

The Interplay of Migration and Population Dynamics in a Patchy World

迁移和离散生境中种群动态的相互作用

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The Interplay of Migration and Population Dynamics in a Patchy World

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Chapter 1

General Introduction

1.1 Simple Spatio-Temporal Models of Population Dynamics

To construct analytical models of spatio-temporal processes, one has to make some basic choices about space, time, and state variables. Each of them may be continuous or discrete, giving eight combinations (Dieckmann et al 1999). Here we briefly introduce two kinds of classical spatial models of population dynamics which are relevant to the approaches in this thesis.

Reaction-Diffusion Equations The classical approach to modelling ecological systems (Volterra 1926) simplifies by ignoring space completely and in essence assumes that every individual is equally accessible to every other individual, which results in the so-called mean-field description of the system. One of the classical methods to take space as well as the movement of organisms into account is the **standard** reaction-diffusion equation (Fisher 1937):

$$u_t = f(u) + D\Delta u \tag{1.1}$$

in which $u = u(t, x)$ is the vector of population densities at time t in spatial position $x \in \Omega \subset \mathbb{R}^n$ (Ω can be either a bounded domain with no-flux on the boundary or an unbounded domain), f is a smooth map, D is a diagonal matrix with constant diagonal elements known as diffusion coefficients. Δ is the Laplace operator. It is seen that the equation is obtained by simply adding a diffusion term (i.e., $D\Delta u$) to the reaction term describing local interaction and growth of populations (i.e. $f(u)$). The basic assumption concerning the diffusion term is that organisms follow Brownian motion in space with a rate which is invariant in time and space. Based on this type of simple models, some well-known theories have been developed, which will be briefly reviewed in the next sections.

Diffusively Coupled Patch Models In a patchy world (either the habitat is patchy or the species assumes a patchy distribution) spatially discrete models (“patch

models”, or “cell models”), in which patches are coupled by dispersal while the within-patch dynamics is described explicitly, turns out to be one of the relevant approaches (e.g., Comins and Blat 1974, Zeigler 1977 1978, Crowley 1981, Sabelis and Diekmann 1988, Reeve 1988, 1990). When organisms migrate among patches by way of unbiased random walk and the rate of migration is constant, this type of models takes the form

$$u_t = f(u) + M\mathcal{B}u \quad (1.2)$$

in which $u = u(t, j)$ is the vector of population densities at time t in patch $j \in \mathbb{N}$ ($\mathbb{N} = \{1, 2, \dots, n\}$, or $\{1, 2, \dots, \}$). M is a diagonal matrix with constant diagonal elements. \mathcal{B} is a certain linear and discrete spatial operator describing how one patch exchanges dispersing organisms with other patches. Essentially, the migration term $M\mathcal{B}u$, in particular the discrete operator \mathcal{B} , can be carefully defined so that the model (1.2) can be taken as a spatially discrete analogue to (1.1) in some extent.

1.2 Pattern Formation in Ecological Systems

The fifty years since Turing (1952) have witnessed the unfolding of a vast literature of theoretical investigations of the pattern formation mechanisms as well as numerous applications to real patterns in a large number of ecological systems (Murray 1993, Bazykin 1998, Nishiura 1994, 2002, Holmes et al 1994, Plahte 2001, Fiedler and Sheel 2003).

Small Amplitude Patterns: Turing Instability It was Turing who firstly exposed that homogeneous, unforced systems of reaction-diffusion equations can exhibit inhomogeneous spatial structures via a symmetry-breaking bifurcation. More precisely, in a reaction-diffusion system, a homogeneous equilibrium which would be predicted to be stable without diffusion becomes unstable. It is hence diffusion that destabilizes the homogeneous equilibrium. This idea is known as **Turing Instability**, or **Diffusion-Driven Instability** (DDI) nowadays. Segel and Jackson (1972) introduced this idea to the ecological field. By a predator-prey system of reaction-diffusion equations they demonstrated the same diffusion-driven instability and gave a biological explanation which is well-known now. In the absence of dispersal, the prey and the predator arrive at a stable equilibrium so that any increase in prey is consumed by the predator, and any increase in predator is reduced by self-limitation. When diffusion is added and the diffusion rate of the predator is sufficiently larger than that of the prey, the stabilizing influence of the predator may be dissipated by diffusion, yielding regular peaks and troughs of prey and predator densities. The striking aspect of the theory is that the spatially periodic patterns are formed due to the Brownian motion of individuals in a homogeneous environment. Under such an assumption of random movement a criterion for DDI in general two-species systems has been established, by which it is concluded that a standard reaction-diffusion system of two-species competition can not exhibit DDI (Okubo 1980, Edelstein-Keshet 1986, Murray 1993). There are also

some new theories which extends the old reaction-diffusion models (e.g., Murray and Oster, 1984a 1984b). However, the analytical methods developed for reaction-diffusion models continue to be of use in the investigation of these alternative models.

Large Amplitude Patterns For some reaction-diffusion systems the spatial inhomogeneous equilibria are far away from any uniform equilibrium. In this case, Turing's method of local bifurcation is of no use in determining both the existence and the stability of such **large amplitude patterns**. Mimura et al (1979) and Nishura (1982) have presented a complete discussion of these patterns in some prey-predator systems of reaction-diffusion equations (in bounded spatial domain with no-flux boundary conditions) (reviewed by Conway (1984)). Gardner and Smoller (1983) have considered analogous problems in unbounded spatial domain while focusing on travelling waves. In general we face a system where one species diffuses much faster than the other. The large amplitude pattern turns to be singular in the sense that they possess some **transition layers**. The approach to constructing such solutions was originated by Fife (1976a,1976b,1977). The Turing approach yields small amplitude patterns because it depends only on the local structure of the interaction terms in a neighbourhood of a point in phase space. In contrast, Fife's method is inherently nonlinear and it depends on certain global features of the interaction terms and yields macroscopic patterns.

1.3 The Fundamental Theories of Metapopulation Dynamics

For more than thirty years, the Levins model (Levins 1969, 1970) has served as a cornerstone of metapopulation studies, providing a conceptual foundation for much of the theory as well as inspiration for empirical studies. Metapopulation theories contain in fact three categories of hypotheses (Taylor 1990)

- i) Local extinctions and recolonization occur frequently.
- ii) Isolated local populations frequently would go extinct, but migration (usually) prevents this.
- iii) Isolated local populations usually would persist but fluctuate wildly, and migration reduces the magnitude of the fluctuation.

Throughout the history two distinct types of models of metapopulations have been studied extensively. One type is called "patch occupancy" models (Levins 1969, Levins and Culver 1971) in which the variable concerned is the fraction of patch occupancy. The other type of models, in contrast, describes within-patch dynamics explicitly, like that given by (1.2). The basic theoretical conclusion reached by studying these models is that persistence can indeed be enhanced by dispersal among populations within a

metapopulation provided some quite loose, and apparently plausible, conditions are met.

The fundamental requirement is **asynchrony** of patch fluctuations because such an asynchrony reduces fluctuations in the total population for purely statistical reasons (Reeve 1990). To see this, suppose that the density of individuals in the i^{th} patch, X_i , is a random variable with mean μ and variance σ^2 . Suppose also that the densities in any two patches have a pairwise correlation of ρ , a measure of their synchrony. The coefficient of variance of average subpopulation density over time is

$$CV(\bar{X}) = \frac{\sqrt{\sigma(1 + (n - 1)\rho)}}{\mu\sqrt{n}}$$

where n is the number of subpopulations. This quantity increase with increasing ρ , i.e., synchrony. Fluctuations in a average density are thus reduced by asynchrony among the subpopulations, for statistical reason alone. What is important is not just whether local populations are asynchronous, but understanding how this situation arises and is maintained.

Early work concerning Turing instability focuses on systems which have a stable equilibrium without diffusion. An isolated local population, however, may settle on a limit cycle. A question associated with the idea of Turing instability is thus whether or not the homogeneous cycle can be destabilized by migration, giving rise to spatially inhomogeneous cycles. The existence and persistence of such cycles have been demonstrated by authors in specific diffusively coupled systems (Gyllenberg et al. 1993, Hastings 1993). In other words, the Turing instability (or, **diffusive instability**) phenomenon may occur in an oscillatory system. The importance of this result has been emphasized by Adler (1993) and Jansen (1994): migration alone results in asynchrony which, as we remarked in the last paragraph, reduces fluctuations in densities across the entire system.

1.4 Beyond Standard Diffusion

It has been the basic assumption behind most early mathematical models of spatial population dynamics that organisms move or disperse in space randomly, which allows for a simple mathematical approach to population dynamics and yet is sufficient to study the fundamental influence of space and dispersal on population dynamics. In the classical applications of partial differential equations to population biology for instance, organisms are assumed to have Brownian motion, the rate of which is invariant in time and space. The assumption leads to the standard reaction-diffusion type of model (1.1).

There is an extensive mathematical literature on reaction-diffusion systems applied to ecological problems (Okubo 1980, Okubo and Levin 2001, Holmes et al 1994). However, in spite of all work that has been devoted to diffusion theory in ecology, the suitability of the most naive diffusion model for the description of animal movements

requires scrutiny. As Skellam (1973) remarked “ it is clearly much better to construct the diffusion model in relation to the realities of the grass-roots situation than to borrow some simple model, such as $\partial u/\partial t \propto \partial^2 u/\partial x^2$, from physical science or mathematical textbooks and trust in its applicability.” For most insect and mamal species the reality of individuals’ movement may be far different from standard diffusion. For instance, individuals may move in response to the local abundance of populations. In some predator-prey systems prey at a certain position usually have increasing inclination to leave when the number of predators near-by increases because of the increasing danger, whereas predators, in contrast, usually have decreasing inclination to leave when the number of prey increases because of the increasing food resource. Obviously the standard reaction-diffusion model (1.1) or the standard diffusively coupled patchy model (1.2) are too naive to describe such movement processes and interactions. The most important question hence is not whether such a mechanism of interspecific influence on mobility exists, but how to implement it mathematically and how to analyse what impacts it would have on those basic theories which we reviewed in the previous two sections.

1.5 The Aims and The Strategy

One of the fundamental issues in spatial ecology is how explicit considerations of space alter the prediction of population models, or what insights they may give into the cause of broad-scale patterns (Tilman and Kareiva 1997). Classical theories, such as diffusion-driven instability and metapopulation dynamics which are developed via simple spatial population models, have profoundly increased our understanding of the issue. In this thesis we scrutinize these theories by considering more complicated processes of spatial interaction of populations. For this purpose we need to construct models in which the migration mechanisms are reflected well. Though there is no absolute standard in this point, it is clearly much better to derive population-level description from the assumptions about behavioural mechanisms of individuals. We shall pay special attention to the interspecific influence on mobility, an important factor that might have significant impact on the dynamical prediction of multi-species interactions. We shall develop a general method to derive spatial population models in which such a factor is naturally incorporated. As we have pointed out in the previous sections, the classical models of spatial population dynamics are the reaction-diffusion equations. The alternatives are spatially discrete models that approximate them. The reaction-diffusion equations, which may have far more complicated diffusion terms than that in (1.1), are often used to understand the origin of patterns and waves (Obubo 1980, Okubo and Levin 2001, Holmes et al 1994). Though reaction-diffusion equations have the advantage in avoiding an arbitrary division of space, they are usually intractable, especially when the diffusion terms have to take a complicated nonlinear form in order to reflect the reality of dispersal. For this reason we will scrutinize in this thesis the theories that concern us by using mainly patchy models.

1.6 A Survey of the Various Chapters

In Chapter 1, we briefly review the two types of simple spatio-temporal models of populations and the well-known theories of diffusion-driven instability and metapopulation dynamics.

In Chapter 2, a predator-prey metapopulation model with two identical patches and only migration of the predator is investigated. Local predator-prey interaction is described by the so-called Rosenzweig-MacArthur model, while the migration term of the predator is put in a nonlinear form, which is derived by extending the Holling time budget argument to migration. In particular, a dimensionless parameter is introduced to quantify the migration tendency of predators while they are handling their prey, which gives rise to a family of models connecting two extremes: predators have no inclination to migrate while handling prey and standard diffusion. We find that the two extremes have both qualitative and quantitative differences in dynamics, leading to different answers to the key question about whether or not spatial structure substantially reduces predator-prey oscillations.

Having realised that a cross-emigration response, i.e. the dependence of the emigration tendency of individuals of one species on the density of some other species, is an ubiquitous feature of multi-species systems we were motivated to study this potential mechanism of pattern formation (i.e. Turing instability) theoretically. In Chapter 3, we formulate a multi-patch multi-species model in which the cross-emigration response is incorporated and quantified (The corresponding model is referred to as “the cross-migration” model). We find that a cross-emigration response has crucial effects on diffusive instability. In the case of competition a cross-emigration response promotes pattern formation by exercising a destabilizing influence; in particular, it may lead to diffusive instability provided that the response is sufficiently strong, which contrasts sharply with the well-known fact that the standard competition system does not exhibit diffusive instability. In the case of prey-predator or activator-inhibitor interaction it acts against diffusive instability by exerting a stabilizing effect; in particular, the diffusive instability, even though it may happen in a standard system, never occurs when the response is sufficiently strong.

In Chapter 4 we present a general method to mechanistically derive “cross-migration models”. We consider a system of multiple species living in a patchy habitat in which the local population of each species consists of some behavioural groups. We then formulate a time-continuous model in which a small positive parameter is present, measuring the time scale of behavioural transitions relative to that of giving birth, death and migration among patches. By the singular perturbation method the model is reduced to a lower dimensional one in which the migration terms are, in general, nonlinear and related to the reaction terms.

In Chapter 5, we examine the stability consequences of a particular migration process in which individuals choose to settle. For this purpose, we formulated a time-continuous multi-species multi-patch model in which individuals migrate by one or two instantaneous jumps while making the second jump with a certain probability that

possibly depends on the conditions at the end point of the first jump. It turned out that a second jump has some quantitative effects on diffusive instability when it occurs with a probability that is density-independent. When a second jump happens as a natural interspecific response of individuals, and such a response is sufficiently strong, it has crucial effects on diffusive instability: it leads to diffusive instability in the case of competitive interactions, whereas it annihilates diffusive instability in the case of prey-predator interactions.

In Chapter 6, we turn to a practical problem of spatial population dynamics. We present a model that describes the dynamical change in the number of host individuals (i.e. peach flowers and fruits) infected by the brown rot fungus (*Monilinia laxa*). The model predicts both the annual incidence of the disease when the infected individuals are spatially homogeneously distributed and the asymptotic velocity of disease spread when the disease initiates at a certain spatial position. Numerical simulations based on the model show that suitable orchard management restrains the epidemic incidence and spread.

Chapter 2

Predator Migration In Response To Prey Density: What Are The Consequences?

Abstract. A predator-prey metapopulation model with two identical patches and only migration of the predator is investigated. Local predator-prey interaction is described by the so-called Rosenzweig-MacArthur model, while the migration term of the predator is put in a nonlinear form, which is derived by extending the Holling time budget argument to migration. In particular, a dimensionless parameter θ is introduced to quantify the migration tendency of predators while they are handling their prey, which gives rise to a family of models connecting two extremes: predators have no inclination to migrate while handling prey ($\theta = 0$) and standard diffusion ($\theta = 1$). Various aspects of the model, including changes in the number and the stability of equilibria and limit cycles, are investigated. We then focus on the key question: "Does spatial structure lead to a substantial damping of the violent oscillations exhibited by many predator-prey models?". It is known that the answer is "yes" if one adopts standard diffusion ($\theta = 1$). However, we present substantial evidence that the answer is "no" if one takes $\theta = 0$. We conclude that the migration submodel is an important constituent of a spatial predator-prey model and that the issue deserves scrutiny, both experimentally and theoretically.

Key words: Predator-Prey Model - Predator Migration - Time Budget - Bifurcations

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2.1 Introduction

Predator and prey populations that live and interact in an ensemble of patches exhibit metapopulation dynamics. One of the hypotheses concerning the crucial role of dispersal and spatial structure in metapopulation dynamics is that isolated local populations fluctuate wildly and that migration among local populations reduces the amplitude of the fluctuations (Taylor, 1990).

Violent oscillations of local predator-prey populations in isolation are both predicted by mathematical models and observed in experiments (Rosenzweig, 1971; 1972). However, oscillations of local populations may proceed out of phase persistently (in an extreme case the peaks in densities of some local populations coincide with the troughs in densities of other local populations) and consequently the amplitude of the global oscillation may be much reduced.

Spatial predator-prey models can be used to scrutinize this idea theoretically. One such model is the spatial variant of the so-called Rosenzweig-MacArthur model. The local predator-prey interaction is then described by the two differential equations:

$$\begin{aligned} v' &= rv\left(1 - \frac{v}{k}\right) - \frac{\alpha vp}{1 + \alpha hv} \\ p' &= \frac{\beta vp}{1 + \alpha hv} - \mu p \end{aligned} \quad (2.1)$$

which reflect the assumptions that prey with density v grow logistically without predators, while predators with density p have Holling type II functional response to prey density. $k, r, \mu, \alpha, h, \beta/\alpha$ are the prey carrying capacity, maximal prey growth rate, predator death rate, predator searching efficiency, predator handling time per prey and the conversion efficiency of prey to predators respectively.

Migration of predator and prey may follow complicated rules, in particular the per capita rate might be density-dependent. The simplest case is that one or both species migrate between two patches and that the per capita rate of emigration is constant (Comins and Blatt, 1974, Crowley, 1981, Holt, 1985, Murdoch et al. 1992, Nisbet, 1992, Jansen, 1995, de Roos et al. 1998, Jansen and de Roos, 1999, Gurney and Veitch, 2000). When migratory rates are assumed to be constant, the bifurcation diagram and the dynamics of the model are surprisingly complicated (Jansen, 1994). However, we maintain that a constant rate of emigration of a predator is not a consistent assumption when a predator is assumed to need a (prey-density dependent) fraction of its time for the handling of prey. (Likewise, if it is the digestive capacity, rather than the time budget, which limits the prey capture rate of a predator, one can imagine that a predator with a full stomach has little inclination to move or emigrate.) In other words, it is reasonable to apply the time budget argument to both local search for prey and more global movement.

In this paper we first extend the Holling searching-handling time budget argument to movement of predators in the spatially discrete case, which results in a special prey density-dependent form of emigration rate of predators. Then we focus on a two patch system in which local interaction is described by the Rosenzweig-MacArthur model, prey is assumed immobile, while the migration rate of the predator is put in

a general form. We will investigate the bifurcations of equilibria and limit cycles, and find that the extension of the Holling time budget argument to movement has essential effects on the dynamics. Our results show that the migration submodel is an important constituent of a spatial prey-predator model and they point the way towards a further investigation of possible spatio-temporal patterns.

2.2 The rationale of the model and some preliminaries

According to the classical Holling time budget argument (Holling, 1966), a predator's total time of food-gathering T consists of two parts : the searching time T_s and the handling time T_h . The number of prey caught by one predator is then proportional to the prey density (v) and the searching time. That is,

$$\text{the total number of prey caught} = \alpha v T_s$$

where α is the searching efficiency of the predator.

Moreover, the total handling time equals the product of the total number of prey caught and the expected handling time h per prey

$$T_h = h \alpha v T_s$$

So the expected number of prey caught per predator per unit of time equals

$$\frac{\alpha v T_s}{T} = \frac{\alpha v T_s}{T_s + T_h} = \frac{\alpha v}{1 + \alpha h v}$$

which is the well known Holling type II functional response .

For the majority of predator species the movement of an individual in space is closely related to its food-gathering activity (namely, the searching and handling of prey). Therefore, we have to consider the effect of the food-gathering activity on the movement, including the propensity to migrate, when we try to establish a model to investigate spatial predator-prey interactions. To do so, we argue as follows.

During a food-gathering time period a predator is, by assumption, in one of the following four states (here we follow an idea of the state classification by Metz & Diekmann (1986))

$$(m, s), (m, h), (n, s), (n, h)$$

where the symbols m, n, s, h correspond to the mobile, immobile, searching and handling state respectively. By "mobile" we mean that there is a certain positive probability per unit of time, say D , that the predator moves from one patch to another.

The time partition is now

$$T = T_{ms} + T_{mh} + T_{ns} + T_{nh}$$

where T_{ms} is the total time that a predator is in the (m, s) state, etc..

If a predator is mobile in a fraction δ of its searching time, while it is mobile in a fraction θ of its handling time, then

$$\begin{aligned} T_{ms} &= \delta T_s, & T_{ns} &= (1 - \delta)T_s & \text{with} & & 0 \leq \delta \leq 1 \\ T_{mh} &= \theta T_h, & T_{nh} &= (1 - \theta)T_h & \text{with} & & 0 \leq \theta \leq 1 \end{aligned}$$

so that $\delta = 1$ & $\theta = 0$ corresponds to the case with mobile-searching and immobile-handling states only, while $\delta = 1$ & $\theta = 1$ corresponds to another extreme case in which the predator is always mobile.

Recall that $T_h = h\alpha v T_s$. So we have

$$m(v) := \frac{T_m}{T} = \frac{T_{ms} + T_{mh}}{T} = \frac{\delta T_s + \theta T_h}{T_s + T_h} = \frac{\delta + \theta \alpha h v}{1 + \alpha h v} \quad (2.2)$$

where $m(v)$ can be interpreted as the probability that a predator is in the mobile state at any moment. So the density of mobile predators is $m(v)p$, where v, p are the prey and predator densities at the spatial position or the local patch.

The two patch Rosenzweig-MacArthur model with immobile prey then takes the following form:

$$\begin{aligned} \frac{dv_i}{dt} &= r v_i \left(1 - \frac{v_i}{k}\right) - \frac{\alpha v_i p_i}{1 + \alpha h v_i} \\ \frac{dp_i}{dt} &= -\mu p_i + \frac{\beta v_i p_i}{1 + \alpha h v_i} + D \left(\frac{\delta + \theta \alpha h v_j}{1 + \alpha h v_j} p_j - \frac{\delta + \theta \alpha h v_i}{1 + \alpha h v_i} p_i \right) \\ & \quad i, j = 1, 2 \text{ and } j \neq i \end{aligned}$$

where D is the diffusion rate.

Note that the model has, in essence, no difference between $0 < \delta < 1$ and $\delta = 1$ (as follows from the parameter transformation $D\delta \sim D, \theta/\delta \sim \theta$). So we restrict to the case $\delta = 1$ in the rest of the paper.

After scaling

$\beta v_i/r \sim v_i, (\alpha/r)p_i \sim p_i, \beta k/r \sim k, \mu/r \sim \mu, r\alpha h/\beta \sim h, D/r \sim D, rt \sim t$
the system has the form:

$$\begin{aligned} \frac{dv_i}{dt} &= v_i \left(1 - \frac{v_i}{k}\right) - \frac{v_i p_i}{1 + h v_i} \\ \frac{dp_i}{dt} &= -\mu p_i + \frac{v_i p_i}{1 + h v_i} + D \left(\frac{1 + \theta h v_j}{1 + h v_j} p_j - \frac{1 + \theta h v_i}{1 + h v_i} p_i \right) \\ & \quad i, j = 1, 2 \quad \text{and} \quad i \neq j \end{aligned} \quad (2.3)$$

We consider θ as a homotopy parameter, linking the traditional "diffusion" model $\theta = 1$ to the "only mobile while searching" model $\theta = 0$.

Throughout the rest of this paper we assume that $h\mu < 1$ (because otherwise the predator goes extinct no matter how abundant the prey is).

We follow Jansen & Lloyd (to appear) to write the state variable in a matrix form

$$X := (x_{.1}, x_{.2}) = (x_{1.}, x_{2.})^T = \begin{pmatrix} v_1 & v_2 \\ p_1 & p_2 \end{pmatrix}$$

In order to link up with the bifurcation theory of symmetric systems we define a symmetry transformation on \mathbb{R}_+^4 by

$$R : \begin{pmatrix} v_1 & v_2 \\ p_1 & p_2 \end{pmatrix} \mapsto \begin{pmatrix} v_2 & v_1 \\ p_2 & p_1 \end{pmatrix}$$

It is obvious that if X is a solution of (2.3), so is $R(X)$. Hence the system (2.3) is, since $R^2 = I$, a so-called \mathbb{Z}_2 -equivariant system (Kuznetsov, 1998).

In addition to the symmetry transformation R , the following three subspaces are helpful for the description of the bifurcations and the dynamics of the system:

$$\text{Diagonal space: } W = \{X = (x_{.1}, x_{.2}) \in \mathbb{R}_+^4 \mid x_{.1} = x_{.2}\}$$

$$\text{Boundary space: } W_i^b = \{X \in \mathbb{R}_+^4 \mid v_i = 0\}, \quad i = 1, 2$$

W, W_1^b and W_2^b are all invariant sets of the flow generated by (2.3).

2.3 Equilibria and Their Classification

The system (2.3) has a maximum of 9 equilibria which can be divided into 4 categories (see **Appendix A**):

- Trivial equilibria

$$E_{00} = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix} \quad E_{kk} = \begin{pmatrix} k & k \\ 0 & 0 \end{pmatrix}$$

$$E_{k0} = \begin{pmatrix} k & 0 \\ 0 & 0 \end{pmatrix} \quad E_{0k} = R(E_{k0})$$

- Nontrivial symmetric (or, homogeneous) equilibrium

$$E^s = \begin{pmatrix} v^s & v^s \\ p^s & p^s \end{pmatrix}$$

- Nontrivial boundary equilibria:

$$E_1^b = \begin{pmatrix} v^b & 0 \\ p^b & p_0^b \end{pmatrix} \quad E_2^b = R(E_1^b)$$

- Asymmetric equilibria:

$$E_1^a = \begin{pmatrix} v_1^a & v_2^a \\ p_1^a & p_2^a \end{pmatrix} \quad E_2^a = R(E_1^a)$$

The explicit expressions of the equilibrium components in terms of the parameters are derived in **Appendix A.1** and listed in **Table 2.1**.

Table 2.1: Equilibrium components

Symbol	Expression
v^s	$\mu/(1-h\mu)$
p^s	$(1+hv^s)(1-v^s/k)$
v^b	$\frac{\mu(2D+\mu)}{D(1-h\mu-\theta h\mu)+\mu(1-h\mu)}$
p^b	$(1+hv^b)(1-\frac{v^b}{k})$
p_0^b	$\frac{D}{D+\mu}(1+\theta hv^b)(1-\frac{v^b}{k})$
γ	$\frac{D(1-h\mu-\theta h\mu)+(1-h\mu)\mu}{(1-h\mu)(2\theta hD-(1-h\mu))}$
v_1^a	$\frac{1}{2}(k-v^s) - \gamma + \frac{1}{2}\sqrt{(k-3v^s-2\gamma)(k+v^s+2\gamma)}$
v_2^a	$\frac{1}{2}(k-v^s) - \gamma - \frac{1}{2}\sqrt{(k-3v^s-2\gamma)(k+v^s+2\gamma)}$
p_1^a	$(1+hv_1^a)(1-v_1^a/k)$
p_2^a	$(1+hv_2^a)(1-v_2^a/k)$

Throughout the rest of the paper we will say that an equilibrium exists if it is biologically meaningful, i.e. all of its components are non-negative. **Figure 2.1** gives an impression of the position of the 9 equilibria when they exist.

2.4 Local Dynamics and Bifurcations

In this and the following sections, we use certain symbols to denote particular bifurcations and the parameter conditions which characterise them. To enhance the surveyability, these symbols are introduced in **Table 2.2**, **2.3**, **2.4**. A more detailed description is presented in the later subsections.

For the bifurcation theory of \mathbb{Z}_2 -equivariant systems we refer to [65]. Note, however, that the invariance of the boundary subspaces makes transcritical bifurcations a generic possibility in the present system.

In addition, the following terminology is adopted:

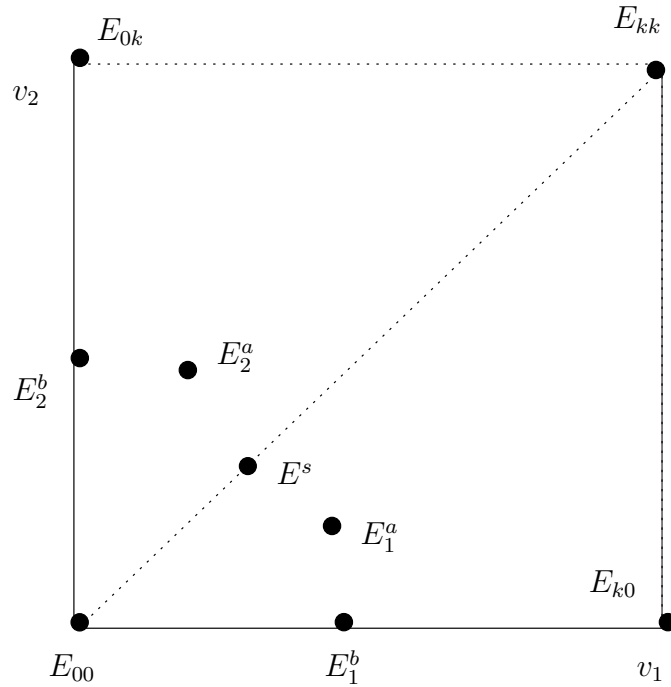


Figure 2.1: Nine non-negative equilibria projected in (v_1, v_2) plane. When $\theta > 0$ the system may have three interior equilibria provided certain parameter conditions are satisfied (see Section 4.3); When $\theta = 0$ only one interior equilibrium (the symmetric one) exists.

1). a limit cycle is called **synchronous** if, pointwise in time, it is invariant under R (i.e., if the two patches oscillate in phase); in [65] a periodic solution with this property is called fixed.

2). a limit cycle is called **asynchronous**, if the orbit, as a set, is invariant under R , yet it is not synchronous; the action of R then corresponds to a phase shift of π , i.e. a translation over half the period; in [65] a periodic solution with this property is called symmetric.

3). a limit cycle for which the orbit is not invariant under R is called **asymmetric**, unless it is contained in one of the boundary subspaces W_i^b , in which case we speak about a **boundary limit cycle**.

Table 2.2: Transcritical bifurcation curves

Symbol	Formula	What happens
l_s	$k = v^s$	E^s and E_{kk} coincide
l_{sa}	$D(\theta k - \frac{1+(2\theta-1)h\mu}{h(1-h\mu)}) = \frac{1-h\mu}{2h}(k - v^s)$	E^s and E_i^a coincide
l_b	$k = v^b$	E_1^b and E_{k0} coincide
l_{ba}	$k = \frac{Dv^b(1+\theta hv^b)}{\theta h Dv^b - \mu}$	E_i^b and E_i^a coincide

Table 2.3: Hopf bifurcation curves

Symbol	Formula	Limit cycle
H_s^+	$k = \frac{1+h\mu}{h(1-h\mu)} =: k^*$	Γ_+^s
H_s^-	(2.26) & (2.27)	Γ_-^s
H_b	not available	Γ_i^b
H_a	not available	Γ_i^a

As the system has five parameters, a choice has to be made when we want to visualise the subdivision of the parameter space according to these stability and bifurcation conditions. In **Figure 2.2** we choose to fix h and μ at a particular value and to picture, for three different values of θ , the various conditions as curves in the (k, D) -plane.

2.4.1 Equilibria in W

In the diagonal space W there are at most three equilibria E_{00} , E_{kk} and E^s . Local dynamics near, and bifurcations of, the two trivial equilibria E_{00} and E_{kk} are simple. We briefly describe these as follows: E_{00} is unstable for all $k > 0$; E_{kk} is a stable node when $k < v^s = \mu/(1 - h\mu)$, while it is a saddle when $k > v^s$. There is a transcritical bifurcation within the diagonal space at E_{kk} when $k = v^s$. Note that $k > v^s$ is exactly the condition that the predator population can grow when the prey population is held fixed at density k .

Next we focus on the nontrivial equilibrium E^s . Based on computation of the eigenvalues and eigenvectors of the corresponding Jacobian matrix in **Appendix B.1** (where a decomposition of the linearized system into two decoupled $2 - d$ systems is also given to elucidate both the symmetry and the biological meaning of the local dynamics), we now present a survey of local stability and bifurcation results:

- A transcritical bifurcation happens at l_s : E^s exists if and only if $k > v^s$.
- E^s is a stable equilibrium if and only if $v^s < k < k^*$, where $k^* = (1 + h\mu)/(h(1 - h\mu))$.

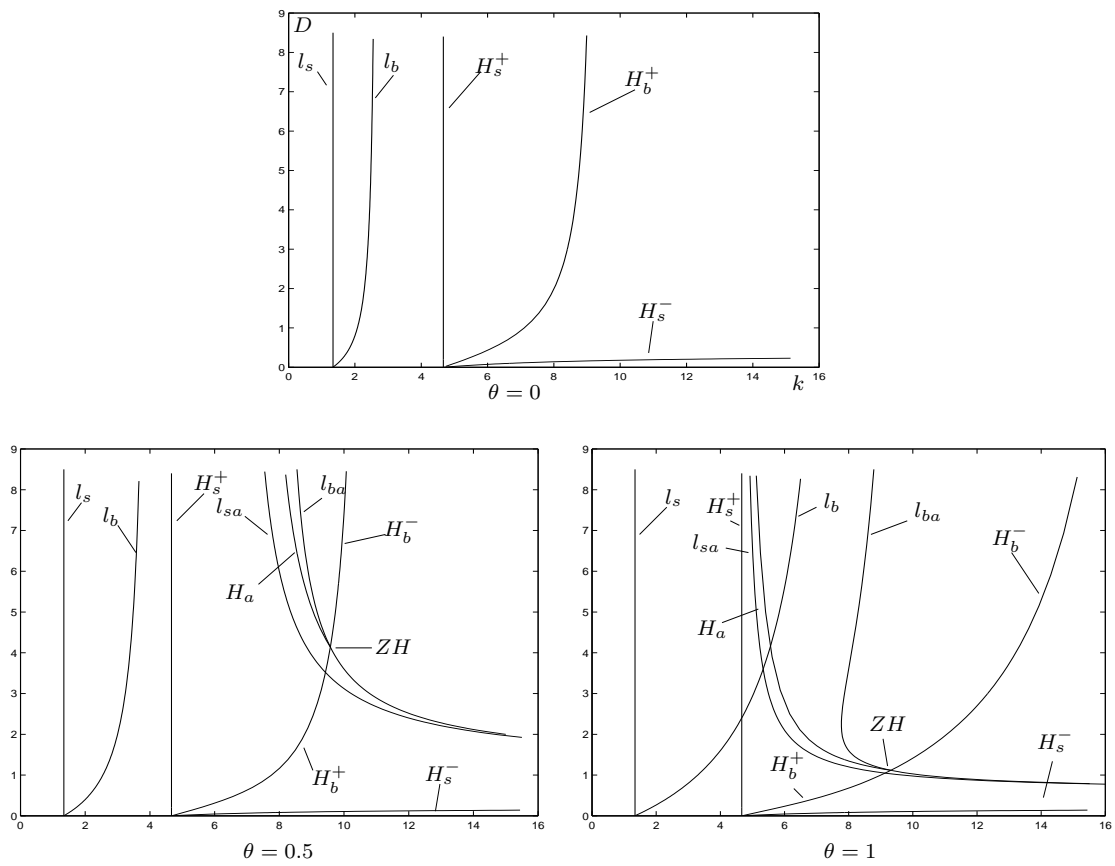


Figure 2.2: Two parameter bifurcation diagrams of equilibria. H_b^- and H_b^+ are actually two parts of one curve separated by the point "ZH". The intersection of H_s^- and l_{sa} is not shown. See text for the meaning of the symbols. ($h = 0.5, \mu = 0.8$.)

Table 2.4: A partial list of limit cycles

Symbol	Name
Γ_+^s	synchronous limit cycle
Γ_-^s	asynchronous limit cycle
Γ_i^b	boundary limit cycle
Γ_i^a	asymmetric limit cycle

- A Hopf bifurcation happens at H_s^+ : at $k = k^*$ a unique limit cycle Γ_+^s supercritically bifurcates within W from E_s (Cheng, 1981) and hence Γ_+^s is a global attractor for the flow restricted to this invariant subspace. Note that Γ_+^s describes synchronous (in-phase) oscillations in the two patches.
- A pitchfork bifurcation happens at l_{sa} : the two asymmetric equilibria E_i^a originate from E^s at l_{sa} defined by (2.25) in the **Appendix B.1**.
- A Hopf bifurcation happens at H_s^- : an unstable limit cycle Γ_-^s , describing asynchronous (i.e. π -out-of-phase) oscillations in the two patches, bifurcates from E^s at H_s^- defined by (2.26)&(2.27) in the **Appendix B.1**.

2.4.2 Equilibria in W_i^b

Because of symmetry we only need to discuss the equilibria in one of the boundary spaces, say W_1^b . In W_1^b there are at most three equilibria E_{00} , E_{k0} and E_1^b . As noted before E_{00} is always unstable. E_{k0} is a stable node when $0 < k < v^b$, while it is a saddle when $k > v^b$. There is a transcritical bifurcation within W_1^b at l_b , i.e. $k = v^b$. In fact, $k > v^b$ is exactly the condition that the two-patch predator population can grow when the prey population is held fixed at density k in one patch and at density zero in the other patch and accordingly E_1^b exists if and only if $k > v^b$.

Next we focus on the local dynamics and bifurcations related to the nontrivial boundary equilibrium E_1^b .

The linearized system of (2.3) around E_1^b can be decomposed into a $3-d$ system that describes the dynamics near E_1^b within W_1^b (i.e. no prey in patch 2) and an equation that describes the behavior of v_2 , the prey density in patch 2, near zero. We call the eigenvalue associated with the one-dimensional system **the transversal eigenvalue**.

We now present a survey of local stability and bifurcation results:

- A transcritical bifurcation happens at l_b : E^b exists if and only if $k > v^b$.
- A transcritical bifurcation happens at l_{ba} : E_1^a and E_1^b meet at l_{ba} defined by (2.28) (i.e. the transversal eigenvalue equals zero). (see **Appendix B.2**.)

- A Hopf bifurcation happens at H_b : a limit cycle Γ_1^b within W_1^b , describing an oscillation among predators in both patches and prey in one patch, bifurcates from E_1^b . (see **Appendix B.2** for the definition and the computation of H_b)

As H_b and l_{ba} intersect, we need a two parameter bifurcation analysis to obtain more detailed information. This is postponed till the next section

2.4.3 The asymmetric equilibria

The asymmetric equilibria exist if and only if the following three conditions are satisfied (see **Appendix A.2**)

$$\theta D > \frac{1 - h\mu}{2h} \quad (2.4)$$

$$D\left(\theta k - \frac{1 + (2\theta - 1)h\mu}{h(1 - h\mu)}\right) \geq \frac{1 - h\mu}{2h}(k - v^s) \quad (2.5)$$

$$k \leq \frac{Dv^b(1 + \theta hv^b)}{\theta h D v^b - \mu} \quad (2.6)$$

Note that when (2.4) holds, the subset of the parameter space given by, respectively, (2.5) and (2.6) with the equality sign is, respectively, l_{sa} and l_{ba} .

Apart from the transcritical bifurcations at l_{sa} and l_{ba} we have

- A Hopf bifurcation happens at H_a : an asymmetric limit cycle Γ_i^a bifurcates from E_i^a . With reference to **Figure 2.2**, where H_a is computed numerically by **CONTENT** (Kuznetsov, 1998a), we can say that E_i^a is stable in between l_{ba} and H_a and unstable in between l_{sa} and H_a .

2.5 The Zero-Hopf point

As is clear from the two diagrams in **Figure 2.2** corresponding to $\theta > 0$, the codimension two point "ZH" (for Zero-Hopf: three simple eigenvalues on the imaginary axis, one at zero and one conjugate pair) is an organizing centre. At this point the curves H_a , H_b and l_{ba} intersect. In **Figure 2.3** we present a blow-up of a neighbourhood of this point featuring yet another curve called TC_b , which corresponds to a transcritical bifurcation of the boundary limit cycles Γ_i^b (this curve is found numerically by continuing Γ_i^b from H_b^-). The curves divide the neighbourhood of "ZH" into six regions and for each of these we have sketched phase portraits in terms of tailor made coordinates: amplitude ρ of the boundary limit cycle and distance to the boundary space ξ .

In particular the existence and stability of the relevant equilibria and limit cycles in each of the six regions can be observed. We summarise the results in **Table 2.5**.

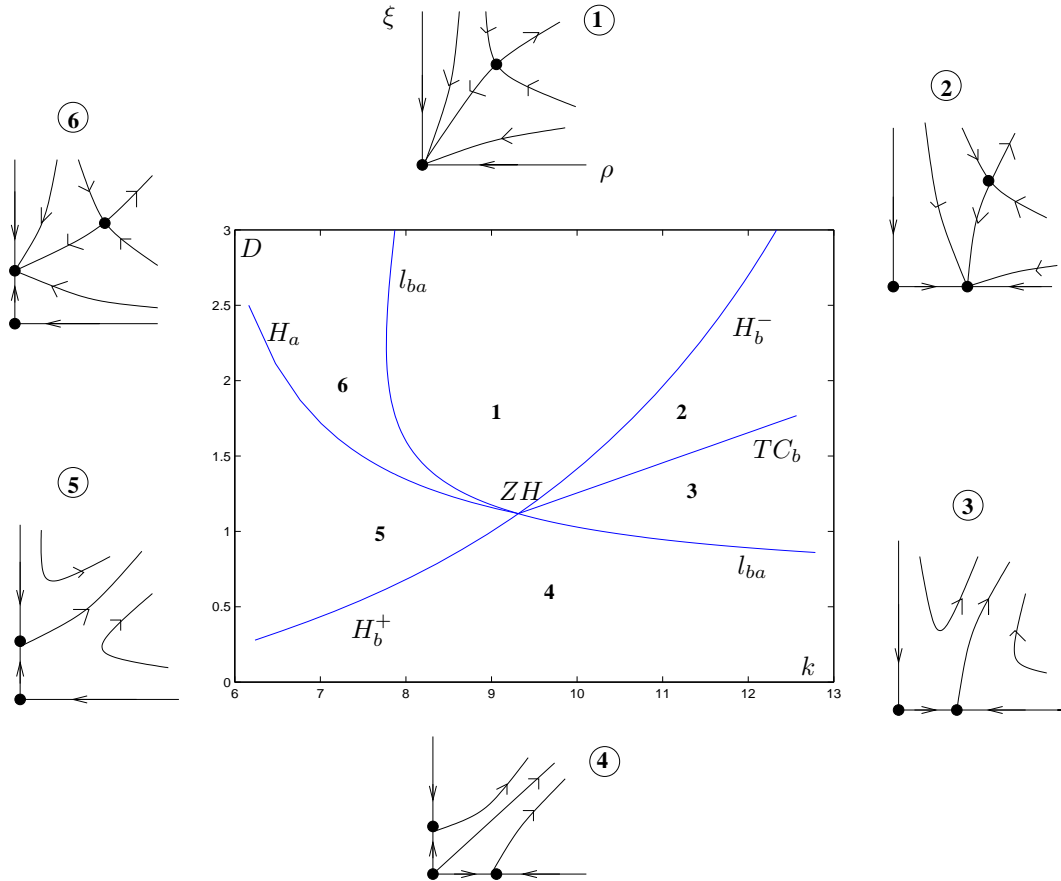


Figure 2.3: A two parameter bifurcation diagram and typical phase portraits in the vicinity of the Zero-Hopf point (labeled by "ZH" in the figure). The meaning of the curves l_{ba} , H_a , H_b and TC_b are stated in the text. In the phase portraits, the symbol ρ represents the amplitude of the limit cycle Γ_i^b , while ξ is a coordinate in the direction transversal to the boundary space. The origin corresponds to E_i^b . The dot on the horizontal axis, the vertical axis and in the interior of the positive cone respectively corresponds to Γ_i^b , E_i^a and Γ_i^a . (The value of the other fixed parameters is $\theta = 1, h = 0.5, \mu = 0.8$)

Table 2.5: Existence and stability of the relevant equilibria and limit cycles: the symbols "n", "s" and "u" mean, respectively, non-existent, stable and unstable

	E_i^b	E_i^a	Γ_i^b	Γ_i^a
Region 1	s	n	n	u
2	u	n	s	u
3	u	n	u	n
4	u	u	u	n
5	u	u	n	n
6	u	s	n	u

At this stage the status of **Figure 2.3** is that of an educated guess strongly supported by numerical evidence. A rigorous justification of the information presented in **Figure 2.3** requires more detailed calculations, in particular the normal form analysis (see Kuznetsov & Rinaldi, 1996, for a similar yet somewhat different situation; also see Jansen, 1994).

2.6 Contrasting $\theta = 0$ with $\theta = 1$

The aim of this section is to pinpoint the qualitative differences that exist between $\theta = 0$ and $0 < \theta \leq 1$ (in particular $\theta = 1$).

Equilibria By fixing θ, h and μ , the conditions l_{sa} and l_{ba} define curves in the (k, D) -plane (see **Figure 2.2**). Both have

$$D = \frac{1 - h\mu}{2\theta h} \quad (2.7)$$

as a lower horizontal asymptote and l_{sa} has

$$k = \frac{1 + (2\theta - 1)h\mu}{\theta h(1 - h\mu)} = \frac{1}{\theta h} + \frac{2\mu}{1 - h\mu} \quad (2.8)$$

as a left vertical asymptote. So the region between these curves (which, according to (2.4)-(2.6), is exactly the region where E_i^a exists) is pushed up and right as θ varies from 1 to 0 and disappears when $\theta = 0$. Likewise, the region between l_{ba} and H_b^- , i.e. the region of stability of the boundary equilibria E_i^b , moves off to infinity as $\theta \searrow 0$.

We conclude:

both the condition for the existence of the asymmetric equilibria E_i^a and the condition for the stability of the boundary equilibria E_i^b become more and more restrictive as θ decreases and can not be met when $\theta = 0$.

Limit cycles We summarize our (incomplete!) knowledge about the existence and the stability of limit cycles:

- i) Γ_i^a is unstable (it arises in a subcritical Hopf bifurcation) and does not exist for $\theta = 0$ (since H_a lies in between l_{sa} and l_{ba}).
- ii) Γ_i^b can be stable (see region 2 in **Figure 2.2**), but not for $\theta = 0$ (since the point "ZH" moves off to infinity when $\theta \searrow 0$).
- iii) Γ_-^s is unstable (it arises by Hopf bifurcation from the equilibria E^s with two eigenvalues in the right half plane)
- iv) Γ_+^s can be stable (in fact, it is stable close to the Hopf bifurcation)

We conclude:

both the condition for the existence of asymmetric limit cycles Γ_i^a , arising by Hopf bifurcation from E_i^a , and the condition for the stability of the boundary limit cycles Γ_i^b become more and more restrictive as θ decreases and can not be met when $\theta = 0$.

However, as is pointed out by Jansen (1994), asynchronous limit cycles can arise from a flip (i.e. period doubling) bifurcation of Γ_+^s . So we can not exclude the existence of attractors that exhibit spatio-temporal patterns and further numerical bifurcation studies, especially the bifurcation of the symmetric limit cycle Γ_+^s , are needed. Yet we like to state the following preliminary conclusion of our numerical experiments so far:

when $\theta = 0$ the amplitude of the prey-predator fluctuations in the two patch system is never substantially reduced relative to the amplitude of Γ_+^s .

2.7 Conclusions and Discussion

The time budget of a predator for searching and handling leads to the functional response, i.e. a prey density-dependent catch rate. The movement of a predator is often closely related to its food-gathering activity. Therefore it is not only natural, but also necessary, to consider the effect of the time budget on movement. Such a consideration leads to a prey density-dependent rate of diffusion (in the spatially continuous case) or migration (in the spatially discrete case) of the predator.

In this paper we introduced and studied a family (parametrised by θ) of models such that at one extreme, viz. for $\theta = 0$, the effect is fully included, while at the other extreme, viz. for $\theta = 1$, the effect is fully neglected and the migration is described by standard diffusion.

One of the motivations to investigate patchy predator-prey systems is to show that spatial structure reduces predator-prey oscillations by maintaining spatial differences (i.e. spatial patterns (Turing, 1952)), which is a significant idea in metapopulation dynamics (Jansen, 1994). Two kinds of mechanisms have been suggested in some

recent investigations (Jansen, personal communication, Jansen, 1994, Jansen and de Roos, 1999):

I. For large predator migration rate, the pattern is formed by persistent asymmetry, in particular prey missing in parts of the space.

II. For small predator migration rate, predator and prey are present everywhere and the spatio-temporal pattern is formed by the out-of-phase fluctuations in the local densities.

The behaviour of the model for $\theta > 0$ corroborates both the mechanisms I and II. However, the dynamics of the system for $\theta = 0$, which corresponds to an arguably more realistic assumption about predator migration, does not exhibit the mechanism I. In fact, there is a continuous change: when θ decreases from 1 to 0 the conditions for the other parameters to obtain asymmetric persistent behaviour become more and more severe until ultimately, for $\theta = 0$, they cannot be met by any parameter combination.

The underlying reason is the following. Peaks in prey density lead to peaks in the predator birth rate. In the case of standard diffusion with a large rate these then serve as a local source of predators which at other positions prevent the growth of the prey population. When $\theta = 0$, however, the predators basically stay where they are born as long as the prey density is high.

Mechanism II may still operate for $\theta = 0$, but its quantitative effect seems to be far less pronounced than in the standard diffusion case $\theta = 1$. Again the reason seems to be that predators don't move away from local peaks in prey density.

It has been suggested repeatedly (Jansen 1994, Jansen and de Roos 1999, Gurney et al 2000) that spatial structure may, by itself, lead to a substantial damping of the violent oscillations exhibited by reasonable predator-prey models. As such suggestions are based on coupling local systems by standard diffusion, the present paper shows they are premature. In our view, this paper serves as an invitation to experimental and field biologists to investigate in detail how the tendency to migrate (i.e. move in a short time over a long distance, where both the "short" and the "long" are relative to the scale of the food-gathering activity) is related to the success (or lack thereof) of predation. Moreover, to ascertain the extent to which asynchronous or asymmetric spatio-temporal patterns show reduced amplitudes, a detailed study (by numerical bifurcation methods) of various types of attractors should be carried out, in particular for the system with $\theta = 0$.

2.8 Appendix A. Computation of Equilibria

2.8.1 A.1. Expression of equilibria

In this appendix we use the symbols x and y instead of v_i and v_j and correspondingly p_x and p_y instead of p_i and p_j . An equilibrium is a solution of the following system of equations

$$\begin{aligned}
x\left(1 - \frac{x}{k} - \frac{p_x}{1+hx}\right) &= 0 \\
y\left(1 - \frac{y}{k} - \frac{p_y}{1+hy}\right) &= 0 \\
\frac{(1-h\mu-\theta hD)x-(D+\mu)}{1+hx}p_x + \frac{D(1+\theta hy)}{1+hy}p_y &= 0 \\
\frac{(1-h\mu-\theta hD)y-(D+\mu)}{1+hy}p_y + \frac{D(1+\theta hx)}{1+hx}p_x &= 0
\end{aligned} \tag{2.9}$$

a) The restriction $x = y$ (symmetry in prey density) leads to three equilibria

$$E_{00}: \quad x = y = 0 \quad p_x = p_y = 0$$

$$E_{kk}: \quad x = y = k \quad p_x = p_y = 0$$

$$E^s: \quad x = y = v^s := \frac{\mu}{1-h\mu} \quad p_x = p_y = p^s := (1+hv^s)\left(1 - \frac{v^s}{k}\right)$$

b) If $x \neq y$ (asymmetry in prey density) equilibria occur in pairs, one being the R -image of the other. Whenever appropriate we list one of each pair.

E_{k0} and E_{0k} : If $x = 0, y = k$ we immediately have $p_x = p_y = 0$;

E_i^b : If $x = 0, y \neq 0, k$, we have

$$y = v^b := \frac{\mu(2D + \mu)}{D(1 - h\mu - \theta h\mu) + \mu(1 - h\mu)}$$

$$p_y = p^b := (1 + hv^b)\left(1 - \frac{v^b}{k}\right)$$

$$p_x = p_0^b := \frac{D}{D + \mu}(1 + \theta hv^b)\left(1 - \frac{v^b}{k}\right)$$

E_i^a : If $x, y \neq 0, k$, it must be that

$$p_x = (1 + hx)(1 - x/k) \quad \text{and} \quad p_y = (1 + hy)(1 - y/k)$$

and therefore that

$$[(1 - h\mu - \theta hD)x - (D + \mu)](1 - x/k) + D(1 + \theta hy)(1 - y/k) = 0 \tag{2.10}$$

$$[(1 - h\mu - \theta hD)y - (D + \mu)](1 - y/k) + D(1 + \theta hx)(1 - x/k) = 0 \tag{2.11}$$

Now we follow the computational procedure by Jansen (1994).

Addition of the last two equations yields (using the notation $a := 1 - h\mu$)

$$(ax - \mu)(k - x) + (ay - \mu)(k - y) = 0$$

or, after elaboration,

$$\left[x - \frac{(k + v^s)}{2}\right]^2 + \left[y - \frac{(k + v^s)}{2}\right]^2 = \frac{(k - v^s)^2}{2} \quad (2.12)$$

y can be solved from (2.10) and (2.11) as

$$y = \frac{[a(D + \mu) - \theta h \mu D]x - \mu(2D + \mu)}{a(a - 2\theta h D)x - [a(D + \mu) - \theta h \mu D]} \quad (2.13)$$

If we introduce another compound parameter

$$\gamma := \frac{\theta h \mu D - a(D + \mu)}{a(a - 2\theta h D)} = \frac{(a - \theta h \mu)D + a\mu}{a(2\theta h D - a)} \quad (2.14)$$

then we can write (2.13) as

$$y = \frac{-\gamma x + v^s(v^s + 2\gamma)}{x + \gamma} \quad (2.15)$$

By plugging (2.15) into (2.12) and then multiplying both sides by $(x + \gamma)^2$ we find

$$\begin{aligned} (x + \gamma)^2 \left[(x - v^s) - \frac{k - v^s}{2} \right]^2 + \left[\left(\frac{k - v^s}{2} + v^s + \gamma \right) (x - v^s) + \frac{k - v^s}{2} (v^s + \gamma) \right]^2 \\ - \frac{1}{2} (k - v^s)^2 (x + \gamma)^2 = 0 \end{aligned} \quad (2.16)$$

Note that $x + \gamma = (x - v^s) + (v^s + \gamma)$. So the left hand side of the above equation is a fourth order polynomial with respect to the variable $(x - v^s)$:

$$(x - v^s)^2 \left[(x - v^s)^2 + 2(v^s + \gamma - \frac{1}{2}(k - v^s))(x - v^s) + 2(v^s + \gamma)(v^s + \gamma - \frac{1}{2}(k - v^s)) \right] = 0 \quad (2.17)$$

The two roots that are different from v^s therefore are

$$x = v_1^a := \frac{1}{2}(k - v^s) - \gamma + \frac{1}{2}\sqrt{(k - 3v^s - 2\gamma)(k + v^s + 2\gamma)} \quad (2.18)$$

and

$$x = v_2^a := \frac{1}{2}(k - v^s) - \gamma - \frac{1}{2}\sqrt{(k - 3v^s - 2\gamma)(k + v^s + 2\gamma)} \quad (2.19)$$

It is due to the symmetry that $y = v_j^a$ when $x = v_i^a$ ($j \neq i$, $i, j=1,2$). Hence, we have one pair of such equilibria. When $x = v_i^a$, the corresponding p component is

$$p_x = p_i^a := (1 + h v_i^a)(1 - v_i^a/k) \quad i=1,2$$

2.8.2 A.2. When does E_i^a exist ?

E_i^a exists (i.e. non-negative) if and only if $0 \leq v_1^a, v_2^a \leq k$, which holds if and only if

$$(k - 3v^s - 2\gamma)(k + v^s + 2\gamma) \geq 0$$

and

$$0 \leq \frac{1}{2}(k - v^s - 2\gamma) \mp \frac{1}{2}\sqrt{(k - 3v^s - 2\gamma)(k + v^s + 2\gamma)} \leq k$$

So we have the following three conditions:

$$k - 3v^s - 2\gamma \geq 0 \iff k \geq 3v^s + 2\gamma \quad (2.20)$$

$$\sqrt{(k - 3v^s - 2\gamma)(k + v^s + 2\gamma)} \leq k - v^s - 2\gamma \iff \gamma k \leq (v^s + \gamma)(v^s + 2\gamma) \quad (2.21)$$

$$\sqrt{(k - 3v^s - 2\gamma)(k + v^s + 2\gamma)} \leq k + v^s + 2\gamma \iff v^s + \gamma \geq 0 \quad (2.22)$$

Since

$$\begin{aligned} v^s + \gamma &= \frac{(1 - h\mu + \theta h\mu)D}{(1 - h\mu)(2\theta hD - (1 - h\mu))} \\ v^s + 2\gamma &= \frac{2D + \mu}{2\theta hD - (1 - h\mu)} \\ 3v^s + 2\gamma &= \frac{2D(1 - h\mu + 2\theta h\mu) - (1 - h\mu)\mu}{(1 - h\mu)(2\theta hD - (1 - h\mu))} \end{aligned}$$

one finds that (2.20) & (2.21) & (2.22) can be rewritten as (2.4) & (2.5) & (2.6) in **Section 4.3**, which, as a whole, is a sufficient and necessary condition for E_i^a to exist.

2.9 Appendix B. Computation of Eigenvalues

The Jacobian matrix of the linearized system of (2.3) at an equilibrium

$$E_0 = \begin{pmatrix} v_{i0} & v_{j0} \\ p_{i0} & p_{j0} \end{pmatrix}$$

is

$$M = \begin{pmatrix} A_i & B_j \\ B_i & A_j \end{pmatrix}$$

Where

$$\begin{aligned} A_i &= \begin{pmatrix} 1 - \frac{2v_{i0}}{k} - \frac{p_{i0}}{(1+hv_{i0})^2} & -\frac{v_{i0}}{1+hv_{i0}} \\ \frac{1+(1-\theta)hD}{(1+hv_{i0})^2} p_{i0} & \frac{(1-h\mu-\theta hD)v_{i0}-(D+\mu)}{1+hv_{i0}} \end{pmatrix} \\ B_i &= \begin{pmatrix} 0 & 0 \\ -\frac{(1-\theta)hD}{(1+hv_{j0})^2} p_{j0} & \frac{D(1+\theta hv_{j0})}{1+hv_{j0}} \end{pmatrix} \end{aligned}$$

$i \neq j, i, j = 1, 2.$

2.9.1 B.1. Eigenvalues corresponding to E^s

In this case we have $v_{i0} = v_{j0} = v^s$, $p_{i0} = p_{j0} = p^s$. It follows that $A_i = A_j =: A$, $B_i = B_j =: B$. The matrix

$$M = \begin{pmatrix} A & B \\ B & A \end{pmatrix}$$

has exactly the same eigenvalues as the block-diagonal matrix

$$\begin{pmatrix} A + B & 0 \\ 0 & A - B \end{pmatrix}$$

Accordingly, the linearized system of (2.3) around E^s can be decomposed into two 2-dimensional linear systems by considering mean prey and predator densities supplemented by the differences:

$$\begin{pmatrix} \bar{v} \\ \bar{p} \end{pmatrix}' = (A + B) \begin{pmatrix} \bar{v} \\ \bar{p} \end{pmatrix} \quad (2.23)$$

$$\begin{pmatrix} \hat{v} \\ \hat{p} \end{pmatrix}' = (A - B) \begin{pmatrix} \hat{v} \\ \hat{p} \end{pmatrix} \quad (2.24)$$

where

$$\begin{aligned} \bar{v} &= \frac{v_1 + v_2}{2} - v^s & \bar{p} &= \frac{p_1 + p_2}{2} - p^s \\ \hat{v} &= v_1 - v_2 & \hat{p} &= p_1 - p_2 \end{aligned}$$

If η is an eigenvector of $A + B$ corresponding to eigenvalue λ , then (η, η) is an eigenvector of M corresponding to λ (in particular, it belongs to the diagonal space W). If ξ is an eigenvector of $A - B$ corresponding to eigenvalue λ , then $(\xi, -\xi)$ is an eigenvector of M corresponding to λ (in particular, it is orthogonal to W).

By substituting the components of E^s into A, B we have, with $k^* = (1 + h\mu)/(h(1 - h\mu))$

$$\begin{aligned} A + B &= \begin{pmatrix} 1 - \frac{2v^s}{k} - \frac{p^s}{(1+hv^s)^2} & -\frac{v^s}{1+hv^s} \\ \frac{p^s}{(1+hv^s)^2} & \frac{(1-h\mu)v^s - \mu}{1+hv^s} \end{pmatrix} \\ &= \begin{pmatrix} h\mu(1 - \frac{k^*}{k}) & -\mu \\ (1 - h\mu)(1 - \frac{v^s}{k}) & 0 \end{pmatrix} =: \begin{pmatrix} a_1 & -a_2 \\ a_3 & 0 \end{pmatrix} \\ A - B &= \begin{pmatrix} 1 - \frac{2v^s}{k} - \frac{p^s}{(1+hv^s)^2} & -\frac{v^s}{1+hv^s} \\ \frac{1+2(1-\theta)hD}{(1+hv^s)^2} p^s & \frac{(1-h\mu-2\theta hD)v^s - (2D+\mu)}{1+hv^s} \end{pmatrix} \\ &= \begin{pmatrix} h\mu(1 - \frac{k^*}{k}) & -\mu \\ (1 - h\mu)[1 + 2(1 - \theta)hD](1 - \frac{v^s}{k}) & -2D[1 - h\mu(1 - \theta)] \end{pmatrix} =: \begin{pmatrix} a_1 & -a_2 \\ a_4 & -a_5 \end{pmatrix} \end{aligned}$$

The eigenvalues of $A + B$ are

$$\lambda_{1,2} = \frac{a_1 \pm \sqrt{a_1^2 - 4a_2a_3}}{2}$$

and the eigenvalues of $A - B$ are

$$\lambda_{3,4} = \frac{(a_1 - a_5) \pm \sqrt{(a_1 - a_5)^2 - 4(a_2a_4 - a_1a_5)}}{2}$$

We now check when these eigenvalues are zero or purely imaginary:

l_s : $A + B$ has a zero eigenvalue if and only if $a_2a_3 = 0$, i.e. $k = v^s = \mu/(1 - h\mu)$. Moreover, the zero eigenvalue is simple because $a_1 < 0$. We denote the subset of parameter space where this condition is satisfied by l_s .

H_s^+ : Two eigenvalues (i.e. $\lambda_{1,2}$) of $A + B$ are purely imaginary if and only if $a_1 = 0$, i.e. $k = k^*$ (see Section 4.1 for the definition of k^*). We denote the subset of parameter space where this condition is satisfied by H_s^+ .

l_{sa} : $A - B$ has a zero eigenvalue if and only if $a_2a_4 - a_1a_5 = 0$ or, after elaboration,

$$D\left(\theta k - \frac{1 + (2\theta - 1)h\mu}{h(1 - h\mu)}\right) = \frac{1 - h\mu}{2h}\left(k - \frac{\mu}{1 - h\mu}\right) \quad (2.25)$$

We denote the subset of parameter space where this condition (with $k > v^s$) is satisfied by l_{sa} .

H_s^- : $A - B$ to have purely imaginary eigenvalues if and only if $a_1 = a_5$ and $a_2a_4 - a_1a_5 > 0$, which can be expressed, respectively, as

$$2D = \frac{h\mu}{1 - h\mu(1 - \theta)}(1 - k^*/k) \quad (2.26)$$

$$D\left(\theta k - \frac{1 + (2\theta - 1)h\mu}{h(1 - h\mu)}\right) < \frac{1 - h\mu}{2h}\left(k - \frac{\mu}{1 - h\mu}\right) \quad (2.27)$$

We denote the subset of parameter space where (2.26) and (2.27) are satisfied by H_s^- . Note that the boundary of the subset, where (2.27) is satisfied, is just l_{sa} . So $A - B$ has double zero eigenvalue if and only if both (2.26) and l_{sa} are satisfied.

2.9.2 B.2. Eigenvalues corresponding to E_i^b

In this case we have $v_{i0} = v^b, v_{j0} = 0, p_{i0} = p^b, p_{j0} = p_0^b$. The Jacobian matrix M necessarily has an eigenvalue

$$\lambda_1 = 1 - p_0^b = 1 - \frac{D}{D + \mu}(1 + \theta hv^b)\left(1 - \frac{v^b}{k}\right)$$

Clearly $\lambda_1 > 0$ if $\theta = 0$, an observation that is of some importance.

The other three eigenvalues are the roots of a third order polynomial with coefficients that can be expressed in terms of the parameters, but these expressions are both extremely lengthy and uninformative.

The criticality conditions are as follows:

l_{ba} : $\lambda_1 = 0$ if and only if

$$1 - \frac{D}{D + \mu}(1 + \theta h v^b)\left(1 - \frac{v^b}{k}\right) = 0$$

which can be rewritten as

$$k = \frac{Dv^b(1 + \theta h v^b)}{\theta h D v^b - \mu} \quad (2.28)$$

We denote the subset of parameter space where this condition is satisfied by l_{ba} .

H_b : By definition, H_b is the subset of parameter space for which a pair of complex conjugate eigenvalues lie on the imaginary axis. Its intersection with a plane (e.g. the (k, D) plane) is a curve that can be easily computed by means of the numerical software **CONTENT**. The intersection of H_b and l_{ba} divides H_b into two parts, labeled by H_b^- and H_b^+ in **Figure 2.2** and **Figure 2.3**. So, $H_b = H_b^- \cup H_b^+$.

2.9.3 B.3. Eigenvalues corresponding to E_i^a

The eigenvalues corresponding to E_i^a satisfy a fourth order polynomial equation. As follows indirectly from the expression of E_i^a that we obtained in **Appendix A**, the condition for zero to be an eigenvalue yields the already known curves l_{sa} and l_{ba} .

H_a : By definition H_a is the subset of parameter space for which there is a pair of purely imaginary eigenvalues. To compute H_a we use **CONTENT**.

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Chapter 3

Interspecific Influence On Mobility And Turing Instability

Abstract. In this paper we formulate a multi-patch multi-species model in which the per capita emigration rate of one species depends on the density of some other species. We then focus on Turing instability to examine if and when this cross-emigration response has crucial effects. We find that the type of interaction matters much. In the case of competition a cross-emigration response promotes pattern formation by exercising a destabilizing influence; in particular, it may lead to diffusive instability provided that the response is sufficiently strong, which contrasts sharply with the well-known fact that the standard competition system does not exhibit Turing instability. In the case of prey-predator or activator-inhibitor interaction it acts against pattern formation by exerting a stabilizing effect; in particular, the diffusive instability, even though it may happen in a standard system, never occurs when the response is sufficiently strong. We conclude that the cross-emigration response is an important factor that should not be ignored when pattern formation is the issue.

Key words: Emigration Response, Cross-migration, Cross-diffusion, Pattern Formation, Diffusive Instability

AMS subject classification: 37G40, 37N25, 92D25

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3.1 Introduction

Throughout the history of theoretical biology, spatially continuous models formulated as reaction-diffusion equations (Okubo 1980, Murray 1993, Holmes et al. 1994, Grindrod 1996, Okubo&Levin 2000) have been intensely used to describe spatio-temporal dynamics and to investigate mechanisms for pattern formation. When individuals undergo unbiased random walk and the mobility of individuals of the various species is independent of the densities of both its own and other species, the standard system of reaction-diffusion equations

$$u_t = D\Delta u + f(u) \quad (3.1)$$

arises, where $u = u(t, x)$ is a vector of functions of t and x , f is a smooth map, D is a diagonal matrix with constant components and Δ is the Laplace operator.

However, there exist both experimental evidence (Takafuji 1977, Sabelis 1981, Bernstein 1984, Pels 2001) and theoretical arguments (e.g. Shigesada et al. 1979, Huang and Diekmann 2001) in favour of an emigration response, in particular, cross-emigration response: the inclination to emigrate depends on the densities of other species. For predator-prey interactions, for instance, prey at a certain position shall have increasing inclination to emigrate when the number of predators near-by increases because of the increasing danger, whereas predators, in contrast, shall have decreasing inclination to emigrate when the number of prey increases because of the increasing food resource.

When a cross-emigration response is incorporated, the corresponding reaction-diffusion model has the form

$$u_t = \Delta\phi(u) + f(u) \quad (3.2)$$

featuring a nonlinear vector diffusion term $\Delta\phi(u) = \Delta(D(u)u)$ with a diagonal matrix $D(u)$ (Okubo 1980, Aronson 1985). With the well-known theory of Turing instability in mind, a natural question then arises: Does such a cross-emigration response lead to crucially different stability results? Or, more specifically, does it promote or act against diffusive instability?

The system (3.2) is a *cross-diffusion* system in the sense that the temporal change of the density of a certain species is influenced by the spatial distribution of some other species. Such quasilinear systems are not at all easy to handle mathematically (Amann 1990, 1993, 1995, Lou&Ni 1996, Ni 1998). A spatially discrete model hence has certain advantages. In fact, when small amplitude pattern formation is the issue, spatially explicit multi-patch models and coupled map lattice models have often been used as an alternative (see e.g. some early work by Allen (1975) and Crowley (1981) and some recent work by Jansen&Lloyd (2000) and Plahte (2001)). The choice of the “right” model requires a careful assessment of the scale over which interactions and movement are taking place (Hastings 1990, Durrett&Levin 1994). Fortunately, however, the two types of model can be formulated and, at a formal level (i.e., ignoring the technicalities of justification), even analysed in an identical manner.

In this paper, we shall formulate a time-continuous multi-patch model analogous to (3.2) and then focus on the stability of homogeneous steady state solutions in the two species case to examine the effects of a cross-emigration response. Our strategy is to measure the strength of the cross-emigration response by real parameters related to the “size” of the quantities $\partial D_{ii}(u)/\partial u_j$ for $i \neq j$ and then to investigate how the stability of homogeneous steady state solutions changes as these parameters vary. By elaborating the second derivatives in $\Delta(D(u)u)$ one obtains the sum of a full (as opposed to a diagonal) matrix acting on the vector of second order derivatives and first order terms. Previous authors (Jor ne 1974, Almirantis and Papageorgiou 1991, Capasso and Di Liddo 1994, Chattopadhyay and Tapaswi 1993 1997, Farkas 1997) have studied the effect of the non-diagonal terms in this matrix. Our analysis is just a slight twist which, as we hope to demonstrate, has the advantage of allowing a clear biological interpretation yielding a general insight.

The organization of the paper is the following: In Section 2 we formulate the time-continuous multi-patch model in which the cross-emigration response is incorporated by way of a nonlinear map. In Section 3 we present a stability principle that simplifies the linear stability analysis. In Section 4 we examine the effects of the cross-emigration response on the stability of a homogeneous equilibrium by distinguishing different types of interactions.

3.2 The Model Formulation

Consider a system of k species living in a habitat of n identical patches linked by migration. (To assume that the patches are identical, facilitates the bookkeeping, since we do not have to elaborate how conservation of numbers works out on densities; but it is not really essential for the conclusions we shall obtain.)

Let

$$u_i(t, j) = \text{density of species } i \text{ in patch } j$$

$$u(t, j) = (u_1(t, j), \dots, u_k(t, j))^T$$

then the time-continuous model to be investigated can be formulated as a system of differential equations

$$\frac{\partial}{\partial t} u(t, j) = f(u(t, j)) + \sum_{l=1}^n c_{lj} \phi(u(t, l)), \quad j = 1, \dots, n \quad (3.3)$$

which is specified in terms of three ingredients f , ϕ and C that are defined as follows:

- $f : \mathbb{R}^k \rightarrow \mathbb{R}^k$ is a (nonlinear) smooth map describing the local interaction. So

$$u' = f(u) \quad \text{for } u \in \mathbb{R}_+^k$$

generates the dynamics in an isolated patch.

- $\phi : \mathbb{R}^k \rightarrow \mathbb{R}^k$ is a given (linear or nonlinear) map describing emigration at the population level. We assume that this map has the form

$$\phi(u) = M(u)u \quad (3.4)$$

and that

$$M(u) = \text{diag} \{d_1\rho_1(u), \dots, d_k\rho_k(u)\} \quad (3.5)$$

where d_i ($i = 1, 2, \dots, k$) is a constant characterising the per capita rate of emigration when individuals of species i emigrate from a certain patch randomly (i.e., with no response to the density of any species), while $\rho_i(u)$ ($i = 1, 2, \dots, k$) is positive and monotone as a function of the various components of u characterising the increase or the decrease of the per capita rate of emigration, relative to the per capita rate of random emigration (i.e. d_i), when individuals of species i emigrate from a certain patch in response to the densities of its own or other species.

We shall term the per capita rate of emigration of a certain species i as the *emigration response* of species i when it is density-dependent. In particular, we refer to it as *self-emigration response* when it depends on the density of the species itself and as *cross-emigration response* when it depends on the density of some other species.

- If $\rho_i(u) \equiv 1, i = 1, 2, \dots, k$ we refer to the system (3.3) as the *standard (diffusively coupled) system*.
- If the system of equations (3.3) involves a cross-emigration response (i.e., $\partial\rho_i(u)/\partial u_j \neq 0$ for some $j \neq i$), we call it a *cross-migration system*.
- $C : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is a linear map describing spatial structure or, in other words, the connectivity between patches. The map is represented by a matrix $C = (c_{ij})_{n \times n}$ whose elements are defined as

$$c_{ij} = \begin{cases} \tilde{c}_{ij} & \text{if } i \neq j \\ -1 + \tilde{c}_{ij} & \text{if } i = j \end{cases} \quad (3.6)$$

where \tilde{c}_{ij} is the probability per unit of time that an individual lands at patch j when it starts from patch i . Namely, the map \tilde{C} defined by the matrix

$$(\tilde{c}_{ij})_{n \times n}$$

describes the instantaneous redistribution.

We make, motivated by the properties of redistribution, two fundamental assumptions concerning C :

$$\text{Symmetry: } \quad c_{ij} = c_{ji}, \quad \text{for } 1 \leq i, j \leq n \quad (3.7)$$

$$\text{Conservation: } \quad \sum_{j=1}^n c_{ij} = 0 \quad \left(\text{i.e., } \sum_{j=1}^n \tilde{c}_{ij} = 1 \right) \quad (3.8)$$

The former expresses that migration is non-directional (for instance, governed only by relative distance), while the latter implies that individuals do not die in the process of migration.

Hence, C has n real eigenvalues $\lambda_1, \lambda_2, \dots, \lambda_n$ (see e.g. Marcus and Minc, 1964), satisfying

$$0 = \lambda_1 > \lambda_2 \geq \dots \geq \lambda_n \quad (3.9)$$

The system (3.3) may be written in a matrix form (Jansen&Lloyd 2000) as

$$U' = F(U) + \Phi(U)C \quad (3.10)$$

where

$$U = (u(t, 1), \dots, u(t, n)) = (u_i(t, j))_{k \times n}$$

and where $F, \Phi : \mathbb{R}^{k \times n} \rightarrow \mathbb{R}^{k \times n}$ are defined by “lifting” $f, \phi : \mathbb{R}^k \rightarrow \mathbb{R}^k$ in the sense that

$$F(U) = (f(u(t, 1)), \dots, f(u(t, n))) = (f_i(u(t, j)))_{k \times n}$$

$$\Phi(U) = (\phi(u(t, 1)), \dots, \phi(u(t, n))) = (\phi_i(u(t, j)))_{k \times n}$$

3.3 Stability Principle

In this section we shall establish a stability principle (due to Othmer&Scriven (1971), Jansen&Lloyd (2000), see also Plahte (2001)) for the homogeneous solutions of (3.10), to facilitate the forthcoming investigation.

Theorem 3.1 *Suppose that f, ϕ are two smooth $\mathbb{R}^k \rightarrow \mathbb{R}^k$ maps and that C is a $n \times n$ matrix which has n independent eigenvectors. The linearized system of (3.10) about a homogeneous solution $\bar{U} = (\bar{u}, \bar{u}, \dots, \bar{u})$ with \bar{u} taking values in \mathbb{R}_+^k , can be transformed by a similarity transformation into n decoupled k -dimensional subsystems*

$$y' = B_j y \quad (j = 1, 2, \dots, n)$$

where $B_j := Df(\bar{u}) + \lambda_j D\phi(\bar{u})$ in which λ_j is an eigenvalue of C .

The proof is put in the appendix of this chapter.

Remark The two assumptions (3.7) and (3.8) that we made in the last section guarantee that the matrix C has n independent eigenvectors. Moreover, they also allow the system (3.10) to have homogeneous solutions because it follows from them that $\sum_{i=1}^n c_{ij} = 0$ for all $j = 1, \dots, n$. The subsystem corresponding to $\lambda_1 = 0$ describes the linearized dynamics of (3.10) near \bar{U} within the homogeneous space $W = \{U = (u, u, \dots, u) \in \mathbb{R}_+^{k \times n} | u \in \mathbb{R}_+^k\}$, whereas the other subsystems describe the perturbations with spatial structure (i.e., the differences between patches).

When the homogeneous solution \bar{U} is an equilibrium we immediately have the following corollary

Corollary 3.2 *The homogeneous equilibrium $\bar{U} = (\bar{u}, \bar{u}, \dots, \bar{u})$ of (3.10) is linearly stable if and only if all eigenvalues of B_j ($j = 1, 2, \dots, n$) have negative real parts*

Remark If the eigenvalues of B_1 lie in the left half of the complex plane (i.e., \bar{U} is stable with respect to spatially homogeneous perturbations), while one or more eigenvalues of B_j ($j = 2, 3, \dots, n$) are to the right of the imaginary axis, we have the well-known **Turing instability**: small non-constant (in space) perturbations to the homogeneous equilibrium will grow and develop into spatial patterns. If the eigenvalues of B_1 do not lie in the left half of the complex plane (i.e., \bar{U} is homogeneously unstable), the homogeneous dynamics presumably leads to other attractors such as another steady state or periodic oscillations. We will not consider the latter case in this paper.

3.4 The Effects of a Cross-Emigration Response

For simplicity we consider only the two species case (i.e., $k = 2$) hereafter.

Suppose that $\bar{U} = (\bar{u}, \dots, \bar{u})$ is a positive homogeneous equilibrium of (3.3) whose uniform component \bar{u} is a stable equilibrium of the one-patch model. Let

$$Df(\bar{u}) = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \quad (3.11)$$

then we have the following two inequalities which are the general assumptions for the forthcoming discussion:

$$(I) \quad \begin{cases} a_{11} + a_{22} < 0 \\ a_{11}a_{22} - a_{12}a_{21} > 0 \end{cases} \quad (3.12)$$

According to the assumption for the map ϕ (see (3.4) and (3.5)) the Jacobian matrix $D\phi(\bar{u})$ can be computed and next be written as

$$D\phi(\bar{u}) \equiv \begin{pmatrix} m_1 & m_1\alpha \\ m_2\beta & m_2 \end{pmatrix} \quad (3.13)$$

where

$$m_i = d_i \left(\frac{\partial \rho_i(\bar{u})}{\partial u_i} \bar{u}_i + \rho_i(\bar{u}) \right), \quad i = 1, 2 \quad (3.14)$$

$$\alpha = \left(\frac{\partial \rho_1(\bar{u})}{\partial u_2} \bar{u}_1 \right) / \left(\frac{\partial \rho_1(\bar{u})}{\partial u_1} \bar{u}_1 + \rho_1(\bar{u}) \right) \quad (3.15)$$

$$\beta = \left(\frac{\partial \rho_2(\bar{u})}{\partial u_1} \bar{u}_2 \right) / \left(\frac{\partial \rho_2(\bar{u})}{\partial u_2} \bar{u}_2 + \rho_2(\bar{u}) \right) \quad (3.16)$$

We assume that $m_1, m_2 > 0$. The magnitude of the parameters α and β measures *the strength* of the cross-emigration response, while their sign indicates *the type*: *attraction* (negative sign) or *repulsion* (positive sign).

It is easier to contrast the cross-migration system with the standard system and to interpret the differences biologically if the per capita emigration rates are not self-density dependent (i.e., $\partial \rho_i(u)/\partial u_i = 0$, for $i = 1, 2$). One then sees that the system (3.3) is a standard system if and only if $\alpha = \beta = 0$.

Scaling m_1 to 1 (with the consequence that C and its eigenvalues change; we do not incorporate this in our notation; note, therefore, that the eigenvalues of C below are the scaled ones) and dropping the superfluous index 2 in m_2 the matrices B_j ($j = 2, \dots, n$) defined in the previous section can be written as

$$B(\alpha, \beta, m, \sigma^2) = \begin{pmatrix} a_{11} - \sigma^2 & a_{12} - \sigma^2 \alpha \\ a_{21} - \sigma^2 m \beta & a_{22} - \sigma^2 m \end{pmatrix} \quad (3.17)$$

where

$$\sigma \in \Lambda := \{ \sqrt{-\lambda_j} | j = 2, \dots, n \}$$

According to the corollary in the previous section, the equilibrium \bar{U} is linearly stable if and only if, for any $\sigma \in \Lambda$, the following two inequalities hold

$$(II) \quad \begin{cases} a_{11} + a_{22} - \sigma^2(1 + m) < 0 \\ K(\alpha, \beta, m, \sigma^2) > 0 \end{cases} \quad (3.18)$$

where

$$K(\alpha, \beta, m, \sigma^2) = [m\sigma^4 - (ma_{11} + a_{22})\sigma^2 + a_{11}a_{22} - a_{12}a_{21}] + [\sigma^2 a_{21} \alpha + m\sigma^2 a_{12} \beta - m\sigma^4 \alpha \beta] \quad (3.19)$$

It is clear that the first inequality in (II) always holds because of the general assumption (I) (see (3.12) and (3.18)). Therefore the linearized stability of the equilibrium \bar{U} is fully determined by the signs of the functions $K(\alpha, \beta, m, \sigma^2)$ for the various $\sigma \in \Lambda$. Namely,

$$\begin{array}{l} \text{Stability} \\ \text{Instability} \end{array} \quad \iff \quad \begin{array}{ll} K > 0 & \text{for all } \sigma \in \Lambda \\ K < 0 & \text{for some } \sigma \in \Lambda \end{array} \quad (3.20)$$

Now we are ready to check how the strength and the type of the cross-emigration response, as measured by α and β , affect the stability of \bar{U} . To proceed, we distinguish different types of interactions.

3.4.1 Competitive Interaction

For competitive interaction, a_{12}, a_{21} and α, β should satisfy

$$a_{12} < 0, a_{21} < 0, \alpha \geq 0, \beta \geq 0 \quad (3.21)$$

where the positive sign of α and β corresponds to the inclination of individuals of one species to leave from a certain patch due to the repulsion by the competitors in the patch.

Combining the general assumption (I) (i.e. (3.12)) with the sign assumption on a_{12}, a_{21} made here, we immediately find that $a_{11} < 0, a_{22} < 0$ which implies that

$$K(0, 0, m, \sigma^2) > 0, \text{ for all } \sigma \in \Lambda \text{ and for all } m > 0 \quad (3.22)$$

Therefore, \bar{U} remains stable when $\alpha = \beta = 0$ (no matter how big the parameter m is), corresponding to the well-known fact that the standard competition system does not exhibit Turing instability (Edelstein-Keshet 1987).

We now check the stability of \bar{U} when $\alpha \neq 0$ or/and $\beta \neq 0$ to see if the cross-emigration response can lead to diffusive instability.

Checking the expression of the function K defined in (3.19) we find that all terms involving α or/and β are negative when $\alpha \neq 0, \beta \neq 0$ according to the sign assumption (3.21) and that the sum of these terms decreases at a rate bounded away from zero as α or/and β increase. Therefore the function K shall be negative sooner or later as α or/and β increase. In other words, the diffusive instability shall arise when the cross-emigration response is sufficiently strong. To illustrate such a destabilizing effect of the cross-emigration response we visualize the neutral stability condition $K = 0$ in the $(\alpha, \beta, \sigma^2)$ space while the rest of the parameters are chosen to be fixed (see **Fig.3.1**).

3.4.2 Mutualism

For mutualistic interaction, a_{12}, a_{21} and α, β should satisfy

$$a_{12} > 0, a_{21} > 0, \alpha \leq 0, \beta \leq 0 \quad (3.23)$$

where the negative sign of α and β corresponds to the inclination of individuals of one species to stay at a certain patch due to the attraction by the other species in the patch.

For this type of interaction, we have the same conclusion about the effects of the cross-emigration response on the stability of the equilibrium \bar{U} as for the competitive

interaction because the signs of $\alpha\beta$, $a_{12}\beta$ and $a_{21}\alpha$ in the two types of interactions are the same.

3.4.3 Prey-Predator and Activator-Inhibitor Interaction

For prey-predator (or activator-inhibitor) interaction, if the prey and the predator correspond to, respectively, the indices 1 and 2, we should have

$$a_{12} < 0, a_{21} > 0, \alpha \geq 0, \beta \leq 0 \quad (3.24)$$

where the positive sign of α describes the inclination of a prey (or an activator) to leave from a certain patch because of the danger (or the inhibition), whereas the negative sign of β corresponds to the tendency of a predator (or an inhibitor) to stay at a certain patch because of the presence of prey (or the activator).

For this type of interaction \bar{U} may be diffusively stable or unstable when $\alpha = \beta = 0$, depending on the precise local interaction terms (Segel&Jackson 1972). Let us first assume that \bar{U} is diffusively stable when $\alpha = \beta = 0$, namely

$$K(0, 0, m, \sigma^2) > 0, \quad \text{for all } \sigma \in \Lambda \text{ and all } m > 0 \quad (3.25)$$

Then we have, according to the sign assumptions on a_{12}, a_{21} and α, β , that

$$K(\alpha, \beta, m, \sigma^2) > 0 \quad \text{for all } \sigma \in \Lambda \text{ and for all } m > 0$$

as well when $\alpha \neq 0$ or/and $\beta \neq 0$ (because all terms involving α or/and β are positive when $\alpha \neq 0, \beta \neq 0$ according to the sign assumption (3.24)). Therefore, the equilibrium \bar{U} can not be destabilized by the cross-emigration response.

Next, we assume that \bar{U} is diffusively unstable when $\alpha = \beta = 0$, namely

$$K(0, 0, m, \sigma^2) < 0, \text{ for some } \sigma \in \Lambda \text{ and for some } m > 0 \quad (3.26)$$

Now, the fact that all terms involving α or/and β in the expression of the function K are positive and that the sum of these terms increases at a rate bounded away from zero as α or/and $|\beta|$ increase means that the function K shall be positive sooner or later as α or/and $|\beta|$ increase. In other words, the equilibrium \bar{U} shall be stable when the cross-emigration response is sufficiently strong. To illustrate such a stabilizing effect of the cross-emigration response we visualize the neutral stability condition $K = 0$ in the $(\alpha, \beta, \sigma^2)$ space while the rest of the parameters are chosen to be fixed (see **Fig.3.2**). Note that it is required that $ma_{11} + a_{22} > 0$ because of the assumption (3.26).

3.4.4 Summary

Now we summarise the results as follows

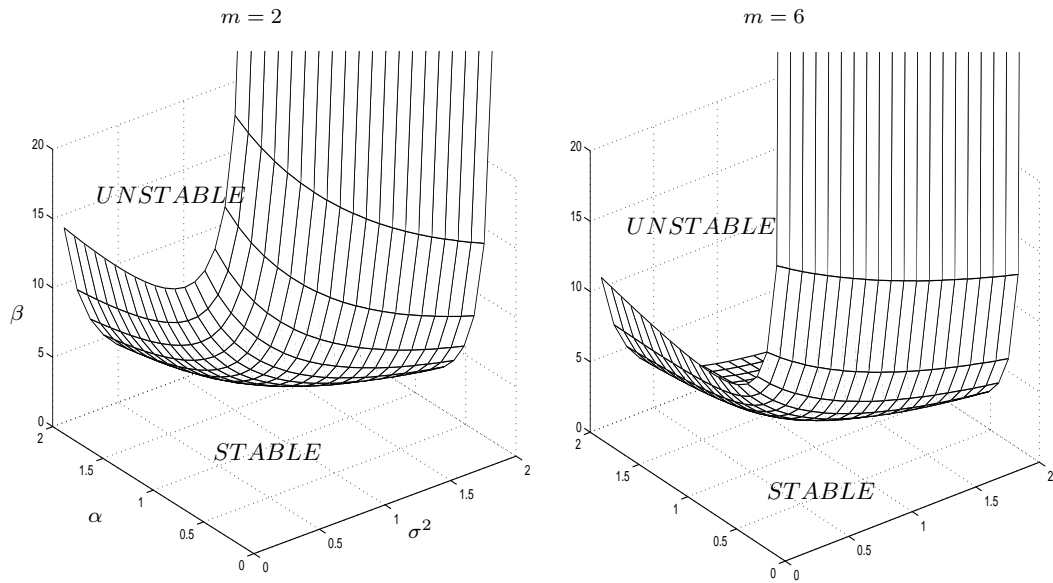


Figure 3.1: Neutral stability surfaces in the case of competition. When $\alpha = \beta = 0$ the equilibrium \bar{U} is stable. When α or/and β are sufficiently large the equilibrium becomes unstable. The other fixed parameters are as follows: $a_{11} = -2$, $a_{22} = -2$, $a_{12} = -0.4$, $a_{21} = -0.5$.

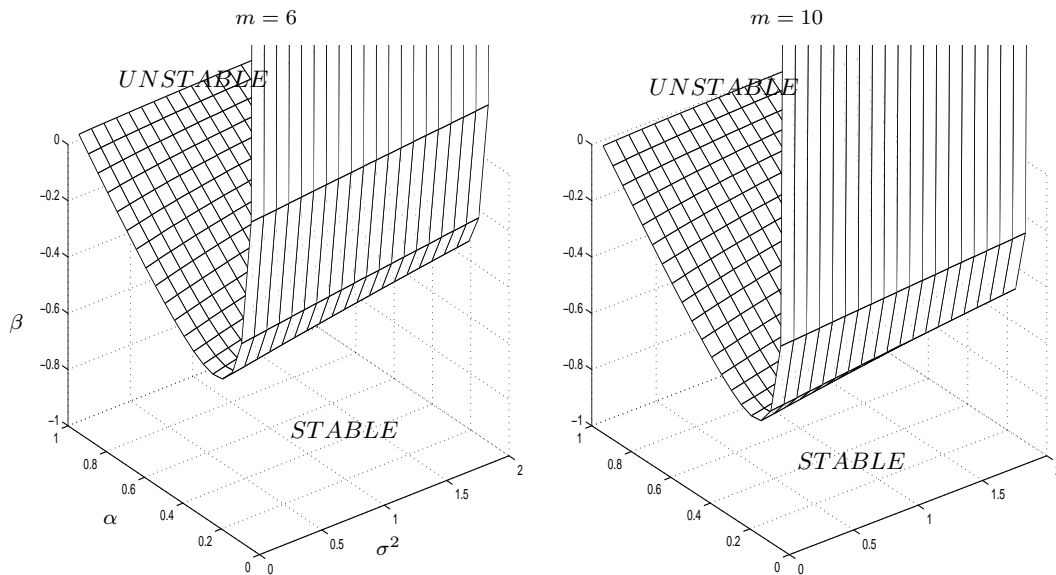


Figure 3.2: Neutral stability surfaces in the case of prey-predator or activator-inhibitor interaction. When $\alpha = \beta = 0$ the equilibrium \bar{U} is unstable. When α and/or $|\beta|$ are sufficiently large the equilibrium becomes stable. The other fixed parameters are as follows: $a_{11} = 2$, $a_{22} = -1$, $a_{12} = -2$, $a_{21} = 1.5$.

Proposition 3.3 *For a competitive type of interaction (or mutualism), random emigration never results in diffusive instability, but a cross-emigration response may lead to diffusive instability provided that the response is sufficiently strong. For a prey-predator (or an activator-inhibitor) type of interaction, a standard system with no emigration response may be either stable or unstable. A cross-emigration response, in particular that of the predator or inhibitor, can stabilize an unstable standard system provided that the response is sufficiently strong, but it can never destabilize a stable standard system.*

3.5 Discussion

In the study of a competition model proposed by Shigesada et al.(1979), several authors (Lou&Ni 1996, Ni 1998) found that a cross-emigration response characterised by a specific nonlinear diffusion term leads to inhomogeneous solutions that do not exist in the standard diffusion system. In the study of a two-patch prey-predator model in which a specific nonlinear form of the emigration map is incorporated, however, we found that inhomogeneous equilibria that exist in the standard diffusively coupled system disappear (Huang&Diekmann 2001). Having noticed these two specific examples and, more importantly, having realised that a cross-emigration response is an ubiquitous feature of multi-species systems (Sabelis 1981, Bernstein 1984, Pels 2001) we were motivated to study this potential mechanism of pattern formation theoretically. For this purpose we formulated a coupled multi-patch multi-species model in which the cross-emigration response is reflected by the nonlinearity of the emigration map. Here we did restrict ourselves to increased or decreased random movement rather than directional movement (Segel 1984, Aronson 1985), so that we could contrast the behaviour of the cross-migration systems with that of the standard system.

The cross-emigration response reflects density-dependence. We may distinguish an attractive cross-emigration response, in which an emigration rate is reduced, and a repulsive cross-emigration response, in which it is enhanced (the terminology has a tendency to be ambiguous, as there might very well be an asymmetry in the costs and benefits for the species A and B , when A exerts an influence on the emigration rate of B). Essentially we could quantify it by way of real parameters and could study its effect through bifurcation analysis. Our main result is that repulsive cross-emigration promotes pattern formation in competition systems while the natural combination of attractive and repulsive cross-emigration response for prey-predator or activator-inhibitor systems inhibits pattern formation.

The purpose of this paper is to emphasize the importance of the cross-emigration response as an ecological phenomenon. Our method of contrasting the cross-migration system with the standard system is quite similar to that which leads to the well-known theory of diffusion-driven instability (Segel&Jackson 1972, Edelstein-Keshet 1987, Grindrod 1996), where the conclusion is reached by contrasting the spatial system with the nonspatial system. Our results suggest that the cross-emigration response

might play a crucial stabilizing or destabilizing role in real biological systems and that it has so far not yet received the attention it deserves. In other words, spatial ecological theory based on simple standard diffusion should be subjected to a careful re-assessment and reinterpretation.

Since the emigration response is a highly uncontrollable factor in real biological systems, it is difficult (but perhaps not impossible) to experimentally examine whether or not it plays a crucial stabilizing or destabilizing role in the field. This difficulty is probably the reason that the issue has often been ignored. We hope that this work, although it is merely a theoretical argument at this stage, serves to alert the ecologists and to stimulate further experimental study of the issue.

3.6 Appendix: The Proof of Theorem 3.1

Let $Z = U - \bar{U}$ be a small perturbation. Then the nonlinear system

$$U' - \bar{U}' = F(U) - F(\bar{U}) + [\Phi(U) - \Phi(\bar{U})]C \quad (3.27)$$

can be approximated by the linear system

$$Z' = DF(\bar{U})Z + [D\Phi(\bar{U})Z]C \quad (3.28)$$

Since the matrix C has n independent eigenvectors, it can be diagonalized by a similarity transformation. Let $\omega_1, \dots, \omega_n$ be the n right eigenvectors with associated eigenvalues, respectively, $\lambda_1, \dots, \lambda_n$. We shall have

$$A^{-1}CA = \Lambda, \quad \text{or} \quad CA = A\Lambda$$

where $A = (\omega_1, \dots, \omega_n)$, while $\Lambda = \text{diag}\{\lambda_1, \dots, \lambda_n\}$. Multiplying (3.28) by A from the right and using the transformation

$$Y = ZA$$

we obtain a $k \times n$ dimensional system

$$Y' = DF(\bar{U})Y + D\Phi(\bar{U})Y\Lambda \quad (3.29)$$

which indeed consists of n decoupled k -dimensional systems

$$y'(t, j) = [Df(\bar{u}) + \lambda_j D\phi(\bar{u})]y(t, j), \quad j = 1, 2, \dots, n \quad (3.30)$$

Acknowledgements We thank Vincent Jansen for his comments and Miklos Farkas for providing some references.

Chapter 4

How Do Cross-Migration Models Arise?

Abstract. In this chapter we present a general method to derive spatial population models mechanistically. We consider a system of multiple species living in a patchy habitat in which the local population of each species consists of some behavioural groups. We then formulate a time-continuous model where a small positive parameter is present, measuring the time scale of behavioural transitions relative to that of giving birth, death and migration among patches. By the singular perturbation method the model is reduced to a lower dimensional one in which the migration terms are, in general, nonlinear and related to the reaction terms. Three examples demonstrating the emergence of cross-migration models, i.e., the models in which the per-capita emigration rate of one species depends on the density of some other species, are given.

*to be submitted

4.1 Introduction

Although it has been widely accepted that an understanding of spatial processes is important in ecological theory, it is not clear how best to proceed when modelling the interplay of dispersal and local interactions.

Classical reaction-diffusion models, in which dispersal is assumed to be a process independent of local interactions, like those studied by Skellam (1951) and Turing (1952), have revealed the fundamental importance of dispersal. Individuals' dispersal, or migration, however, may be far more complicated. Individuals of a species often have different behavioural states in which they have different migration inclinations. When predators are involved in handling a prey caught, or their stomach is full, for instance, they may have little inclination to migrate. When predators are searching, or they are very hungry, they might have a strong inclination to move. On the other hand, individuals may have a distinctive fecundity as well as mortality when they are in different behavioural states. Therefore, a consideration of individuals' behavioural states helps to model migration mechanistically.

There have been many examples of distinguishing different behavioural states of some predators and prey in connection with their foraging and predator avoidance behaviour. Huisman and De Boer (1997) have considered a case where predators have three states: searching, handling and coupling with a certain prey which can still escape. Ruxton et al (1992) have considered the interference between searching predators, so they assume that predators have three behavioural states: searching without interference, handling and a special state in which a forager is in trouble with another forager, so it is neither searching nor handling. Ruxton and Moody (1997) discussed kleptoparasitic interactions among predators, so predators have three different states: searching, handling without interference, being involved in the kleptoparasitic interaction. Various forms of the functional response have been derived in accordance with their assumptions. None of these works, however, addresses the connection of migration of predators to their feeding behaviour.

One of the major questions in spatial ecology is how explicit considerations of space alter the predictions of population models (Tilman and Kareiva 1997). To answer the question we need to extend population models to incorporate the spatial factor. Yet the mechanisms of spatial interactions of populations should be reflected well in the models in order to draw convincing conclusions. Though there is no absolute standard in this point, it is clearly much better to derive population-level description from assumptions concerning the behavioural mechanisms of individuals. In a previous study (Huang & Diekmann, 2001) we have studied a two-patch predator-prey model in which predators are assumed to be immobile when they are handling prey caught and to be mobile only when they are searching for prey. The model did show some qualitative and quantitative differences from the simple model. As we have pointed out in the previous paragraph, individuals of many species do have two or more behavioural states in which they may have different migration inclination. It is therefore natural to consider a general case where individuals have multiple behavioural states.

In this paper we shall formulate a time-continuous multi-patch multi-species model in which each population consists of some behavioural groups. We shall assume that behavioural transitions occur much faster than giving birth, death and migration among patches and that the per-capita rates of transition from one behavioural group to another are in general density-dependent. We then present a rigorous argument to reduce the model to a lower dimensional one. We shall also give some examples to show how cross-migration models, i.e., the models in which the per-capita emigration rate of one species depends on the density of some other species, naturally arise.

4.2 The Full System

Consider a system of K species who interact and grow in N identical habitat patches coupled by migration. Suppose that individuals of species i have S_i behavioural states. Therefore population i at a certain patch consists of S_i behavioural groups (or, subpopulations). The key assumptions concerning the transition between behavioural states are

- i) **Two time scales:** The behavioural transitions occur much faster than the processes of giving birth, death and migration.
- ii) **Nonlinear behavioural kinetics:** The per-capita rate at which individuals of a certain species at a certain patch switch from one behavioural group to another depends, in general, on the density of local behavioural groups of the species itself and/or some other species.

Incorporating these assumptions we have the following system of equations which we shall call **the full system**:

$$\frac{dU_{is}}{dt} = m_{is}\Delta U_{is} + F_{is}(\cdot)U_{is} + \frac{1}{\epsilon} \sum_{q \neq s, q=1}^{S_i} (\lambda_{iqs}(\cdot)U_{iq} - \lambda_{isq}(\cdot)U_{is}) \quad (4.1)$$

$$(i = 1, \dots, K ; s = 1, \dots, S_i ; j = 1, \dots, N)$$

in which we use the symbol i to index species, j to index patches, s and q to index behavioural states. The meaning of the various notations is as follows

$$U_{is} = U_{is}(t, j) = \text{the local density of group } s \text{ of species } i$$

$$U_i = U_i(t, j) = (U_{i1}(t, j), \dots, U_{iS_i}(t, j))^T$$

- ϵ is a small positive constant measuring the timescale of the behavioural transition relative to that of the other processes (viz. birth, death and migration among patches). In order to reformulate the model (4.1) and to apply the singular perturbation theory in the later sections we introduce a **fast time** $\tau = t/\epsilon$. t is hence a **slow time**.

- $F_{is}(\cdot) = F_{is}(U_1, \dots, U_K)$ is a smooth function describing the identical local per-capita rate of change of group s of species i .
- $\lambda_{isq}(\cdot) = \lambda_{isq}(U_1, \dots, U_K)$ is a smooth function describing the per capita rate (measured at the fast time scale $\tau = t/\epsilon$) at which individuals of group s of species i at a certain patch switch to group q of the same species ($s, q = 1, \dots, S_i$). These rates in general are functions of (U_1, \dots, U_K) . Namely, they depend, in general, on the density of various behavioural groups of various species.
- m_{is} is the per-capita emigration rate of individuals of group s of species i which is assumed to be constant.
- Δ is a (linear and discrete) spatial operator defined as

$$\Delta W(t, j) = -c_{jj}W(t, j) + \sum_{l \neq j, l=1}^n c_{lj} \int_0^\infty g(\delta) e^{-\mu\delta} W(t - \tau, l) d\delta, \quad j = 1, 2, \dots, n \quad (4.2)$$

for any density variable W .

- $g(\delta)$ is a species-dependent **probability density function** for the traveling time of an individual. This probability density function may be (behavioural) group-dependent and even (l, j) -dependent. We do not consider such a complicated case in this paper.
- $e^{-\mu\delta}$ is the probability that migrators survive a trip of duration δ . μ is a species-dependent positive constant.

What we consider here is a general situation where individuals spend some time to travel from one patch to another and that individuals may die on the way, as considered by, for instance, van den Bosch et al (1990) and Neubert et al (2002). In the special case where individuals travel instantaneously, we have

$$\Delta W(t, j) = \sum_{l=1}^n c_{lj} W(t, l), \quad j = 1, 2, \dots, n \quad (4.3)$$

$C = (c_{ij})_{n \times n}$ is a matrix (with constant elements) describing the spatial structure (For the detailed explanation of this matrix we refer to Jansen & Lloyd (2000), or Huang & Diekmann (2003), so as to avoid a lengthy repetition). A simple example of this matrix is

$$C = \begin{pmatrix} -1 & 1 & 0 & \cdots & \cdots & 0 \\ 1 & -2 & 1 & \cdots & \cdots & 0 \\ 0 & 1 & -2 & 1 & \cdots & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & & 1 & -2 & 1 & 0 \\ 0 & \cdots & & \cdots & 1 & -2 & 1 \\ 0 & \cdots & & \cdots & 0 & 1 & -1 \end{pmatrix} \quad (4.4)$$

The system of equations (4.1) may be written as

$$\frac{dU_i}{dt} = M_i \Delta U_i + F_i(\cdot) U_i + \frac{1}{\epsilon} \Lambda_i(\cdot) U_i. \quad (4.5)$$

$(i = 1, \dots, K ; j = 1, \dots, N)$

Here

$$F_i(\cdot) = \text{diag}\{F_{i1}(\cdot), \dots, F_{iS_i}(\cdot)\} \quad (4.6)$$

$$M_i = \text{diag}\{m_{i1}, \dots, m_{iS_i}\} \quad (4.7)$$

$$\Lambda_i(\cdot) = \begin{pmatrix} -\sum_{q \neq 1} \lambda_{i1q} & \lambda_{i21} & \cdots & \lambda_{iS_i1} \\ \lambda_{i12} & -\sum_{q \neq 2} \lambda_{i2q} & \cdots & \lambda_{iS_i2} \\ \cdots & \cdots & \cdots & \cdots \\ \lambda_{i1S_i} & \lambda_{i2S_i} & \cdots & -\sum_{q \neq S_i} \lambda_{iS_iq} \end{pmatrix} \quad (4.8)$$

We may compress (4.5) further to

$$\frac{dU}{dt} = M \Delta U + F(U)U + \frac{1}{\epsilon} \Lambda(U)U \quad (4.9)$$

$(j = 1, \dots, N)$

in which

$$U = (U_1, \dots, U_K)^T \quad (4.10)$$

$$F(U) = \text{diag}\{F_1, \dots, F_K\} \quad (4.11)$$

$$\Lambda(U) = \text{diag}\{\Lambda_1, \dots, \Lambda_K\} \quad (4.12)$$

$$M = \text{diag}\{M_1, \dots, M_K\} \quad (4.13)$$

Clearly the three terms in the right hand side of (4.9), i.e., $M \Delta U$, $F(U)U$ and $(1/\epsilon)\Lambda(U)U$, describe, respectively, the global migration, the local increase or decrease and the local behavioural transition.

4.3 Reduction

In most of cases what concerned is often the spatio-temporal evolution of the total abundance of the populations rather than the evolution of the distribution of the abundances of behavioural groups. For this reason, yet noticing that two timescales are present, we seek to reduce the full system (4.1) to a lower dimensional one by the singular perturbation method. We shall continue to omit the time and patch argument of density variables unless it is necessary to show them.

In order to apply the singular perturbation method we rewrite the full system (4.1) as the following $(S - K) \times K$ -dimensional system (with $S = S_1 + \dots + S_K$)

$$\epsilon \frac{dU_{is}}{dt} = \epsilon m_{is} \Delta U_{is} + \epsilon F_{is}(\cdot) U_{is} + \sum_{q \neq s, q=1}^{S_i} [\lambda_{iqs}(\cdot) U_{iq} - \lambda_{isq}(\cdot) U_{is}] \quad (4.14)$$

$$\frac{dU_i}{dt} = \Delta \left(\sum_{s=1}^{S_i} m_{is} U_{is} \right) + \sum_{s=1}^{S_i} F_{is}(\cdot) U_{is} \quad (4.15)$$

$(i = 1, \dots, K ; s = 1, \dots, S_i - 1)$

in which the equation (4.14) is obtained by multiplying the two sides of the equation (4.1) by ϵ , while the second equation (4.15) is obtained by summing up, respectively, the species specific equations in (4.1). Note that

$$U_i = \sum_{s=1}^{S_i} U_{is}, \quad i = 1, \dots, K \quad (4.16)$$

is the total population density of species i in patch j and that for each species i , U_{iS_i} should be understood as a function of $U_{i1}, \dots, U_{i(S_i-1)}$ and U_i , i.e.,

$$U_{iS_i} = U_i - \sum_{s=1}^{S_i-1} U_{is}, \quad i = 1, \dots, K \quad (4.17)$$

Let $\epsilon = 0$ in (4.14) we have following **quasi-steady-state equations** (note that for each species i , U_{iS_i} still has to be understood as a function of $U_{i1}, \dots, U_{i(S_i-1)}$ and U_i)

$$0 = \sum_{q \neq s, q=1}^{S_i} [\lambda_{iqs}(\cdot) U_{iq} - \lambda_{isq}(\cdot) U_{is}] \quad (4.18)$$

$(i = 1, \dots, K ; s = 1, \dots, S_i)$

which, together with (4.17), determines a set in $\mathbb{R}^{(S-K) \times K}$. This set (or its certain subset that is of interest) constitutes the so-called **critical manifold** by the terminology of the Geometric Singular Perturbation theory (Jones, 1994).

Let us assume that (4.18) together with (4.17) has a unique positive solution expressing U_{is} ($i = 1, \dots, K, s = 1, \dots, S_i$) as functions of $U := (U_1, \dots, U_K)^T$ (for $U \in \mathbb{R}_+^K$), say

$$U_{is} = \Psi_{is}(U_1, \dots, U_K)U_i, \quad i = 1, \dots, K, s = 1, \dots, S_i \quad (4.19)$$

which means that the critical manifold is given as the graph of the vector function $\Psi = (\Psi_1, \dots, \Psi_K)^T$ with $\Psi_i = (\Psi_{i1}, \dots, \Psi_{i(S_i-1)})^T$ ($i = 1, \dots, K$). For each species i , U_{is} ($i = 1, \dots, S_i$) given by (4.19) may be called the **quasi-steady state distribution**.

Since every element in any vector U_i now is a function of (U_1, \dots, U_K) according to the quasi-steady-state distribution (4.19) we can indeed obtain a decoupled $K \times N$ dimensional system describing the spatio-temporal evolution of the total densities of populations by substituting (4.19) into (4.15):

$$\frac{dU_i}{dt} = \Delta \left(\sum_{s=1}^{S_i} m_{is} \Psi_{is}(U_1, \dots, U_K) U_i \right) + G_i(U_1, \dots, U_K) \quad (4.20)$$

$(i = 1, \dots, k)$

Here $G(U_1, \dots, U_K) = \sum_{s=1}^{S_i} F_{is}(U_1, \dots, U_K)$.

This lower dimensional system contains **nonlinear migration terms** as long as one or more $\lambda_{iqs}(\cdot)$ are density-dependent; in particular, the system reflects **cross-migration** (i.e., the dependence of the per-capita emigration rate of one species on the density of some other species) if one or more λ_{iqs} depend on the density of some other species j ($j \neq i$) (Huang & Diekmann 2003). Moreover, the migration terms in (4.20) are, in general, nonlinear and related to the local interaction terms.

For the full system (4.1) what we are concerned about are usually some specific dynamical properties, the bifurcation of equilibria for instance. As far as such dynamical properties are concerned, it is sufficient to study the reduced system (4.20) if the critical manifold defined by (4.19) is **normally hyperbolic** and if the reduced system (4.20) is structurally stable (see **Appendix A** for a rigorous argument).

4.4 Examples

4.4.1 Example 1: Predator-Prey Interactions with Predators' Searching-handling Classification

Let us consider a multi-patch predator-prey system. Suppose that the prey is a sessile species and its individuals have only one state. Suppose that predators have two states in connection with their feeding activities: searching and handling. It follows that the predator population in each local patch (with density P) consists of two groups: the searching predators (with density P_s) and the handling predators (with density P_h).

The multi-patch model corresponding to (4.1) may be written, by omitting the time and patch argument of the various density variables, as

$$\frac{dV}{dt} = F(V) - \alpha V P_s \quad (4.21)$$

$$\frac{dP_s}{dt} = m_s \Delta P_s - \mu P_s + e \frac{1}{h} P_h + \left[\frac{1}{h} P_h - \alpha V P_s \right] / \epsilon \quad (4.22)$$

$$\frac{dP_h}{dt} = m_h \Delta P_h - \mu P_h + \left[\alpha V P_s - \frac{1}{h} P_h \right] / \epsilon \quad (4.23)$$

Here α is the searching efficiency. h is the mean handling time per prey item. μ is the per-capita death rate of both searching and handling predators. e is a conversion parameter. m_s and m_h are, respectively, the per-capita emigration rates of the searching and handling predators. The per-capita rate of switching from being searching to being handling (measured at the fast time scale $\tau = t/\epsilon$) is αV , while the per-capita rate of switching from being handling to being searching is $1/h$ (Holling 1959 1966, see also Metz and Diekmann 1986). $F(V)$ is a certain function describing the growth of prey in the absence of predators.

The full system may be rewritten as

$$\epsilon \frac{dP_s}{dt} = \epsilon m_s \Delta P_s + \epsilon \left[-\left(\mu + \frac{e}{h}\right) P_s + \frac{e}{h} P \right] + \left[\frac{1}{h} P - \left(\alpha V + \frac{1}{h}\right) P_s \right] \quad (4.24)$$

$$\frac{dV}{dt} = F(V) - \alpha V P_s \quad (4.25)$$

$$\frac{dP}{dt} = \Delta \left[(m_s - m_h) P_s + m_h P \right] + \left(\frac{e}{h} - \mu \right) P - \frac{e}{h} P_s \quad (4.26)$$

in which the relation $P = P_s + P_h$ has been used. The critical manifold is then given as

$$\begin{aligned} M_0 &= \left\{ (P_s, V, P) : 0 = \frac{1}{h} P - \left(\alpha V + \frac{1}{h}\right) P_s \right\} \\ &= \left\{ (P_s, V, P) : P_s = \frac{1}{1 + \alpha h V} P \right\} \end{aligned}$$

where the expression $P_s = \frac{1}{1 + \alpha h V} P$ is meaningful for any non-negative V, P . A substitution of this expression into the second and the third equation of the rewritten system yields the following reduced multi-patch predator-prey equations:

$$\frac{dV}{dt} = F(V) - \frac{\alpha V}{1 + \alpha h V} P \quad (4.27)$$

$$\frac{dP}{dt} = \Delta \left(\frac{m_s + m_h \alpha h V}{1 + \alpha h V} P \right) - \mu P + e \frac{\alpha V}{1 + \alpha h V} P \quad (4.28)$$

4.4.2 Example 2: Predator-Prey Interactions with Predators' Kleptoparasitism

Let us consider a multi-patch system of predator-prey with predators' kleptoparasitism (i.e. food-stealing) which is inspired by Ruxton and Moody (1997). Suppose that the prey is a sessile species and its individuals have only one state. Suppose that predators have three behavioural states: searching (s -state), handling without interference (h -state) and kleptoparasitic coupling (k -state). It follows that the predator population in each local patch (with density P) consists of three groups: the searching predators (with density P_s), the handling predators (with density P_h) and the predators who are being involved in the kleptoparasitic interaction (P_k). The multi-patch model corresponding to (4.1) may take the form

$$\frac{dV}{dt} = F(V) - \alpha V P_s \quad (4.29)$$

$$\begin{aligned} \frac{dP_s}{dt} = & m_s \Delta P_s - \mu P_s + e \frac{1}{h} P_h \\ & + \left(\left[\frac{1}{h} P_h - \alpha V P_s \right] + \left[\frac{1}{2k} P_k - \beta P_s P_h \right] \right) / \epsilon \end{aligned} \quad (4.30)$$

$$\begin{aligned} \frac{dP_h}{dt} = & m_h \Delta P_h - \mu P_h \\ & + \left(\left[\alpha V P_s - \frac{1}{h} P_h \right] + \left[\frac{1}{2k} P_k - \beta P_s P_h \right] \right) / \epsilon \end{aligned} \quad (4.31)$$

$$\begin{aligned} \frac{dP_k}{dt} = & m_k \Delta P_k - \mu P_k \\ & + \left(\left[\beta P_s P_h - \frac{1}{2k} P_k \right] + \left[\beta P_s P_h - \frac{1}{2k} P_k \right] \right) / \epsilon \end{aligned} \quad (4.32)$$

Here αV is the rate at which searching predators discover a prey. βP_h is the rate at which searching predators discover a handling predator. h is the mean handling time per prey item. k is the mean time per kleptoparasitic interaction. μ is the per-capita death rate of predators. e is a conversion parameter. m_s , m_h and m_k are respectively the per-capita emigration rates of searching predators, handling predators and predators involved in the kleptoparasitic interaction. $F(V)$ is a certain function describing the growth of prey in the absence of predators.

The assumptions concerning the per-capita rates of behavioural transition (measured at the fast time scale $\tau = t/\epsilon$) are the following

- i) Searching predators discover prey (and hence become handling predators) at a rate αV . Handling predators come back to search at a rate $1/h$.
- ii) Searching predators discover handling predators (and hence become involved in the kleptoparasitic interaction) at a rate βP_h . The k - state predators become

searching predators at a rate $\frac{1}{2k}$. (That is, the “klepto-owner” pair dissolves in one searching and one handling predator after an exponentially distributed time with mean k).

- iii) Handling predators are discovered by searching predators (and hence become involved in the kleptoparasitic interaction) at a rate βP_s . The k -state predators become handling predators at a rate $\frac{1}{2k}$.

The quasi-steady state equations are

$$0 = \left[\frac{1}{h}P_h - \alpha V P_s\right] + \left[\frac{1}{2k}P_k - \beta P_s P_h\right] \quad (4.33)$$

$$0 = \left[\alpha V P_s - \frac{1}{h}P_h\right] + \left[\frac{1}{2k}P_k - \beta P_s P_h\right] \quad (4.34)$$

$$0 = 2\beta P_s P_h - \frac{1}{k}P_k \quad (4.35)$$

Note that

$$P = P_s + P_h + P_k \quad (4.36)$$

We may solve for P_s , P_h and P_k as functions of V and P . We indeed have the following unique steady state solution which is biologically meaningful.

$$P_s = \frac{-(1 + \alpha h V) + \sqrt{(1 + \alpha h V)^2 + 8\alpha\beta h k V P}}{4\alpha\beta h k V} := \Phi_s(V, P) \quad (4.37)$$

$$P_h = \frac{-(1 + \alpha h V) + \sqrt{(1 + \alpha h V)^2 + 8\alpha\beta h k V P}}{4\beta k} := \Phi_h(V, P) \quad (4.38)$$

$$P_k = P - \Phi_s(V, P) - \Phi_h(V, P) =: \Phi_k(V, P) \quad (4.39)$$

We then end up with a time-continuous multi-patch predator-prey equations as follows

$$\frac{dV}{dt} = F(V) - \alpha V \Phi_s(V, P) \quad (4.40)$$

$$\begin{aligned} \frac{dP}{dt} &= \Delta[m_s \Phi_s(V, P) + m_h \Phi_h(V, P) + m_k \Phi_k(V, P)] \\ &\quad - \mu P + e\alpha V \Phi_s(V, P) \end{aligned} \quad (4.41)$$

One can see that both the functional response $\alpha V P_s/P$ and the emigration response of searching predators to prey density P_s/P vary with the kleptoparasitic strength ρ defined as $\rho = \frac{\beta k}{\alpha h}$. (see **Fig.4.1.**)

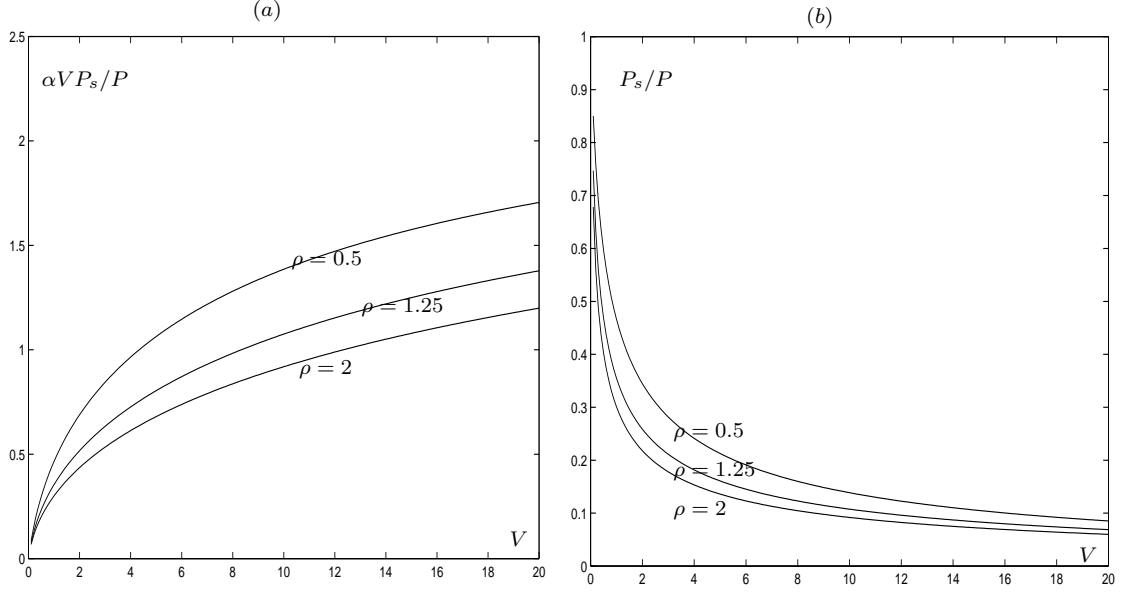


Figure 4.1: The graphs of the functional response $\alpha V P_s / P$ and the emigration response of the searching predators to prey density P_s / P for the various values of the kleptoparasitic strength ρ (see (a) and (b) respectively). Note that the expression of P_s is given as in (4.37). Fixed parameters or variables are $\alpha = 1, h = 0.4, P = 10$.

4.4.3 Example 3: Competition between Two Consumers

Consider a system of two consumers (C_1 and C_2) competing for a single food resource (R) in a patchy environment. Suppose that individuals of each consumer species have two states in connection with their feeding activity: searching and handling. Each consumer population in any patch then consists of a searching group (C_{is}) and a handling group (C_{ih}) ($i = 1, 2$). Ignoring any direct conspecific and interspecific interference among individuals we may have the following full system:

$$\frac{dR}{dt} = R^0 - R - \alpha_1 R C_{1s} - \alpha_2 R C_{2s} \quad (4.42)$$

$$\frac{dC_{1s}}{dt} = m_{1s} \Delta C_{1s} - \mu C_{1s} + e_1 \frac{1}{h_1} C_{1h} + \left[\frac{1}{h_1} C_{1h} - \alpha_1 R C_{1s} \right] / \epsilon \quad (4.43)$$

$$\frac{dC_{1h}}{dt} = m_{1h} \Delta C_{1h} - \mu C_{1h} + \left[\alpha_1 R C_{1s} - \frac{1}{h_1} C_{1h} \right] / \epsilon \quad (4.44)$$

$$\frac{dC_{2s}}{dt} = m_{2s} \Delta C_{2s} - \mu C_{2s} + e_2 \frac{1}{h_2} C_{2h} + \left[\frac{1}{h_2} C_{2h} - \alpha_2 R C_{2s} \right] / \epsilon \quad (4.45)$$

$$\frac{dC_{2h}}{dt} = m_{2h} \Delta C_{2h} - \mu C_{2h} + \left[\alpha_2 R C_{2s} - \frac{1}{h_2} C_{2h} \right] / \epsilon \quad (4.46)$$

The meaning of the parameters α_i, h_i, e_i, m_i ($i = 1, 2$) as well as μ is hopefully clear from the previous two examples. R^0 is the resource production. For simplicity we have assumed that the two consumer populations have the same per-capita death rate.

By the computational procedure of reduction method we end up with the following equations:

$$\frac{dR}{dt} = R^0 - R - \frac{\alpha_1 R}{1 + \alpha_1 h_1 R} C_1 - \frac{\alpha_2 R}{1 + \alpha_2 h_2 R} C_2 \quad (4.47)$$

$$\frac{dC_1}{dt} = \Delta \left(\frac{m_{1s} + m_{1h} \alpha_1 h_1 R}{1 + \alpha_1 h_1 R} C_1 \right) - \mu C_1 + e_1 \frac{\alpha_1 R}{1 + \alpha_1 h_1 R} C_1 \quad (4.48)$$

$$\frac{dC_2}{dt} = \Delta \left(\frac{m_{2s} + m_{2h} \alpha_2 h_2 R}{1 + \alpha_2 h_2 R} C_2 \right) - \mu C_2 + e_2 \frac{\alpha_2 R}{1 + \alpha_2 h_2 R} C_2 \quad (4.49)$$

4.5 Discussion

In this paper we formulated and (mathematically) justified a method to derive spatial population models mechanistically where the migration terms are in general nonlinear and related to the reaction terms. The **algorithm** may be summarized as three steps:

- i) Formulate the full time-continuous multi-species multi-patch model in which each species locally consists of some behavioural groups. The full model contains a submodel describing the kinetics of behavioural transitions of the various species which occur very fast compared to the other processes.
- ii) Specifying the various rates of behavioural transitions and then solve the steady state of the behavioural transition submodel to obtain a quasi-steady-state distribution which expresses the densities of the various behavioural groups as functions of the total local densities of the various species.
- iii) Reformulate the full model by respectively summing up the species-specific equations and then plug the quasi-steady-state distribution, which shall yield a lower dimensional population model containing information about the behavioural processes.

The behavioural transition submodel may be either **linear**, in which those per-capita rates of exchanging from one behavioural group to another are all constant or depend only on some environmental variables that do not change at the short behavioural time scale, or **nonlinear**, in which some transition rates depend on variables that do vary at the behavioural time scale. In this paper, we presented examples of both linear (Examples 1 and Example 3) and nonlinear case (Example 2). (see also Heesterbeek and Metz (1993) for an example of the nonlinear case and the relevant result).

The nonlinearity of migration terms and the connection of migration terms with reaction terms are the two important features that are not reflected in classical spatial models, such as the reaction-diffusion type of models. In a previous work (Huang & Diekmann 2001) we have investigated a specific predator-prey model with these two features and found that it did exhibit both quantitative and qualitative differences from the corresponding simple model. We hope that the method in this paper helps to derive realistic descriptions of spatial interactions of populations, like those models we obtained in the examples in this paper, by which we can understand the impact of dispersal and spatial interaction on population dynamics better.

There are a few practical problems associated with the implementation of the method. First of all, we need to recognize (or classify) the behavioural states (of individuals of species). The well-established concept, like the Holling searching-handling classification of predators, may give a great help in this point. Second, the time scale of behavioural transitions should be very small compared to other processes, in particular the migration among patches. If this is not true then the reduction method introduced in this paper is not applicable. Third, we have to make reasonable assumptions concerning the per-capita rates of transition between behavioural groups. All these problems have to be solved by studying the specific system concerned carefully.

It is no doubt that there are both differences and correspondences in fecundity, mortality and mobility between individuals of a species. In the one extreme, one assumes that every individual is different from others, yielding individual-based models which can only be analyzed by computer simulation. In the other extreme, one simply uses the art of averaging, formulating population models in which such differences and correspondences between individuals are usually ignored. The method in this paper is an attempt to bridge the gap between the two extremes.

Some authors (Weisser and Hassell (1996), Weisser et al (1997)) have considered multi-patch host-parasitoid models where each species is locally divided into a mobile and a stationary group. The local mobile and stationary groups may be thought of as two special behavioural groups. In this point their models are the special cases of the full system in this paper. However, they assumed that the mobile-stationary transition has the same time scale as the other processes and that the per-capita rates of transition between the two groups are constant, which are different from our assumptions. Some other authors (Michalski et al. 1997, Auger and Poggiale 1996) have developed a method to derive complex non-spatial predator-prey models. Our models and method are more general than these mentioned.

4.6 Appendix: Mathematical Justification of the Reduction Method

The mathematical justification of the reduction method relies on the Fenichel's first invariant manifold theorem (Fenichel 1971) which can be formulated and stated as

follows (Jones 1994).

Let

$$\begin{aligned} \epsilon x' &= H(x, y, \epsilon) & x &\in \mathbb{R}^l \\ y' &= G(x, y, \epsilon) & y &\in \mathbb{R}^m \end{aligned} \quad (4.50)$$

be a C^∞ vector field on $\mathbb{R}^l \times \mathbb{R}^m$ with one-dimensional small real parameter ϵ on which H and G depend C^∞ -smoothly. $\cdot' = \frac{d}{dt}$.

Suppose that the critical manifold $M_0 = \{(x, y) : H(x, y, 0) = 0\}$ is **normally hyperbolic**, i.e., the matrix $D_x H(\hat{x}, \hat{y}, 0)$ is invertible for any $(\hat{x}, \hat{y}) \in M_0$. Suppose further that the critical manifold M_0 is given as the graph of the function ψ^0 , i.e.,

$$M_0 = \{(x, y) : x = \psi^0(y)\} \quad (4.51)$$

We then have the following theorem

Theorem 4.1 *If $\epsilon > 0$, but sufficiently small, there is a function $x = \psi^\epsilon(y)$ defined on $\Omega \subset \mathbb{R}^m$, such that the graph*

$$M_\epsilon = \{(x, y) : x = \psi^\epsilon(y)\} \quad (4.52)$$

is locally invariant under (4.50). Moreover, ψ^ϵ is C^r for any $r < \infty$, jointly for y and ϵ .

The theorem implies that we can restrict the flow to a lower dimensional manifold M_ϵ which satisfies

- i) $M_\epsilon = M_0 + O(\epsilon)$ or $\psi^\epsilon(y) = \psi^0(y) + O(\epsilon)$
- ii) M_ϵ is diffeomorphic to M_0

Therefore, the following decoupled system

$$y' = G(\psi^\epsilon(y), y, \epsilon) \quad (4.53)$$

suffices to describe the flow on M_ϵ . One can see that (4.53) is a regular perturbation of

$$y' = G(\psi^0(y), y, 0) \quad (4.54)$$

It is easy to see that the system consisted of (4.14) and (4.15) has exactly the same form as (4.50). The Theorem 4.1 indicates that we can restrict the flow generated by (4.14) & (4.15) to the slow manifold which is $O(\epsilon)$ -close to the critical manifold, in order to find interesting structure. In other words, the full system (4.1) is approximated by (4.20) with an error of order $O(\epsilon)$. If (4.20) is structurally stable this error then can be neglected.

Chapter 5

Double-Jump Migration and Diffusive Instability

Abstract. To look into the stability consequences of a particular migration process in which individuals choose to settle, we formulated a time-continuous multi-species multi-patch model in which individuals migrate by one or two instantaneous jumps while making the second jump with a certain probability that possibly depends on the conditions at the end point of the first jump. It turned out that a second jump has some quantitative effects on diffusive instability when it occurs with a probability that is density-independent. When a second jump happens as a natural interspecific response of individuals, and such a response is sufficiently strong, it has crucial effects on diffusive instability: it leads to diffusive instability in the case of competitive interactions, whereas it annihilates diffusive instability in the case of prey-predator interactions.

*A joint work with Diekmann, O. and Van den Bosch, F., submitted to BMB

5.1 Introduction

One of the major issues in spatial population ecology is how dispersal combined with population dynamics influences stability and persistence of interacting species. Although a tremendous amount of theoretical work has been devoted to investigating the issue (Turing 1952, Okubo 1980, Okubo and Levin 2001, Segel 1984, Kareiva and Odell 1987, Othmer et al. 1988), the underlying mechanisms are far from being completely understood because of the complexity of dispersal processes.

Density-dependence, in particular interspecific density-dependence, might contribute substantially to the complexity of dispersal processes. In the case of predator-prey interactions, for instance, prey at a certain position may have increasing inclination to leave when the number of predators near-by increases because of the increasing danger, whereas predators, in contrast, may have decreasing inclination to emigrate when the number of prey increases because of the increasing food abundance. In the previous study (Huang&Diekmann, 2003) we scrutinized the issue via a time-continuous multi-species multi-patch model and found that such a density-dependence mechanism indeed has crucial effects on the stability of interacting species. The model takes (in somewhat different notation) the form

$$\frac{\partial}{\partial t} u_j = f(u_j) - \Phi(u_j)u_j + \sum_{k=1}^n \tilde{c}_{kj} \Phi(u_k)u_k, \quad j = 1, \dots, n \quad (5.1)$$

in which u_j is the vector of densities of species in a certain patch j , f is a nonlinear map describing the local interactions and $\Phi(\cdot)$ is a diagonal matrix in which the diagonal elements are the per-capita rate of emigration of the various species while \tilde{c}_{ij} is the probability that an individual arrives at patch j instantaneously after emigrating from patch i . The key assumption behind the equation is that individuals migrate in response to the quality of the patch of departure (Aronson 1985, Skellam 1973). In other words, it was assumed that there is a density-dependent mechanism at the emigration stage of the migration process and that individuals travel and land randomly after emigration.

Clearly some biological situations do not fit this description. In fact, for some species, such as benthic populations dispersing in the water and insect populations dispersing in the air, not only the departure but also the arrival could be influenced by density-dependent factors. For example, predatory mites dispersing in the air usually look for a “good place” to settle, while the settlement of free swimming larvae of some rock-shore species is often inhibited by chemical defence mechanisms of competitors. Even bird and mammal species do preferentially settle at places of higher prey density (van den Bosch et al, in press). In short, after travelling to a place, individuals may “choose” to settle or to travel again immediately, depending on the “quality” of the place.

To model such a dispersion process by a time-continuous multi-patch model, we need to extend our previous formulation. Indeed, the dispersal process described in the last paragraph may be regarded as consisting of two or more jumps. The approach

to dividing a spatio-temporal transition process into consecutive subprocesses (e.g., a sedentary stage of growth and interaction and a mobile stage) has been used in formulating time-discrete spatial models (Kot 1992, Neubert et al. 1995, Lewis et al. 2000). In the case where individuals do move by jumps of short duration (Othmer et al. 1988), we may use this method to formulate a time-continuous model.

In this paper, we shall indeed formulate a time-continuous multispecies multipatch model in which migration of individuals of each species is in general a composite of two instantaneous jumps. We shall assume that there is a probability for individuals to make a second jump (which depends in general on the conditions at the end point of the first jump). We shall first examine if and how the second-jump, when it is assumed to be density-independent (so merely featuring the approach of double-jump scheme of migration), changes the conditions for diffusive instability as compared to the standard approach. We then study whether or not the second jump, when it happens as a natural interspecific response of individuals, affects diffusive instability crucially.

5.2 The Model

Consider a system of m species in a habitat consisting of n identical patches. For any species i in any patch j , the rate of change of density matches the sum of the net growth rate and the net migration rate (i.e., immigration minus emigration), yielding the following system of ordinary differential equations:

$$\frac{du_j}{dt} = f(u_j) - Mu_j + (I - \Phi(u_j)) \sum_{k=1}^n q_{kj} Mu_k + \sum_{l=1}^n q_{lj} \Phi(u_l) \sum_{k=1}^n q_{kl} Mu_k$$

$$j = 1, 2, \dots, n \quad (5.2)$$

in which $u_j = (u_{1j}, \dots, u_{mj})^T \in \mathbb{R}^m$ is a m -vector whose element u_{ij} is the density of species i in patch j , while

- $f(\cdot) = (f_1(\cdot), \dots, f_m(\cdot))^T: \mathbb{R}^m \rightarrow \mathbb{R}^m$ is a vector function in which $f_i(\cdot)$ ($i = 1, \dots, m$) is the local growth rate of species i .
- $M = \text{diag}\{m_1, \dots, m_m\}: \mathbb{R}^m \rightarrow \mathbb{R}^{m \times m}$ in which m_i ($i = 1, \dots, m$) is the per-capita emigration rate of species i (from any patch). m_i may be density-dependent in general (which is in fact the case we have studied in the previous work (Huang&Diekmann 2003)), but we assume that m_i is density-independent in this paper in order to focus on our main concerns.
- $\Phi(\cdot) = \text{diag}\{\phi_1(\cdot), \dots, \phi_m(\cdot)\}: \mathbb{R}^m \rightarrow \mathbb{R}^{m \times m}$ in which $\phi_i(\cdot)$ ($i = 1, \dots, m$) is the probability that an individual of species i makes a second jump. For the sake of convenience we introduce one more piece of notation: $\phi(\cdot) = (\phi_1(\cdot), \dots, \phi_m(\cdot))^T: \mathbb{R}^m \rightarrow \mathbb{R}^m$.

- q_{ij} ($i, j = 1, 2, \dots, n$) is the probability that an individual instantaneously jumps to patch j from patch i . Therefore, $Q = (q_{ij})$ is an $n \times n$ matrix describing the instantaneous spatial redistribution of individuals. Note that this redistribution is assumed to be identical for all species. We shall discuss this matrix in detail in the next section.

An important assumption behind the formulation (5.2) is that a migration event in general consists of two jumps (and that neither the jumps, nor the period between jumps, take any time). It is also assumed that individuals make a second jump with a certain probability (which depends in general on the conditions at the end point of the first jump). It is clear, when focusing on a certain patch j , that the term Mu_j is the emigration rate, whereas the term $(I - \Phi(u_j)) \sum_{k=1}^n q_{kj} Mu_k$ is the immigration rate via a single jump and the term $\sum_{l=1}^n q_{lj} \Phi(u_l) \sum_{k=1}^n q_{kl} Mu_k$ is the immigration rate via double jumps.

If we define a new matrix $C = (c_{ij})_{n \times n} \equiv Q - I$ in which I is the $n \times n$ identity matrix, i.e.,

$$c_{ij} = \begin{cases} q_{ij} & \text{if } i \neq j \\ q_{ij} - 1 & \text{if } i = j \end{cases} \quad (5.3)$$

(5.2) can be rewritten as

$$\frac{du_j}{dt} = f(u_j) + \sum_{k=1}^n c_{kj} Mu_k + \sum_{l=1}^n c_{lj} \Phi(u_l) \sum_{k=1}^n q_{kl} Mu_k \quad (5.4)$$

$$j = 1, 2, \dots, n$$

We call (5.4) *the standard or single-jump equation* when $\Phi = \mathbf{0}$, and *the double-jump equation* when $\Phi \neq \mathbf{0}$.

5.3 Jump Redistribution

The matrix Q describing the instantaneous jumps is one of the important components of the model. We assume

$$0 \leq q_{ij} \leq 1 \quad \text{for } i, j = 1, 2, \dots, n \quad (5.5)$$

$$\sum_{j=1}^n q_{ij} = 1 \quad \text{for } i = 1, 2, \dots, n \quad (5.6)$$

The first assumption indicates that the elements of Q are probabilities. The second implies that no death occurs during migration.

In addition, we assume that

$$q_{ij} = q_{ji} \quad \text{for } i, j = 1, 2, \dots, n \quad (5.7)$$

which amounts to assuming that dispersal is non-directional (e.g. governed only by the distance).

Therefore, Q is diagonalizable and it has n real eigenvalues, one of which is one, the others being smaller than one. Indeed, all eigenvalues of Q lie in $[-1, 1]$ as follows from the well-known Gerschgorin Theorem in matrix theory (see e.g. Ortega (1987)). We shall denote the eigenvalues of Q by $\sigma_i, i = 1, 2, \dots, n$ and designate $\sigma_1 = 1$. Therefore

$$1 = \sigma_1 > \sigma_2 \geq \dots \geq \sigma_n \geq -1 \quad (5.8)$$

(see two examples of the matrix in the Appendix). Immediately one finds that the matrix C is diagonalizable as well and it has n real eigenvalues, one of which is zero, the others are negative, lying in $[-2, 0)$. We shall denote the eigenvalues of C by $\lambda_i, i = 1, 2, \dots, n$ and designate $\lambda_1 = 0$. Then

$$0 = \lambda_1 > \lambda_2 \geq \dots \geq \lambda_n \geq -2 \quad (5.9)$$

5.4 Stability Criteria of the Flat Solutions

It is clear that the assumptions about the matrices Q are such that the system (5.4) allows spatially homogeneous (or, flat) solutions. A flat solution has the form

$$S(t) = (s(t), \dots, s(t)) \in \mathbb{R}^{m \times n}$$

where $s(t) \in \mathbb{R}^m$ is the solution to the one-patch problem, i.e.,

$$\dot{s} = f(s)$$

The linear stability analysis of a flat solution to the n -patch system (5.4) can be simplified, as detailed in the following result.

Theorem 5.1 *The linearization of (5.4) around a flat solution $S(t) = (s(t), \dots, s(t))$ can be transformed by a similarity transformation into n decoupled subsystems*

$$\dot{w}_j = \{Df(s) + \lambda_j M[I + H(s) + (1 + \lambda_j)\Phi(s)]\} w_j, \quad j = 1, 2, \dots, n \quad (5.10)$$

Here $H(s) = \text{diag}\{s_1, \dots, s_m\}D\phi(s)$.

Remark A flat solution of (5.4) is linearly stable if and only if the zero solutions of the n subsystems given by (5.10) are all asymptotically stable. Hereafter, we shall call the matrices B_j defined by

$$B_j = Df(s) + \lambda_j M[I + H(s) + (1 + \lambda_j)\Phi(s)], \quad j = 1, 2, \dots, n \quad (5.11)$$

as **the criterion matrices**. When $s(t) = s$ is an equilibrium, the flat solution $S = (s, \dots, s)$ is linearly stable if all eigenvalues of the criterion matrices B_j have negative real parts. When $s(t+T) = s(t)$, i.e., $s(t)$ is periodic with period T , the flat solution $S(t)$ is linearly stable if all non-trivial Floquet multipliers of the system $\dot{w}_j = B_j(s(t))w_j$ for all j lie inside the unit circle.

Proof of Theorem 5.1

For any solution (u_1, \dots, u_n) and a flat solution (s, \cdot, s) of (5.4) we can write

$$\begin{aligned} \dot{u}_j - \dot{s} &= f(u_j) - f(s) + \sum_{k=1}^n c_{kj} M(u_k - s) \\ &+ \sum_{l=1}^n c_{lj} \sum_{k=1}^n q_{kl} M[\Phi(u_l)u_k - \Phi(s)s] \quad j = 1, 2, \dots, n \end{aligned} \quad (5.12)$$

The following Taylor expansion holds for any pair of m -dimensional vectors $x = (x_1, \dots, x_m) \in \mathbb{R}^m$ and $y = (y_1, \dots, y_m) \in \mathbb{R}^m$ with both $x - s$ and $y - s$ small:

$$\Phi(x)y = \Phi(s)s + H(s)(x - s) + \Phi(s)(y - s) + h.o.t. \quad (5.13)$$

in which

$$H(s) = \text{diag}\{s_1, \dots, s_m\} D\phi(s) := \left(\begin{array}{ccc} \frac{\partial \phi_1(x)}{\partial x_1} y_1 & \dots & \frac{\partial \phi_1(x)}{\partial x_m} y_1 \\ \dots & \dots & \dots \\ \frac{\partial \phi_m(x)}{\partial x_1} y_m & \dots & \frac{\partial \phi_m(x)}{\partial x_m} y_m \end{array} \right) \Big|_{x=y=s} \quad (5.14)$$

Let

$$u_j(t) = z_j(t) + s(t), \quad j = 1, 2, \dots, n$$

with $z_j(t)$ small. Then we find, for any $l, k = 1, 2, \dots, n$, that

$$\Phi(u_l)u_k - \Phi(s)s = H(s)z_l + \Phi(s)z_k + h.o.t. \quad (5.15)$$

The dynamics of $z_j(t), j = 1, 2, \dots, n$ can therefore be approximated by the linear system

$$\begin{aligned} \dot{z}_j &= Df(s)z_j + \sum_{k=1}^n c_{kj} M z_k \\ &+ \sum_{l=1}^n c_{lj} \sum_{k=1}^n q_{kl} M [H(s)z_l + \Phi(s)z_k], \quad j = 1, 2, \dots, n \end{aligned} \quad (5.16)$$

Since $\sum_{k=1}^n q_{kl} = 1$ (which follows from (5.6)&(5.7)), we find that

$$\begin{aligned} \dot{z}_j &= Df(s)z_j + \sum_{k=1}^n c_{kj}M(I + H(s))z_k \\ &+ \sum_{l=1}^n c_{lj} \sum_{k=1}^n q_{kl}M\Phi(s)z_k, \quad j = 1, 2, \dots, n \end{aligned} \quad (5.17)$$

To perform a linear transformation, we write the above system in the following matrix form

$$\begin{aligned} (\dot{z}_1, \dots, \dot{z}_n) &= (Df(s)z_1, \dots, Df(s)z_n) \\ &+ (M(I + H(s))z_1, \dots, M(I + H(s))z_n) C \\ &+ \left(\sum_{k=1}^n q_{k1}M\Phi(s)z_k, \dots, \sum_{k=1}^n q_{kn}M\Phi(s)z_k \right) C \end{aligned} \quad (5.18)$$

which may be written, using $Q = C + I$, as

$$\begin{aligned} (\dot{z}_1, \dots, \dot{z}_n) &= (Df(s)z_1, \dots, Df(s)z_n) \\ &+ (M(I + H(s) + \Phi(s))z_1, \dots, M(I + H(s) + \Phi(s))z_n) C \\ &+ (M\Phi(s)z_1, \dots, M\Phi(s)z_n) C^2 \end{aligned} \quad (5.19)$$

Because C is similar to the diagonal matrix $\Lambda = \text{diag}\{\lambda_1, \dots, \lambda_n\}$ in which $\lambda_1, \dots, \lambda_n$ are the n eigenvalues of C , there exists a nonsingular $n \times n$ matrix P such that

$$P^{-1}CP = \Lambda = \text{diag}\{\lambda_1, \dots, \lambda_n\}, \quad \text{or} \quad CP = P\Lambda \quad (5.20)$$

Multiplying (5.19) from the right by P and using the similarity transformation

$$w_j = z_j P, \quad j = 1, 2, \dots, n \quad (5.21)$$

we obtain

$$\begin{aligned} (\dot{w}_1, \dots, \dot{w}_n) &= (Df(s)w_1, \dots, Df(s)w_n) \\ &+ (M[I + H(s) + \Phi(s)]w_1, \dots, M[I + H(s) + \Phi(s)]w_n) \Lambda \\ &+ (M\Phi(s)w_1, \dots, M\Phi(s)w_n) \Lambda^2 \end{aligned} \quad (5.22)$$

which consists of n decoupled m -dimensional subsystems

$$\dot{w}_j = \{Df(s) + \lambda_j M[I + H(s) + \Phi(s) + \lambda_j \Phi(s)]\} w_j, \quad j = 1, 2, \dots, n \quad (5.23)$$

5.5 Effects on Diffusive Instability

Throughout this section we restrict ourselves to the two species case (i.e., $m = 2$). Let $S = (s, \dots, s)$ be a homogeneous equilibrium of (5.4) in which $s = (s_1, s_2)^T$ is a stable equilibrium of the one-patch problem $\dot{u} = f(u)$. For the standard equation ($\Phi = \mathbf{0}$) the criterion matrices are

$$B_j = Df(s) + \lambda_j M, \quad j = 1, 2, \dots, n \quad (5.24)$$

whereas for the double-jump equation ($\Phi \neq \mathbf{0}$) the criterion matrices are

$$B_j = Df(s) + \lambda_j [I + H(s) + (\lambda_j + 1)\Phi(s)]M, \quad j = 1, 2, \dots, n \quad (5.25)$$

Let $Df(s) = (f_{ij})_{2 \times 2}$. The assumption that the equilibrium of the one-patch problem s is linearly stable implies that

$$\begin{cases} f_{11} + f_{22} < 0 \\ f_{11}f_{22} - f_{12}f_{21} > 0 \end{cases} \quad (5.26)$$

Let $D\phi(s) = (\phi_{ij})_{2 \times 2}$. We then find, by definition, that

$$H(s) = \text{diag}\{s_1, s_2\}D\phi(s) = \begin{pmatrix} s_1\phi_{11} & s_1\phi_{12} \\ s_2\phi_{21} & s_2\phi_{22} \end{pmatrix} \quad (5.27)$$

It follows that the criterion matrix B_j (for $\lambda_j \in [-2, 0]$ and $\phi_1, \phi_2 \in [0, 1]$) has the form

$$B(\lambda_j, \phi_1, \phi_2, \alpha, \beta) = \begin{pmatrix} f_{11} + \lambda_j \hat{m}_1 & f_{12} + \lambda_j \alpha \\ f_{21} + \lambda_j \beta & f_{22} + \lambda_j \hat{m}_2 \end{pmatrix} \quad (5.28)$$

in which

$$\hat{m}_i = m_i [1 + (\lambda_j + 1)\phi_i + s_i \phi_{ii}], \quad i = 1, 2 \quad (5.29)$$

$$\alpha = s_1 \phi_{12} \quad \beta = s_2 \phi_{21} \quad (5.30)$$

We shall assume that $\phi_{ii} \geq 0$ for $i = 1, 2$. It follows that $\hat{m}_i \geq 0$ ($i = 1, 2$) for any $\lambda_j \in [-2, 0]$ and $\phi_1, \phi_2 \in [0, 1]$.

S is stable if and only if

$$\begin{cases} f_{11} + f_{22} + \lambda_j(\hat{m}_1 + \hat{m}_2) < 0 \\ K(\lambda_j, \phi_1, \phi_2, \alpha, \beta) > 0 \end{cases} \quad (5.31)$$

in which

$$\begin{aligned} K(\lambda_j, \phi_1, \phi_2, \alpha, \beta) &= f_{11}f_{22} - f_{12}f_{21} + \lambda_j(f_{11}\hat{m}_2 + f_{22}\hat{m}_1) + \lambda_j^2\hat{m}_1\hat{m}_2 \\ &\quad - \lambda_j f_{21}\alpha - \lambda_j f_{12}\beta - \lambda_j^2\alpha\beta \end{aligned} \quad (5.32)$$

Since the first inequality in (5.31) holds for any $\lambda_j \in [-2, 0]$ under the assumption (5.26) (Note that m_1, m_2 are nonnegative and that $\phi_1, \phi_2 \in [0, 1]$), the diffusive instability arises if and only if $K(\lambda_j, \phi_1, \phi_2, \alpha, \beta) < 0$ for some $\lambda_j \in [-2, 0]$.

5.5.1 Density-Independent Second Jump

Let us look in this subsection at the case where Φ is density-independent. In this case $\mathbf{H}(\mathbf{s}) = \mathbf{0}$. It follows that $\alpha = \beta = 0$ and that

$$\begin{aligned} K(\lambda_j, \phi_1, \phi_2, 0, 0) &= f_{11}f_{22} - f_{12}f_{21} + \lambda_j[1 + (\lambda_j + 1)\phi_1]f_{22}m_1 \\ &\quad + \lambda_j[1 + (\lambda_j + 1)\phi_2]f_{11}m_2 \\ &\quad + \lambda_j^2[1 + (\lambda_j + 1)\phi_1][1 + (\lambda_j + 1)\phi_2]m_1m_2 \end{aligned} \quad (5.33)$$

For competitive interaction, it is natural that $f_{12} < 0, f_{21} < 0$. It follows from the general assumption (5.26) that $f_{11} < 0, f_{22} < 0$. Therefore, $K(\lambda_j, \phi_1, \phi_2, 0, 0) > 0$ for all $\lambda_j \in [-2, 0]$, which suggests that the system (5.4) can not exhibit diffusive instability.

For prey-predator (or activator-inhibitor) interaction it is natural that f_{12} and f_{21} have the opposite signs. It follows from the general assumption (5.26) that $f_{11}f_{22} < 0$. Suppose, without loss of generality, that $f_{11} > 0, f_{22} < 0$. The neutral stability condition $K(\lambda_j, \phi_1, \phi_2, 0, 0) = 0$ can then be written as

$$m_2 = \frac{(f_{11}f_{22} - f_{12}f_{21}) + f_{22}\lambda_j[1 + (\lambda_j + 1)\phi_1]m_1}{-\lambda_j[1 + (\lambda_j + 1)\phi_2]\{f_{11} + \lambda_j[1 + (\lambda_j + 1)\phi_1]m_1\}} \quad (5.34)$$

which defines a curve in the (m_1, m_2) plane (while $0 \leq m_1 \leq -\frac{f_{11}}{\lambda_j[1 + (\lambda_j + 1)\phi_1]}$) when the other parameters are fixed. It is clear that the homogeneous equilibrium S becomes unstable in the j^{th} eigenmode as the point (m_1, m_2) move upwards over the curve. Some simple algebra shows that the curve moves upwards as ϕ_2 increases from 0 to 1 for any $|\lambda_j| \leq 1$ (while the other parameters are fixed) and that the curve moves downwards as ϕ_2 increases from 0 to 1 for any $|\lambda_j| > 1$ (while the other parameters are fixed) (see the two upper pictures in **Fig.5.1** where we plot the curve for the two extremes of ϕ_2 only). It can be shown similarly that the curve moves to the left as ϕ_1 increases for any $|\lambda_j| \leq 1$ and that the curve moves to the right as ϕ_1 increases for any $|\lambda_j| > 1$ (see the two lower pictures in **Fig.5.1** where we plot the curve for the two extremes of ϕ_1 only). In summary, we have

Proposition 5.2 *Without density-dependent mechanisms in making jumps both the double-jump equation and the standard equation exhibit no diffusive instability for competitive interactions. For predator-prey (or activator-inhibitor) interactions, both equations could exhibit diffusive instability, for which some quantitatively different conditions are required.*

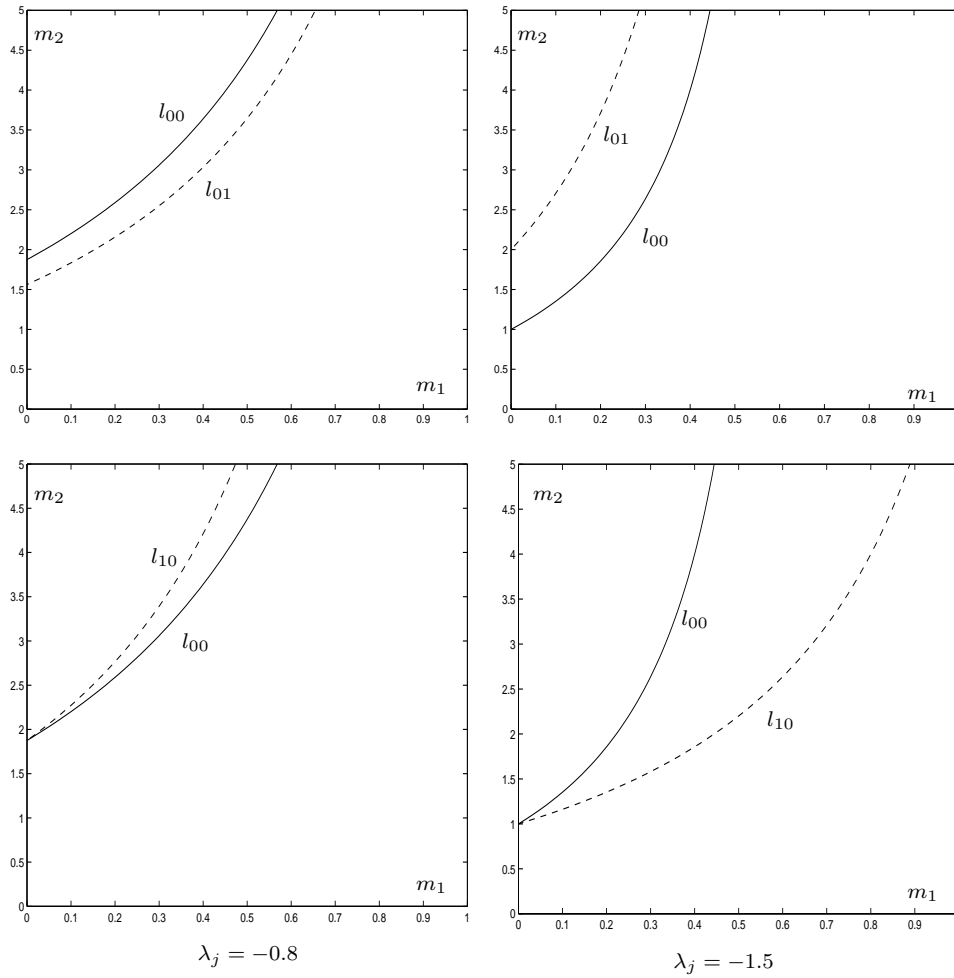


Figure 5.1: Neutral stability curves (l_{ij} corresponds to the neutral stability condition $Det(B(\lambda_j, \phi_1, \phi_2, 0, 0)) = 0$ for $\phi_1 = i, \phi_2 = j, i, j = 0, 1$). The homogeneous equilibrium becomes linearly unstable in the j^{th} eigenmode of the linearized system when the point (m_1, m_2) moves upwards over a curve in each picture. The other fixed parameters are: $f_{11} = 1, f_{22} = -1.5, f_{12} = -2, f_{21} = 1.5$.

5.5.2 Density-Dependent Second Jump

In this subsection we consider the case where one or both diagonal elements of Φ are density-dependent. We shall speak of **the cross-response second jump** if the probability that individuals of species i make a second jump (i.e. ϕ_i) depends on the density of the other species. Now, one finds that $H(s) = \text{diag}\{s_1, \dots, s_m\}D\phi(s)$ is a full matrix (rather than a diagonal matrix) and that $\alpha \neq 0, \beta \neq 0$. Note that $|\alpha|$ and $|\beta|$ measure **the strength** of the cross-response of the second-jump.

For competitive interaction, f_{12}, f_{21} and α, β should satisfy

$$f_{12} < 0, f_{21} < 0, \alpha \geq 0, \beta \geq 0 \quad (5.35)$$

where the positive sign of α and β means that the inclination of individuals of one species to make a second jump increases as the number of the competitors increases.

Checking the expression of the function K defined in (5.32) we find that all terms involving α or/and β are negative when $\alpha \neq 0, \beta \neq 0$ according to the sign assumption (5.35) and that the sum of these terms decreases at a rate bounded away from zero as α or/and β increase. Therefore the function K shall be negative sooner or later as α or/and β increase. In other words, the diffusive instability shall arise when the cross-response (of the second jump) is sufficiently strong.

For prey-predator (or activator-inhibitor) interaction, if the prey and the predator correspond to, respectively, the indices 1 and 2, we should have

$$f_{12} < 0, f_{21} > 0, \alpha \geq 0, \beta \leq 0 \quad (5.36)$$

where the positive sign of α implies that the inclination of prey to make a second jump increases as the number of predators increases, whereas the negative sign of β suggests that the tendency of predators to make a second jump decreases as the number of prey increases.

For this type of interaction S may be diffusively stable or unstable when $\alpha = \beta = 0$, depending on the precise local interaction terms (Segel&Jackson 1972). Let us first assume that S is diffusively stable when $\alpha = \beta = 0$, namely

$$K(\lambda_j, \phi_1, \phi_2, 0, 0) > 0, \quad \text{for all } \lambda_j \in [-2, 0) \quad (5.37)$$

Then we find, according to the sign assumptions on f_{12}, f_{21} and α, β , that

$$K(\lambda_j, \phi_1, \phi_2, \alpha, \beta) > 0, \quad \text{for all } \lambda_j \in [-2, 0) \quad (5.38)$$

as well when $\alpha \neq 0$ or/and $\beta \neq 0$ (because all terms involving α or/and β are positive when $\alpha \neq 0, \beta \neq 0$ according to the sign assumption (5.36)). Therefore, the equilibrium S can not be destabilized by the cross-response (of the second jump).

Next, we assume that S is diffusively unstable when $\alpha = \beta = 0$, namely

$$K(\lambda_j, \phi_1, \phi_2, 0, 0) < 0, \quad \text{for some } \lambda_j \in [-2, 0) \quad (5.39)$$

Now, the fact that all terms involving α or/and β in the expression of the function K are positive and that the sum of these terms increases at a rate bounded away from zero as α or/and $|\beta|$ increase means that the function K shall be positive sooner or later as α or/and $|\beta|$ increase. In other words, the equilibrium \bar{U} shall be stable when the cross-response (of the second jump) is sufficiently strong. In summary, we have

Proposition 5.3 *For a competitive type of interaction (or mutualism), a standard equation does not exhibit diffusive instability, but a cross-response second jump may lead to diffusive instability provided that the response is sufficiently strong. For a prey-predator (or an activator-inhibitor) type of interaction, a standard equation may be either stable or unstable. A cross-response second jump can stabilize an unstable standard equation provided that the response is sufficiently strong, but it can never destabilize a stable standard equation.*

5.6 Examples

5.6.1 Competition

Let us consider a multi-patch two-species competitive system (formulated as (5.4)) in which the identical local dynamics is described by the following Lotka-Volterra equations

$$\begin{aligned} \dot{u} &= u(a_1 - b_1u - c_1v) \\ \dot{v} &= v(a_2 - b_2u - c_2v) \end{aligned} \quad (5.40)$$

where all the constants $a_i, b_i, c_i, i = 1, 2$ are positive. u and v are respectively the population densities of the two competing species. In the “weak competition” case, i.e.,

$$\frac{b_1}{b_2} > \frac{a_1}{a_2} > \frac{c_1}{c_2} \quad (5.41)$$

(5.40) has a positive steady state

$$(u^*, v^*) = \left(\frac{a_1c_2 - a_2c_1}{b_1c_2 - b_2c_1}, \frac{b_1c_2 - b_2a_1}{b_1c_2 - b_2c_1} \right)$$

Standard Equation The corresponding equation is (5.4) with $\Phi = \mathbf{0}$. It is well-known that the homogeneous steady state of (5.4), i.e., $S = (s, \dots, s)$ with $s = (u^*, v^*)^T$, is globally asymptotically stable no matter how large the constants m_1, m_2 are.

Double-Jump Equation The corresponding equation is (5.4) with $\Phi \neq \mathbf{0}$. Let us assume that the probability that individuals of species 1 make a second jump is constant and that the probability that individuals of species 2 make a second jump depends on the density of species 1, i.e., $\Phi = \text{diag}\{\phi_1, \phi_2(u)\}$. Suppose that

$$\phi_2(u) = \frac{u^\theta}{(u^*)^\theta + u^\theta}, \quad u \geq 0, \theta \geq 0 \quad (5.42)$$

(see **Fig.5.2**). One can easily compute that

$$\beta = [\phi_2'(u)v]|_{u=u^*, v=v^*} = \phi_2'(u^*)v^* = \frac{v^*}{4u^*}\theta$$

So the parameter θ measures the strength of the second-jump response of species 2 to the density of species 1.

By Proposition 5.3, S becomes unstable when θ is sufficiently large. (see **Fig.5.3**.)

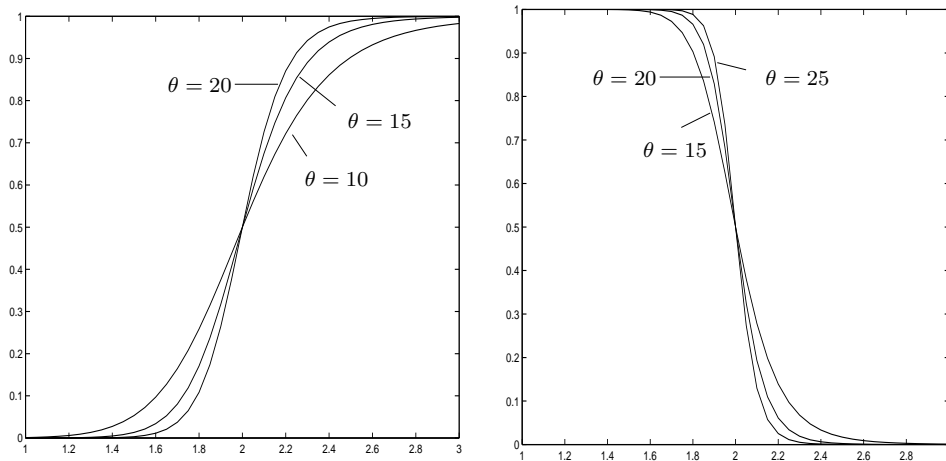


Figure 5.2: Left picture: the graphs of the function $\phi(x) = \frac{x^\theta}{x^\theta + 2^\theta}$ for the various values of θ . Right picture: the graphs of the function $\phi(x) = \frac{2^\theta}{x^\theta + 2^\theta}$ for the various values of θ .

5.6.2 Predator-Prey Interaction

Let us consider a multi-patch phytoplankton-herbivore system (formulated as (5.4)) in which the identical local dynamics is determined by the equations (Levin and Segel 1976)

$$\begin{aligned} \dot{v} &= av + ev^2 - b_1vp \\ \dot{p} &= -cp^2 + b_2vp \end{aligned} \quad (5.43)$$

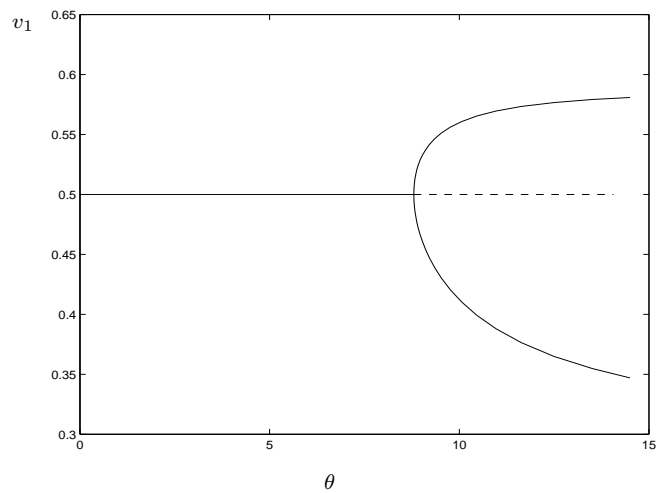


Figure 5.3: A one-parameter bifurcation diagram of the two-patch competition system with a double-jump scheme of migration. The local dynamics is determined by (5.40). $\phi_1 = \text{const}$, ϕ_2 is given by (5.42). It is clear that inhomogeneous equilibria arise as the parameter θ , which measures the strength of the second-jump response of the species 2 to the density of species 1, increases. The other relevant parameters are $a_1 = b_1 = c_1 = 1$, $a_2 = 2, b_2 = 1, c_2 = 3$; $m_1 = 0.1, m_2 = 2.5$; The redistribution matrix Q is set to be $q_{11} = q_{12} = q_{21} = q_{22} = 0.5$.

which reflect the assumptions that there is an autocatalytic effect in the growth rate of phytoplankton (v) and that the mortality of the herbivore (p) is density-dependent. All parameters a, b_1, b_2, c and e are positive.

When $b_1 b_2 > ce$ and $b_2 > e$, (5.43) has an asymptotically stable steady state

$$(v^*, p^*) = \left(\frac{ac}{b_1 b_2 - ce}, \frac{ab_2}{b_1 b_2 - ce} \right)$$

Standard Equation The corresponding equation is (5.4) with $\Phi = \mathbf{0}$. It is known that when

$$\frac{m_2}{m_1} > \frac{1}{[\sqrt{b_1/c} - \sqrt{b_1/c - e/b_2}]^2} \quad (5.44)$$

diffusive instability occurs.

Double-Jump Equation The corresponding equation is (5.4) with $\Phi \neq \mathbf{0}$. Let us assume that the probability that individuals of species 1 make a second jump is constant and that the probability that individuals of species 2 make a second jump depends on the density of species 1, i.e., $\Phi = \text{diag}\{\phi_1, \phi_2(u)\}$. Suppose that

$$\phi_2(v) = \frac{(v^*)^\theta}{(v^*)^\theta + v^\theta}, \quad u \geq 0, \theta \geq 0 \quad (5.45)$$

(see **Fig.5.2**). One can easily compute that

$$\beta = [\phi_2'(v)p]|_{v=v^*, p=p^*} = \phi_2'(v^*)p^* = -\frac{p^*}{4v^*}\theta$$

So the parameter θ measures the strength of the second-jump response of predators to the density of prey.

Thus, diffusive instability never occurs when θ is sufficiently large according to Proposition 5.3.

5.7 Discussion

The migration process of some animal and insect species might be so complicated that it can not be considered as a simple Markov process, as has been the standard approach to describe the spatial transition of organisms. In this paper we considered the case where a migration event consists of one or two instantaneous jumps (by a jump we mean an instantaneous take-off-and-landing process). It turned out that a density-independent second jump has some quantitative effects on diffusive instability. When a second jump happens as a natural interspecific response of individuals, and such a response is sufficiently strong, it has crucial effects on diffusive instability: it leads to diffusive instability in the case of competitive interactions, whereas it annihilates diffusive instability in the case of prey-predator interactions. So the present results

reinforce our earlier (Huang&Diekmann, 2003) conclusion that it is the interspecific influence on mobility, occurring in one way or another, that crucially affects diffusive instability.

Clearly the type of interaction is crucial in leading to our results. In the case of two-species competition, the local growth of one species decrease as the abundance of the other species increases, while the inclination of individuals of one species to make a second jump increases as the abundance of the other species increases. In the case of predator-prey interactions, the local growth of predators increase as the abundance of prey increases, while the inclination of predator to make a second jump decreases as the abundance of prey increases. So there is a natural configuration between the local interaction and the second-jump response in each type of interaction. It is such a natural configuration determined by the interaction type that leads to our results.

We may extend the model (5.4) further to let M be cross-density-dependent. Namely, we may further consider the case where both a cross-emigration response and a cross-second-jump-response exist. Apart from that some expressions could be more lengthy the computation procedure in Section 5.5 should carry over. It is hence expected that the resulting model with both mechanisms (viz, both the cross-response of second jump and the cross-response of emigration) should exhibit diffusive instability easier in the case of competition, but more difficult in the case of predator-prey interactions as compared to the model with only one mechanism.

5.8 Appendix: Examples of the Matrix Q

In the case that n patches are arranged in a one-dimensional linear chain, Q may have, for instance, the form

$$Q = \begin{bmatrix} \frac{1}{2} & \frac{1}{2} & 0 & \cdots & \cdots & 0 \\ \frac{1}{2} & 0 & \frac{1}{2} & \cdots & \cdots & 0 \\ 0 & \frac{1}{2} & 0 & \frac{1}{2} & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & 0 & \frac{1}{2} & 0 & \frac{1}{2} \\ 0 & \cdots & \cdots & 0 & \frac{1}{2} & \frac{1}{2} \end{bmatrix} \quad (5.46)$$

The n eigenvalues are $\sigma_i = \cos \frac{i-1}{n}\pi, i = 1, \dots, n$, which lie in $[-1, 1]$. It follows that the n eigenvalues of $C = Q - I$ are $\lambda_i = -1 + \cos \frac{i-1}{n}\pi, i = 1, \dots, n$

In the case that n patches ($n \geq 3$) form a ring, Q typically is a circulant matrix. For instance

$$Q = \begin{bmatrix} a & b & 0 & \cdots & 0 & b \\ b & a & b & \cdots & \cdots & 0 \\ 0 & b & a & b & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \cdots & 0 & b & a & b \\ b & 0 & \cdots & 0 & b & a \end{bmatrix} \quad (5.47)$$

where $a, b > 0$ and $a + 2b = 1$. The n eigenvalues are $\sigma_i = a + 2b \cos \frac{2(i-1)}{n} \pi$, $i = 1, \dots, n$, which lie in $[-1, 1]$. It follows that the n eigenvalues of $C = \hat{Q} - I$ are $\lambda_i = -1 + a + 2b \cos \frac{2(i-1)}{n} \pi = -2b + 2b \cos \frac{2(i-1)}{n} \pi, i = 1, \dots, n$.

Chapter 6

Incidence And Spread Of Peach Brown Rot: Modelling And Analysis

Abstract. This paper presents a model that describes the dynamic change in the number of host individuals (i.e. peach flowers and fruits) infected by the brown rot fungus (*Monilinia laxa*). The disease is physically transmitted from a diseased individual (“an infective”) to a healthy one (“a susceptible”) in a form of inoculum known as conidium. Three phases of an infection cycle, viz. the production, diffusion and germination of conidia, are formulated as submodels. The model predicts both the annual incidence of the disease when the infected individuals are spatially homogeneously distributed and the asymptotic velocity of disease spread when the disease initiates at certain spatial position. Numerical simulations based on the model show that suitable orchard management restrains the epidemic incidence and spread.

Key words: *M.laxa* - Fungus Disease - Peach Fruit - Orchard Management

*A joint work with F. Lescourret, R. Habib and V. Mercier, submitted to *Ecological Modelling*

6.1 Introduction

In western Europe, the brown rot fungus *Monilinia laxa* is known as an important pathogen on apricots, sour cherry (*Prunus cerasus* L.), sweet cherry (*Prunus avium* L.) etc. (Batra 1991, Tamm 1993). In southern France, *M.laxa* has recently become a major problem on peach [*Prunus persica* (L.) Batsch] fruits. The disease can seriously cause blossom blight and fruit rot.

The life history of the fungus is closely related to the season and the physiological age of the host (Byrde and Willetts, 1976). In the spring, when climate conditions are suitable, mummies left in the orchard in last winter begin to sporulate, producing abundant conidia. When conidia alight on blossoms or other susceptible tissues by dissemination which usually coincides with the emergence of blossoms, infections are initiated under favorable climatic conditions.

Plenty of experimental and field work has contributed to the knowledge of the influence of climate conditions, such as temperature, relative humidity and moisture, on the development of the fungus (Tamm and Fluckiger 1993, Hong and Michailides 1999). However, not sufficient attention has been paid to the effects of technical operations. For instance, irrigation is often intensively conducted in order to promote the growth of fruit, but it may in turn result in physiological vulnerability of fruits to disease transmission (Børve et al 2000).

Models can be established and operate at different time scales: a few weeks (one infectious cycle), a year (an entire growth period of fruits), or many years. Typically, the effects of some climatic factors such as relative humidity and temperature on sporulation and germination of the fungus are of prime concern in some short time scale modelling work. In this paper, we intend to develop a general model of fungus disease that can be applied over various time scales. The effects of orchard technical operations on disease incidence will be the main concern in this paper.

6.2 Site, Materials and Methods

Observations on disease incidence were undertaken in an experimental peach orchard, situated in INRA Gotheron (Valence, southern France). Daily temperature and relative humidity data over several decades are available in the local meteorological database. The peach trees [*Prunus persica* (L.) Batsch] were planted in 1993 (with column-distance 4m and row-distance 4m). Routine horticultural care, such as winter pruning, summer pruning, irrigation in the summer was conducted. No fungicide was applied. The number of infected individuals (flowers or fruits) on randomly selected trees has been weekly recorded from bud break to harvest in 1999 and 2000.

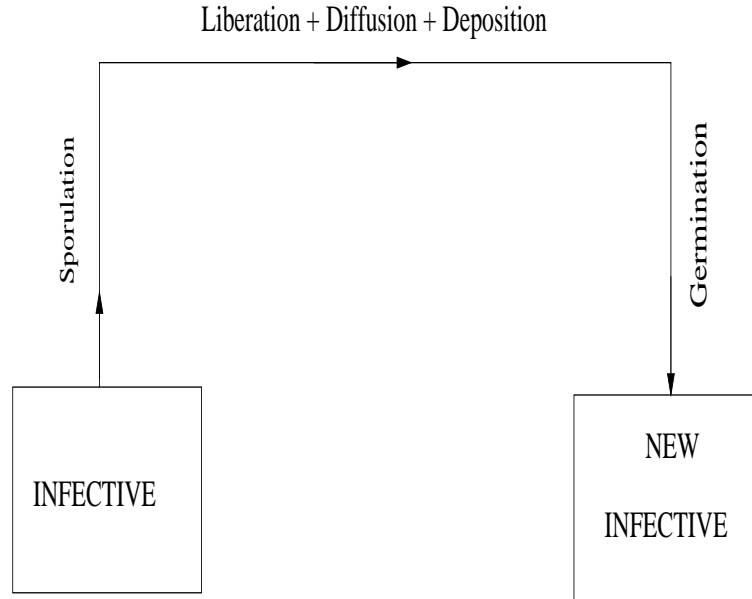


Figure 6.1: Graphical representation of the disease transmission cycle.

6.3 Model Construction

The Host Population The host population consists of individuals that are spatially distributed in \mathbb{R}^2 . These are called susceptibles when they are not infected. The infected individuals are called "infectives". The change in the number of susceptibles caused by factors other than disease is neglected.

The Disease and Inoculum The disease is transmitted from an infective to susceptibles in the form of inocula (i.e. conidia) which may generally be referred to as infectious agents. An infective continually produces conidia after a latent period. Conidia are driven by wind, air current or water splash to disperse. Germination of conidia deposited on a susceptible gives rise to a new infective. (**Fig.6.1**).

Spatio-Temporal Evolution of the Density of Infectives

The equation for the density of infectives, according to our assumptions about the physiology of host and the disease transmission process, is (van den Bosch et al. 1988a, Diekmann and Heesterbeek 2000)

$$\frac{\partial v(t, x)}{\partial t} = [s_0(x) - v(t, x)]g(\gamma N(t, x), E(t)) \quad (6.1)$$

$$v(0, x) = m_0(x) \quad (6.2)$$

where

$$N(t, x) = \int_0^t \int_{\mathbb{R}^2} \frac{\partial v(t - \tau, y)}{\partial t} K(t, \tau) C(y, x) d\tau dy \quad (6.3)$$

The main components of the model are functions K , C and g that will be specified and explained below. Notations and their meaning are listed in **Tab.6.1**.

Table 6.1: A list of symbols and their meaning

Symbol	Meaning
t	the chronological time
$x \in \mathbb{R}^2$	the spatial position
$v(t, x)$	the local density of infectives
$s_0(x)$	the initial density of susceptibles
τ	the age of infection (i.e. the time since infection)
$E(t)$	a relative number measuring the physiological vulnerability of the susceptibles to the disease
$\gamma(t)$	the occupied area per susceptible
$m_0(x)$	the local density of overwintered mummies
$K(t, \tau)$	the density of conidia produced by an infective
$C(y, x)$	the probability that a spore released at position y will (instantaneously) settle at position x
g	a function describing the local infectivity. i.e., the probability per unit of time that a susceptible is infected

Spore Production: Time Kernel

The mean production of conidia per infective can be described as

$$K(t, \tau) = M(t)k(\tau) \quad (6.4)$$

where τ is the time since infection. $k(\tau)$ is a probability density function. $M(t)$ is the number of conidia produced, or more strictly speaking, discharged per infective at time t . $M(t)$ is a function of time because the conidial production is related to both the physiological age of a susceptible and climatic conditions (Rossi et al. 2000). In this paper we use the following shifted gamma distribution to describe $k(\tau)$

$$k(\tau) = [\beta^i (\tau - p)^{i-1} \exp(-\beta(\tau - p))] / \Gamma(i) \quad \text{when } \tau \geq p \quad (6.5)$$

where $\Gamma(i)$ is the gamma function. p is the latency period (i.e., no spore is produced when $\tau < p$). i, β are two constants that determine the mean (i/β) and variance (i/β^2).

Conidial Diffusion: Spatial Redistribution

The conidia of brown rot fungi are dry air spores (Zoberi, 1961). The spores are not violently discharged but are set free to diffuse by air currents, wind and water splash. A simple conventional assumption is that they follow the Brownian motion (i.e. unbiased random walk). For simplicity we further assume that the probability that a spore disperses from one site to another depends only on the distance between the two sites. Therefore

$$C(y, x) = C(0, |x - y|) =: \hat{C}(|x - y|) \quad (6.6)$$

holds for any $x, y \in \mathbb{R}^2$. Note that we shall remove the hat from \hat{C} to write the function $\hat{C}(x)$ as $C(x)$ for any $x \in \mathbb{R}^2$ hereafter in order to reduce the number of notations. It is well-known, under the above assumptions, that the probability density of a spore's position $x = (x_1, x_2)$ after traveling a period of time ξ from the source lesion $(0, 0)$ is a Gaussian

$$C(x) = \frac{1}{4\pi D\xi} \exp\left\{-\frac{x_1^2 + x_2^2}{4D\xi}\right\} \quad (6.7)$$

where D is the diffusion coefficient (Pielou, 1976).

More realistic form of $C(x)$ is a Bessel distribution

$$C(x) = \frac{1}{4\pi\delta^2} \int_0^\infty \frac{1}{\xi} \exp\left\{-\xi - \frac{x_1^2 + x_2^2}{4\xi\delta^2}\right\} d\xi \quad (6.8)$$

which is derived by assuming that spores settle asynchronously with a settlement rate. δ^2 is a constant determined by the diffusion coefficient and the settlement rate.

The marginal distribution of $C(x)$ is a leptokurtic Laplace or double-exponential distribution (Neubert et al. 1995)

$$C(x_i) = \frac{1}{2\delta} \exp\left\{-\frac{|x_i|}{\delta}\right\} \quad (6.9)$$

Conidial Germination: Infectivity Function

In addition to the rate at which a susceptible contacts with infectious agents, the physiological vulnerability of the host also contributes to germination, leading a susceptible to an infective. Therefore, the local infectivity (i.e. the probability per unit of time that a susceptible is infected) should depend on not only the number of the infectious agents arrived per unit of time, but also the physiological vulnerability of the host, which can be quantified by a relative number $E(t)$ ($0 \leq E(t) \leq 1$). The vulnerability increases as E increases. In this paper, we assume

$$g(\gamma(t)N(t, x), E(t)) = aE(t) \cdot \gamma(t)N(t, x) \quad (6.10)$$

Here a is a positive constant, $\gamma(t)$ is the occupied area per susceptible.

6.4 Results and Analyses

6.4.1 Annual Incidence of Disease

Table 6.2: Input and parameter values

t (day)	p(day)	M	E	$\gamma(m^2)$
[0, 30]	$p_1 = 3$	$M_1 = 5000$	$E_1 = 0.2$	$\gamma_1 = 0.01$
(30, 90]	$p_2 = 5$	$M_2 = 12000$	$E_2 = 0.15$	$\gamma_2 = 0.02$
(90, 160]	$p_3 = 2$	$M_3 = 20000$	$E_3(\text{vary})$	$\gamma_3 = 0.05$
$s_0 = 10$		$\delta = 1$	$a = 0.01$	

In this subsection, we apply the model to a simple case in which susceptibles, infectives and initial inocula are spatially homogeneously distributed (which implies that all components in (6.1) are independent of space). We focus on the annual disease incidence to examine the effect of horticultural management measures.

The chronological changes in the density of infectives from bud break to harvest of the host are simulated by a daily time step. Individuals of the host population have three physiological stages: Flowers, Young fruits (or Green fruits) and Ripe fruits. For each stage we assume a constant parameter regime in the model. The simulation using various combinations of parameter values show that the general trend of annual disease incidence is consistent with the field observation: before being ripe (i.e. during the bloom and green fruit period) the infection rate maintains at a stable level. However, the infection increases rapidly once the host reaches the ripe period (see **Fig.6.2**). Two reasons explain the sharp increase of infection in the ripe fruit period: the delay effect of latency infection in the previous periods and the high susceptibility of ripe fruits (Hall, 1972). Input and parameter values that are used in the simulations are listed in **Tab.6.2**.

Effect of Initial Inoculum Density

The density of initial inocula (i.e. the number of overwintered mummies) is one of the parameters that can be controlled by routine horticultural care such as pruning. Numerical simulation shows that when the number of the initial inocula is controlled under a low level there is no outbreak in the fruit-ripening period. (see **Fig.6.3**).

Effect of Microcracks

In the model, we have generally introduced a time-dependent parameter $E(t)$ to measure the physiological vulnerability of a susceptible to the disease. In the later period of the fruit growth, such a vulnerability is mainly characterised by the microcracks (or cuticular fractures) on the surface of fruits (Sekse 1998; Børve et al 2000). Intu-

itively, the incidence of the disease should be positively related to the microcracks that promote the conidial germination. To look at the quantitative influence of microcracks, we conduct a sensitivity analysis by changing the value of $E(t)$ in the maturing period of fruit (i.e. E_3). We find that a small change of this value results in a significant change in the density of infectives (**Fig.6.4**).

Because the microcracks are often caused by intensive or irregular irrigation (Børve et al 2000), the result here suggests that irrigation should be conducted with care and prudence.

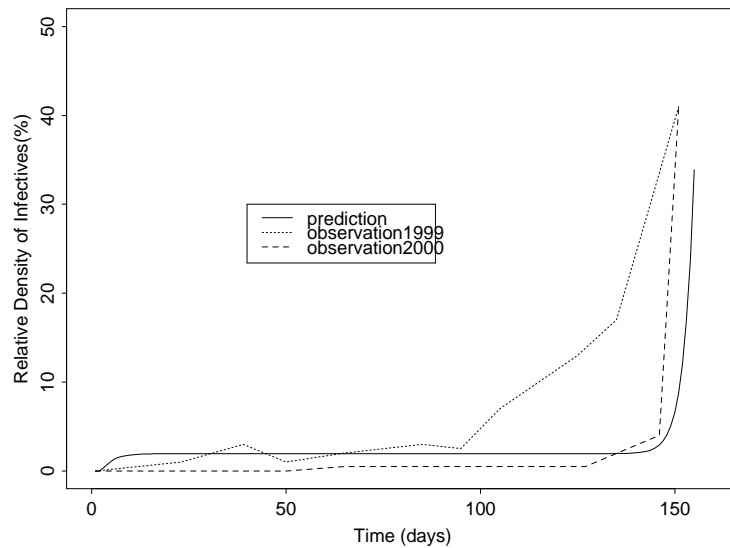


Figure 6.2: Annual incidence: a comparison of model predictions with observations. The solid line represents the annual incidence predicted by the model with a group of artificial parameter values. The dotted line and the dashed line, respectively, are the field incidence in the year 1999 and 2000

6.4.2 Velocity of Epidemic Spread

The model (6.1) can also be used to calculate the typical velocity c_0 for the disease to spread (i.e., the disease spreads in space in a planar front) provided that the parameters M, E, γ are constant (see appendix) and to examine the effects of various parameters on the velocity. Since it is well-known (e.g. Minogue and Fry 1983) that the wave velocity increases linearly with diffusion parameter δ^2 we shall focus on other interesting parameters like E and p etc.

In our model, both parameter E and p are linked to the so-called **basic reproduction ratio** R_0 (see Diekmann and Heesterbeek 2000 for the definition and (6.13) in

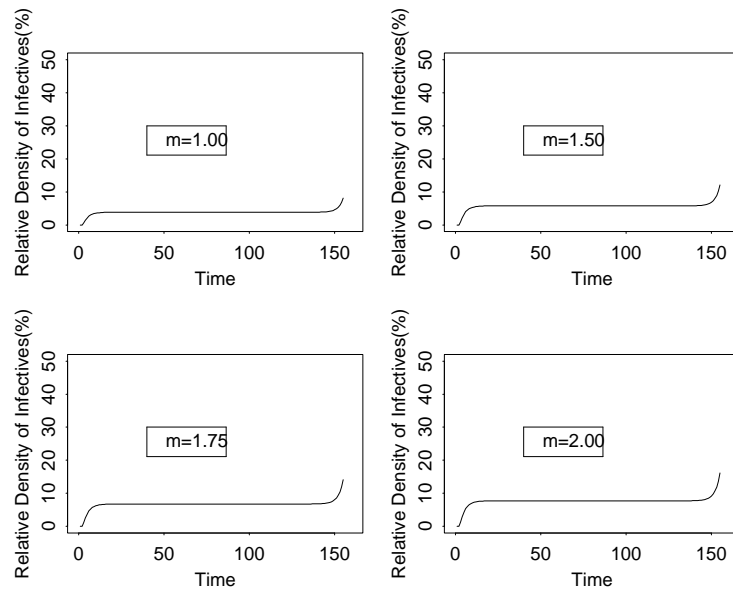


Figure 6.3: The effect of initial inoculum density on disease incidence. Note that in this figure we have used the notation m instead of m_0 to denote the initial inoculum density.

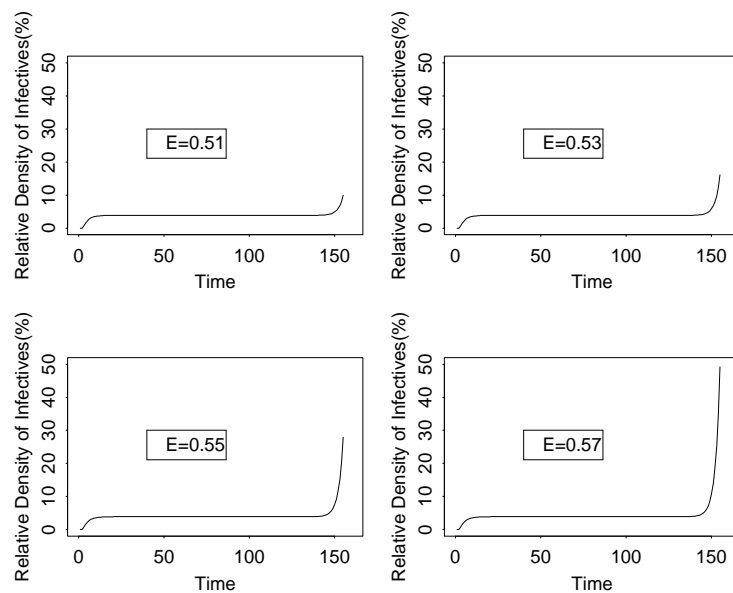


Figure 6.4: The effect of microcracks of fruits on disease incidence. Note that in this figure we have denoted the entry point parameter in the ripe fruit stage by E instead of E_3 .

the appendix for the expression). Numerical simulation shows that the velocity is positively related to E_3 , the entry point parameter in the ripe fruit period, but negatively related to the latency parameter p (**Fig.6.5**).

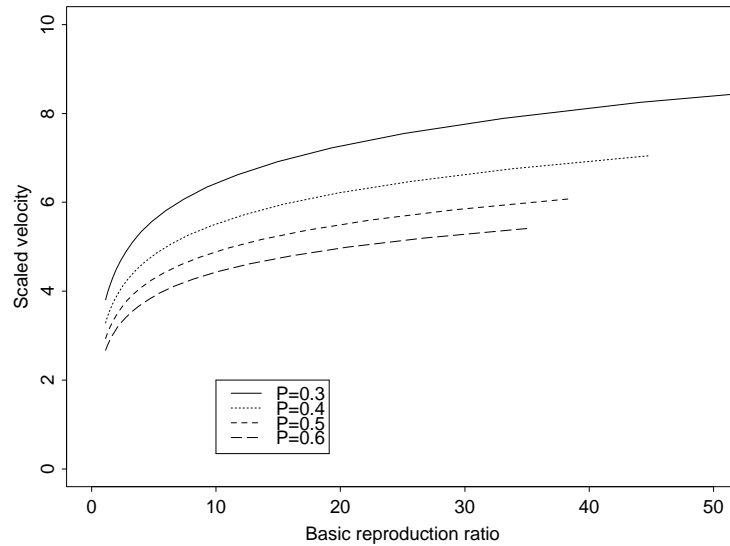


Figure 6.5: The relationship between the asymptotic velocity and the basic reproduction ratio for the various values of the scaled latency period.

6.5 Discussion

The main purpose of this paper is to examine the influence of orchard technical operations on the disease incidence. For this purpose, we have discussed two cases: the homogeneous incidence and the focus expansion. We found that the model was capable of providing both the qualitative and the quantitative information about the integrated influence of the orchard technical operations on disease incidence and spread.

Incidence of the fungal disease is expressed as an overlapping process of infection cycles. Each infection cycle consists of three stages referred to as sporulation, diffusion and germination. A susceptible is infected if and only if some infective agents arrive, settle and successfully germinate. Hence the infectivity is, in essence, the germination probability. The usual "law of mass action" assumes that the infectivity linearly depends on the number of infective agents. We extend it to consider the dependence of infectivity on a newly introduced entry point parameter, which characterises the physiological vulnerability of the host to the disease. Moreover, we establish a dose-response relation between the infectivity and the number of arriving infectious agents. Although

our model is developed for the peach brown rot, one can see that it is applicable to the fungal diseases of other fruit plants.

The factors that directly affect the incidence and spatial spread of the brown rot can be classified into two categories: the climatic conditions and the orchard technical operations. The climate factors such as temperature and relative humidity etc., although they play a very important role in the development of the fungus, are not explicitly included in our model as parameters.

The main components of our model: the time kernel, the spatial redistribution are supposed to be fitted or estimated by either laboratory or field data. The normalized time kernel can be fitted by data of sporulation (Rossi et al. 1999 and 2000). The method of linear regression can be used to estimate the effectivity parameter a in the infectivity function when data are available. The unique parameter δ in the contact distribution can be estimated by fitting the marginal distribution. To get data we can experimentally put only one infective (e.g. a mummy) as the source of inocula in a sufficiently large area and then count the number of new infectives at various distance along a straight line (van den Bosch 1988b), which gives a frequency distribution after normalization. This frequency distribution can be used as the fitting data for (6.9).

We have introduced a relative number to characterise the degree of microcracks on fruits which is believed to be closely related to irrigation (Lescourret et al. 2001) and examined the relation of this parameter to the incidence and spreading velocity of the disease. Combination of our disease model with a fruit growth model that quantify the relation between irrigation and microcrack would constitute a management system that guides the orchard technical operations.

6.6 Appendix: Calculation of Asymptotic Velocity

Since we are concerned about the asymptotic behaviour, the initial inoculum is not important. To guarantee the existence of traveling wave solutions we assume that the density of infectives is much smaller than the density of host and that the density of host is homogeneously distributed (i.e. $s_0(x) \equiv s_0$). Moreover, we restrict to the one-dimensional space in order to simplify the calculation of the asymptotic velocity. With these assumptions the equation from which we are going to calculate the asymptotic velocity is

$$\frac{\partial v(t, x)}{\partial t} = s_0 \cdot aE\gamma \int_0^t \int_{\mathbb{R}} \frac{\partial v(t - \tau, y)}{\partial t} Mk(\tau)C(|y - x|)d\tau dy \quad (6.11)$$

in which $x, y \in \mathbb{R}^1$. This equation typically has wave solutions. Setting

$$v(t, x) = u(x - ct)$$

and using the trial solution

$$u(x - ct) = \exp \{-\omega(x - ct)\}$$

one obtains the characteristic equation $1 = L(c, \omega)$ in which ω is the so-called characteristic number, c is the asymptotic velocity, while

$$L(c, \omega) := R_0 \int_0^{\infty} e^{-\omega c \tau} k(\tau) d\tau \int_{-\infty}^{+\infty} e^{-\omega \xi} C(|\xi|) d\xi \quad (6.12)$$

in which

$$R_0 := s_0 \cdot aE \cdot \gamma M \quad (6.13)$$

is the basic reproduction ratio.

The minimum of the velocity is a solution of the following pair of equations (Diekmann 1979)

$$1 = L(c, \omega) \quad (6.14)$$

$$0 = \frac{\partial L(c, \omega)}{\partial \omega} \quad (6.15)$$

When the two functions $k(\tau)$ and $C(x)$ are given by, respectively, (6.5) and (6.9), (6.14) and (6.15) can be calculated, according to van den Bosch (1988b), as

$$\log R_0 - \log(1 - (\omega^*)^2/2) - \omega^* c^* p^* - \alpha^* \log(1 + c^* \omega^*/\alpha^*) = 0 \quad (6.16)$$

$$\omega^*/(1 - \omega^*/2) - c^* p^* - c^*/(c^* \omega^*/\alpha^* + 1) = 0 \quad (6.17)$$

here $\alpha^* = \beta^2$, $p^* = p\beta/n$, $c^* = cn/(\beta\delta)$, $\omega^* = \omega\delta$

The two equations (6.16) and (6.17), when other parameters are fixed, characterise the dependence of c^* on R_0 .

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Samenvatting

Een belangrijk probleem in de spatiële ecologie is na te gaan hoe resultaten verkregen met behulp van populatiemodellen afhangen van de precieze aannames over de spatiële structuur en in hoeverre patronen op veel grotere schaal hiermee verklaard kunnen worden. Klassieke theorieën, zoals door diffusie aangedreven instabiliteit en metapopulatiodynamica, die ontwikkeld zijn aan de hand van zeer eenvoudige spatiële populatiemodellen, hebben veel inzicht gegeven in deze materie. In dit proefschrift onderzoeken we in hoeverre de conclusies uit de betreffende theorieën stand houden als de ruimtelijke interacties tussen populaties gecompliceerder zijn.

In hoofdstuk 2 wordt een roofdier-prooi-metapopulatiemodel met twee identieke, bewoonbare gebieden (patches) onderzocht waarin alleen de roofdieren zich kunnen verplaatsen van de ene naar de andere patch. We beschrijven de lokale interactie tussen roof- en prooidieren met het zogenaamde Rosenzweig-MacArthur model. Voor de migratieterm van de roofdieren is een niet-lineaire uitdrukking gekozen die verkregen is door Hollings argument over het tijdsbudget ook toe te passen op migratie. We introduceren een dimensieloze parameter die de neiging tot verhuizen van roofdieren beschrijft als ze net een prooi consumeren. De verkregen familie modellen heeft twee extrema: Roofdieren verhuizen niet als ze een prooi consumeren en standaard diffusie. De dynamica van deze twee extrema zijn zowel kwantitatief als kwalitatief verschillend en geven verschillende antwoorden op de kernvraag of spatiële structuur de roof-prooidieroscillaties significant kan verminderen.

De neiging tot migratie van één soort hangt af van de dichtheid van andere soorten. Dit verschijnsel, ook wel emigratie-interactie genoemd, is van zeer algemene aard. Daarom zijn we dit mogelijke mechanisme van patroonvorming (i.e. Turing instabiliteit) theoretisch gaan onderzoeken. In hoofdstuk 3 formuleren we een model met veel soorten en veel patches, waarin de emigratie-interactie expliciet is verwerkt en gekwantificeerd. (We noemen dit het “kruismigratiemodel”.) De emigratie-interactie blijkt een cruciale invloed te hebben op de diffusie-geïnduceerde instabiliteit. In het geval van competitie, bevordert de emigratie-interactie de patroonvorming omdat ze destabiliserend werkt. Als de interactie voldoende sterk is kan er zelfs diffusie-geïnduceerde instabiliteit optreden. Dit is opmerkelijk aangezien het algemeen bekend is dat er geen diffusie-geïnduceerde instabiliteit optreedt in standaard competitie modellen. In het geval van roof- prooidier interactie of een “activator-inhibitor”-interactie zorgt emigratie-interactie juist voor een stabiliserend effect. Wanneer de emigratie-interactie voldoende sterk is, treedt er nooit diffusie-geïnduceerde instabiliteit op, zelfs niet als dit wel het geval was in het standaard systeem.

In hoofdstuk 4 introduceren we een algemeen model om op mechanistische wijze “kruismigratiemodellen” af te leiden. We beschouwen een model waarin veel soorten individuen leven in een wereld die uit vele patches bestaat. Bovendien worden de individuen gekenmerkt door bepaalde gedrageigenschappen. We formuleren een model waarin een kleine parameter voorkomt. Deze parameter bepaalt de relatieve tijdschaal

van gedragsveranderingen ten opzichte van geboorte-, sterfte- en migratieprocessen. Met behulp van singuliere storingsrekening kan een lager dimensionaal model verkregen worden waarin de migratietermen in het algemeen niet-lineair zijn en gerelateerd zijn aan de reactietermen.

In hoofdstuk 5 onderzoeken we wat de consequenties zijn voor de stabiliteit in het geval van een migratieproces waarbij individuen kunnen kiezen of ze zich ergens vestigen. Daartoe formuleren we een model waarin vele soorten individuen leven in veel verschillende patches. Individen kunnen instantaan verhuizen van een patch naar een andere patch via een of twee sprongen. De kans dat het individu een tweede sprong maakt mag afhangen van de situatie in de patch waar het na de eerste sprong terecht komt. De stabiliteit wordt kwantitatief beïnvloed door de tweede sprong als de kans om een tweede sprong te maken afhangt van de dichtheid. Als de tweede sprong op een natuurlijke en voldoende sterke manier afhangt van de interactie tussen individuen van verschillende soorten, zijn er cruciale effecten op de diffusie-geïnduceerde instabiliteit: In geval van competitie treedt er diffusie-geïnduceerde instabiliteit op, terwijl in geval van roofdier-prooi-interacties de diffusie-geïnduceerde instabiliteit wordt opgeheven.

In hoofdstuk 6, beschouwen we een praktisch probleem uit de spatiële populatie dynamica. We beschrijven een model dat de verandering in het aantal gastheren (te weten, perzikbloesem en fruit) dat geïnficeerd is met de vruchtrot veroorzakende schimmel *Monilinia laxa*. Het model beschrijft zowel het aantal nieuwe infecties per jaar als de geïnficeerde gastheren spatieel homogeen verdeeld zijn, alsmede de asymptotische snelheid waarmee de ziekte zich verspreid als de infectie op een bepaalde plaats begonnen is. Numerieke simulaties, op basis van het model, laten zien dat een geschikte indeling van de boomgaard zowel de verspreidingssnelheid als het aantal nieuwe gevallen kan beperken.

迁移和离散生境中种群动态的相互作用

摘要

空间生态学的一个基本问题是空间因素如何改变种群动态模型的预测结果。为了回答这一问题，扩散不稳定性和异质种群动态等经典理论逐步发展起来。不过，这些经典理论所依据的一般是一些非常简单的空间种群模型。在这篇博士论文中，我们将通过考虑较为复杂的空间种群相互作用过程对这些理论进行进一步的审查和探索。

在第二章，我们考虑一个仅含两个镶嵌子种群的捕食---被捕食异质种群动态模型。每个块内的捕食---被捕食相互作用过程由所谓的 Rosenzweig--MacArthur 模型来描述。根据 Holling 关于捕食者“搜索”--“处理”食物的观点，我们推导出了一个描述捕食者迁移的非线性项。特别是我们引进了一个反映捕食者在处理食物过程中的迁移倾向性的无量纲参数。由此我们得到一个包含两个极端情形的模型组。一个极端对应于标准扩散，而另一个极端对应于捕食者在处理食物的过程中根本不想迁移的情形。我们发现对应于这两个极端情形的模型的动态之间存在着显著的定性和定量差异。据此，我们认为对“空间因素是否降低捕食---被捕食系统的波动幅度”这一重要理论问题的回答实际上取决于我们对捕食者迁移的假定，至少这一问题值得进一步研究。

在多种系统中，有一种十分普遍的现象：就是某种个体从某个生境块中迁出的倾向性受到该块内某些其他相关种的密度的影响。我们将这种现象称之为“交叉---迁出反应”。在第三章，我们从理论上研究这种现象对格局形成（或扩散不稳定性）的影响。为此我们建立了一个将这种“交叉--迁出--反应”定量化的多种多块“交叉--迁移模型”。通过对该模型的同质平衡点的稳定性进行研究，我们发现“交叉--迁出--反应”确实对扩散不稳定性发生具有重要影响。具体结果如下：如果种群之间的关系是竞争型的，那么“交叉--迁出--反应”促进扩散不稳定性发生。当这种反应足够强时，扩散不稳定性确实可以发生。这一点同竞争系统不能显

示扩散不稳定性现象的经典结论形成鲜明的对比。如果种群之间是捕食-被捕食关系，那么交叉--迁出--反应限制扩散不稳定性会发生。

在第四章，我们给出了一个从行为机理上推导交叉--迁移模型的一般方法。我们仍然考虑一个栖息在块状生境中的多种系统，其中每个种由一些行为子种群构成。我们注意到，行为转换的时间尺度通常要比象生殖，死亡和迁移这样一些过程的时间尺度小的多。也就是说，两者之间的比率是一个非常小的参数。结合种群各行为子种群之间的转换机制以及行为子种群本身的生殖，死亡和迁移过程。我们构造出了一个含有这一小参数的连续时间模型。通过奇异摄动理论，这一模型最终被简化为一个描述各完全种群密度时空演变的模型。它正是我们所定义的交叉--迁移模型。本章给出的方法自然的将行为水平上的机制反映在一个描述完全种群密度时空变动的模型中。

个体在迁移过程中一般是有选择地而非随机地着陆。在第五章中，我们考察了这种特殊的迁移现象的稳定性后果。为了反映这一迁移现象，我们假定个体通过一次或两次瞬间跳跃来完成一次迁移过程，并且假定个体进行第二次跳跃的概率取决于第一次跳跃到达点的环境条件。在此假设的基础上，我们构造了一个多种多块连续时间模型。对模型稳定性的研究结果表明，如果第二次跳跃产生于第一次跳跃后的一种自然的种间排斥或吸引反应，那么它对系统稳定性，尤其是对扩散不稳定性现象的发生有决定性的影响。

在第六章，我们研究了一个应用型的空间种群动态问题。研究对象是一个受到棕色腐烂菌(*M.Laxa*)感染的桃种群(包括桃花和桃果)。我们给出了描述这一种群密度的时空变动模型。这个模型既可以用来预测这种病害的年度发生，也可以用来预测该病害在较大范围果园区的传播速度。数值模拟显示，合理的果园管理措施，特别是灌溉措施，可以有效的控制该病害的发生和传播。

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Curriculum Vitae

Yunxin Huang was born in Hubei (China) in June 21, 1963. From September of 1980 to June of 1984, he studied in the Mathematical Department of Hubei university and got the B.Sc degree. From July of 1984 to August of 1987, he taught mathematics in Jian-Gang high school. From September of 1987 to July of 1990, he followed a master degree program (of mathematical ecology) sponsored by the Mathematical Department of Hubei University and supported by the Institute of Zoology (IZ), Chinese Academy of Science. He got the M.Sc degree from the IZ in July of 1990. From July of 1990 to September of 1997, he worked in both the Mathematical Department and the Institute of Ecology of Hubei University as a junior researcher. From September of 1997 to June of 1998, he attended a master class organized by the Mathematical Department of Utrecht University (in the Netherlands) and got a certificate when this study is concluded. From 1998 to the present time he has been working on his phd thesis supervised by Professor O. Diekmann for which he spent most of time in Utrecht, a part of time in China and half a year in INRA (Avignon of France). He shall obtain his Phd degree in June, 2003.

