PREDATOR - PREY PROCESSES

by

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DECLARATION

The following record of research work is submitted as a Thesis for the Degree of Master of Philosophy of the University of Edinburgh, having been submitted for no other Degree.

The research was carried out under the supervision of Dr. E. Renshaw. Except where due acknowledgement is made, the work is original.

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ABSTRACT OF THESIS

This thesis is a study of predator-prey models, with particular emphasis on the effects of spatial separation. It is divided into two sections - spatial and non-spatial.

In the non-spatial section we study the deterministic equations of the general two-species interaction model. The equations are linearised about an equilibrium point, and thus linear solutions are found. To examine stochastic models, we develop a technique of probability linearisation. Using this technique, we find that the Normal distribution is an approximate solution for the probability structure of the stochastic model.

The element of spatial distance is introduced in the form of the stepping-stone model - that is, the population is divided into colonies which may be considered to be situated at the integer points of a single coordinate axis. We simplify the problem by first considering the two colony case. Deterministic linear solutions are found, as before, for models with certain restrictions on migration, and approximate stochastic solutions are found using the probability linearisation method. The effect of migration between colonies is seen by comparing these results with those of the non-spatial case. These methods are then extended to cover the case where the number of colonies in infinite. Finally, we look at the diffusion model, where the habitat is continuous and the populations diffuse throughout the region. A survey is given of the effects of spatial diffusion in predator-prey models, and a comparison is made between this continuous diffusion and the discrete migration model.

ACKNOWLEDGEMENTS

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NOTATION

Symbol	Usual Meaning
$H(t)$	number of prey at time t
$P(t)$	number of predators at time t
$H_i(t)$	number of prey in colony i at time t (spatial model)
$P_i(t)$	number of predators in colony i at time t (spatial model)
λ	birth rate of prey
α	death rate of prey
β	birth rate of predators
μ	death rate of predators
c	self-inhibiting factor in birth rate of prey
η_i	migration rate of prey (spatial model)
ν_i	migration rate of predators (spatial model)
η_+, ν_+	migration rates of populations to the right (spatial model)
η_-, ν_-	migration rates of populations to the left (spatial model)
E	equilibrium point of system of equations

$\hat{H}$ equilibrium value for prey

$\hat{P}$ equilibrium value for predators

h   small deviations of prey from equilibrium

p   small deviations of predator from equilibrium

F   quadratic function of H and P, representing rate of change of H

G   quadratic function of H and P, representing rate of change of P

$\dot{H}$ dH/dt

$|_E$ evaluation at the equilibrium point

(H,P)   H prey and P predators present in the system

$P_{ij}(t)$ probability of i prey, j predators at time t

$P_{ijkl}(t)$ two-colony model: probability of i prey, j predators in colony 1, and the k prey, 1 predators in colony 2 at time t

P'_{ij} $\frac{d}{dt}(P_{ij})$

π_{ij} stationary probability of i prey, j predators — that is, $\lim_{t \to \infty} P_{ij}(t) = \pi_{ij}$

$G(z_1,\ldots,z_N,t)$ probability generating function

$K(\theta_1,\theta_2,t)$ cumulant generating function

z_i,θ_j dummy variables

$\left[\dfrac{\partial G}{\partial z_i}\right]_{(1)}$ derivative of G with respect to z_i to be evaluated at

$z_1 = z_2 = z_N = 1$

$\Gamma(x)$ Gamma function

$j!$ factorial j, that is $j(j-1)\ldots1$

m_i first moments of distribution

V_{ij} second factorial moments of distribution

$E(H,t)$ mean of H, at time t

$Var(H,t)$ variance of H, at time t

σ_H^2 variance of H

$CV(H)$ coefficient of variation of H

p_i, q_j stationary probability values for prey and predators calculated using Karlin and Taylor's method

$p(x_1, x_2, t)$ probability of x_1 prey, x_2 predators at time t, with x_1 and x_2 as continuous variables

$p(x_1, \ldots, x_{2N}, t)$ spatial model: probability of x_1 prey, x_2 predators in colony 1, ..., x_{2N-1} prey, x_{2N} predators in colony N at time t

$\underline{X}$ 2N-dimensional vector of continuous variables x_i, where x_{2K-1}, x_{2K} represent the number of prey, predators in colony K (2-dimensional vector also used in non-spatial case)

$\underline{x}_0$ value of the vector $\underline{X}$, when $t=0$

$m_t(\underline{x}_0)$ — the mean of the distribution of $\underline{X}$ at time t, given the initial value of $\underline{x}_0$

$V_t(\underline{x}_0)$ — the variance of the distribution of $\underline{X}$ at time t, given the initial value of $\underline{x}_0$

$\underline{A}$ — matrix A

$\underline{A}^T$ — transpose of A

$\text{Diag}\{a,b\}$ — 2x2 matrix with a,b on the diagonal, and 0 elsewhere (can be n-dimensional)

Q — $c\hat{H}-\beta\hat{P}-\beta\hat{H}$

$S_1(x\ t)$ — density of prey at position x and time t

$S_2(x,t)$ — density of predators at position x and time t

$F_i(S_j,x,t)$ — population interaction terms for species S_i

D_{x_i} — diffusion coefficient of the i'th species in the x direction

A_{x_i} — coefficient of advection for the i'th species in the x direction

JS — flux of S

$\nabla^2 S$ — $\dfrac{\partial^2 S}{\partial x^2} + \dfrac{\partial^2 S}{\partial y^2} + \dfrac{\partial^2 S}{\partial z^2}$

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CHAPTER 1

INTRODUCTION TO THESIS

1.1. General Introduction

This thesis is a theoretical study of predator-prey modelling, with particular emphasis on the effect of spatial separation.

A predator-prey model is a model of two interacting species, where one species depends on the other for survival. By modelling, we intend to give a mathematical description of the behaviour of the species. This description can be used to tell us, for example, if the two species can exist in the same habitat, or, perhaps it could indicate what patterns of interaction are most likely to lead to stability. Most predator-prey models concentrate on how behaviour alters through different forms of interaction, ignoring any effects that might arise from geographical separation. In this study, we incorporate a spatial element into the model.

Predator-prey models fall into two main categories - deterministic and stochastic. The deterministic approach is to look at the rate of change of numbers of individuals, and to determine the exact outcome at a given time. It ignores all effects of statistical fluctuations. In the stochastic model, it is the change in the probability which is examined. The stochastic model will, of course, give a better indication of how the species will react (because of allowing for statistical variation). But this does not mean that deterministic models should be forgotten. Deterministic models are easier to deal with, mathematically, while most stochastic models are

intractable (to an exact solution, at least). Furthermore, when the population numbers are large, they should give a good indication of the behaviour of the system. For these reasons, we study predator-prey models from both the stochastic and deterministic aspects.

Because of the nature of the interaction between predators and prey, the models are non-linear. Non-linear models are generally difficult to solve. If a solution can be found, it is usually so mathematically complicated, that it gives no ready indication of how the model behaves. Deterministically, at least, linear solutions appear to be good approximations to the solutions of non-linear models (indeed better than they deserve). Because of the difficulties involved in non-linear mathematics, we generally consider linear solutions. Thus, most of our results are merely approximations, but, where possible, we show that these approximations are close to the true solutions.

The thesis is divided into two sections - non-spatial (Chapters 2-4) and spatial (Chapters 5-8). In the non-spatial section, we outline the main developments in predator-prey modelling, both deterministic and stochastic, and introduce some ideas that we will find useful in the spatial section.

1.2. Non-Spatial Models

The development of deterministic predator-prey modelling is discussed in Chapter 2. To see what types of behaviour are possible, we study the general quadratic two-species equation, and find the solutions to the equations linearised about the equilibrium point. We see that the solutions are either exponential or oscillatory, which may be damped or undamped. These types of behaviour are illustrated using two examples of predator-prey models, one stable (which means that small perturbations from the equilibrium value decay) and the

other unstable (it exhibits constant amplitude oscillations).
Because these two models represent all types of deterministic
behaviour possible (from linear solutions), we shall usually use
these as examples of predator-prey systems.

In Chapter 3, we introduce the stochastic model in the form of
the stochastic analogue of the unstable example above, and discuss
the difficulties that arise in stochastic modelling. We derive the
forward equation for the probability distribution, which is a
difference-differential equation, but cannot solve it. The moments
of the distribution cannot be found either, because the equations do
not form a closed system. We try to extend other methods often used
in the stochastic modelling of single-species systems, but without
success. In an attempt to simplify the forward probability equation,
we approximate the discrete state space by a continuous one, and
arrive at a diffusion equation. Though this equation is now intract-
able, we will later simplify it, so that a solution can be found.

We investigate techniques using linearisation in stochastic
models in Chapter 4. Three methods are discussed - Bartlett's sto-
chastic linearisation, probability linearisation and linearisation of
the continuous model. In the first two methods, approximations can
be found for the moments of the distribution. In the third method,
the discrete process is approximated by a continuous one, as before,
but now, using probability linearisation, the diffusion equation can
be solved. Hence, this method provides an approximate solution
(which is the Normal distribution) for the probability distribution
of the stochastic model. Another advantage of this third method is
that it is possible to extend it for use in spatial models.

1.3. Spatial Models

To introduce a spatial element, we consider that the habitat is

divided into a number of colonies. Within each colony, spatial separation is ignored, but, between colonies, migration is common. We assume that migration is instantaneous, so the effects of it are immediate. We also assume that there are no losses during migration, so that an individual leaving one colony arrives at another.

We first try to generalise our results to the 'spatial' model when the number of colonies is two. Deterministic two-colony models are studied in Chapter 5. Because the solution to the general deterministic model is too mathematically complicated to give any indication of the general behaviour of the species, the solutions to some special cases are discussed. When individuals are allowed to migrate between colonies at the same rate in both directions, we see that migration has no long-term effect on the model. In the case of the unstable model, in a single colony, the populations oscillate with constant amplitude. However, in the two-colony unstable model, if a species is allowed to migrate in one direction only, from colony 2 to colony 1, say, then, after a time t, both colonies oscillate with constant amplitude, but out of phase. If predators are migrating, colony 2 lags colony 1, whereas if prey migrate, colony 2 leads colony 1.

Two-colony stochastic models are investigated in Chapter 6. Using the three stochastic linearisation methods developed in Chapter 4, we study the effect of migration on a stochastic model. The model we choose is the stable model where the predators migrate at the same rate in both directions. We choose this model because it enables us to simplify the equations. The approximations for the means and variances found using all three methods are identical. We see how migration affects the model by comparing these with the one-colony solutions. The approximate solution to a more general two-colony model is found using the third method (of continuous approximation).

Multi-colony models are discussed, in Chapter 7, in terms of 'stepping-stone' models. A (one-dimensional) stepping-stone model is a model in which we consider the colonies to be situated at the integer points of a single coordinate axis, with migration possible between nearest neighbours only. The solution to the deterministic model in which each colony is undergoing the same process is given. The same results appear as in the two-colony model. That is, if migration parameters are equal in both directions, no long-term effect is noticed, but in the unstable model, when migration is in one direction only, the colonies oscillate out of phase. An approximate solution is found for the N-colony stochastic model, using the method of continuous approximation and linearisation.

Thus, we incorporate spatial separation into the model by considering the populations to be separated into discrete colonies, and looking at the effect of migration between colonies. An alternative method of introducing spatial distance into the model is to regard the habitat as a continuous region, and allow the populations to diffuse continuously throughout the region. In recent years, much progress has been made in investigating the effect of spatial diffusion in predator-prey models. A survey of these developments is given in Chapter 8, and a comparison is made between continuous diffusion and discrete migration models.

CHAPTER 2

DETERMINISTIC MODELS

2.1. Introduction

As an introduction to predator-prey modelling, we will discuss the origins and development of non-spatial deterministic models.

The first predator-prey model, the Lotka-Volterra model, will be defined in Section 2.2. Because we will be referring to this model throughout the thesis, we will describe its behaviour in detail, and give the solution to the linearised form of the equations. Developments in predator-prey modelling will be outlined in Section 2.3. These developments will be considered from two aspects: more general reaction rates, and time delays in systems. To see what types of behaviour are possible in predator-prey models, in Section 2.4 we study the general quadratic two-species equations, and find the solution for linear perturbations from the equilibrium value. From this solution it will be seen that only four types of behaviour may result. In Section 2.5, examples of predator-prey models displaying these different types of behaviour, are given. We will discuss in detail the example described in Section 2.5.2, known as the Volterra-Gause-Witt model, because it is an example we will often return to. In Section 2.6, we introduce different population processes which are algebraically similar to predator-prey models, emphasising that results from other population studies may often be useful. We discuss non-linear effects in Section 2.7, and consider the consequences of using linear approximations.

2.2. The Lotka-Volterra Model

2.2.1. Description of model

The first predator-prey model was proposed by Lotka (1925) and independently by Volterra (1931). According to Goel et al. (1971), Volterra was motivated to study fluctuations in animal populations by discussions with a young zoologist friend, D'Ancona. D'Ancona had made a statistical analysis of fish catches in the Upper Adriatic. There were two types of fish, one type feeding on the other. It was noticed that the population of both species varied with the same period, but out of phase. To describe this behaviour, Volterra (1931) proposed the mathematical model below.

Let the number of prey at time t be denoted by $H(t)$, and the number of predators by $P(t)$. Let λ, α be the birth and death rates, respectively, for the prey, and β, μ the birth and death rates for the predators. Then the Lotka-Volterra model is defined by the differential equations:

$$\frac{dH}{dt} = \lambda H - \alpha HP$$

$$\frac{dP}{dt} = \beta HP - \mu P \quad . \tag{2.1}$$

As we can see from the equations, the birth rate of the prey is assumed independent of the number of predators, while the death rate of the prey is proportional to the number of predators. The situation is reversed in the predator equation.

The behaviour of the system described by these equations may be graphically represented by using a phase diagram: that is, the change in the system with time may be plotted as a single trajectory on a

graph with axes H and P. In the case of system 2.1, first notice that

$$\frac{dH}{dP} = \frac{(\lambda - \alpha P)H}{(\beta H - \mu)P} , \qquad (2.2)$$

which integrates to

$$\mu \ln H - \beta H + \lambda \ln P - \alpha P = \text{constant}, \qquad (2.3)$$

where the constant is determined by the initial conditions.

Using 2.3, Pielou (1977) illustrated three different representations of the Lotka-Volterra model on the phase diagram (see Figure 2.1).
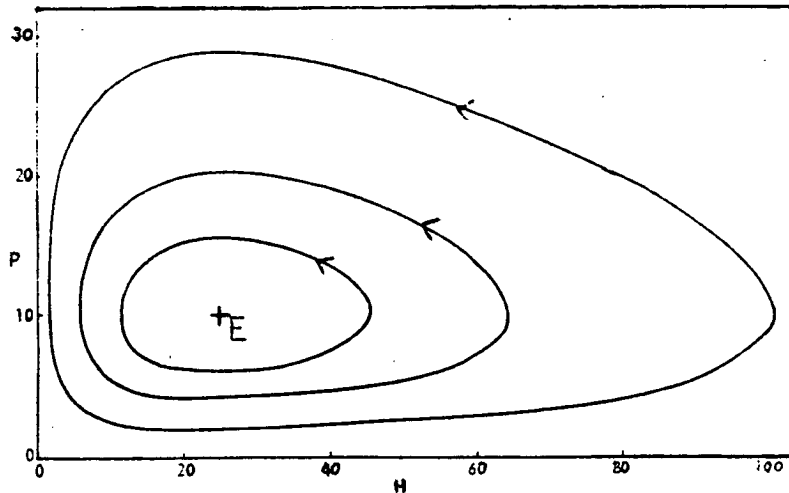
Figure 2.1. Phase diagram showing three representations of the Lotka-Volterra model, with $\lambda = 1$, $\alpha = 0.1$, $\beta = 0.02$, $\mu = 0.5$. The equilibrium is at $\hat{H} = 25$, $\hat{P} = 10$.

E is the equilibrium value of the system, that is, where the

rate of change of the population numbers is zero:

$$\frac{dH}{dt} = \frac{dP}{dt} = 0 .$$

(2.4)

In each curve, the same parameter values are used, but with different initial conditions. Because the curves are closed, the population will continue indefinitely to follow the trajectory on which it starts, travelling in an anti-clockwise direction.

2.2.2. Solution to the linearised equations

The behaviour of the system in the neighbourhood of this equilibrium point may be investigated algebraically (see, for example, Pielou, 1977). Let the equilibrium values of the prey and predator be $\hat{H}$ and $\hat{P}$, respectively. By setting the left hand side of equations 2.1 equal to zero, these values are seen to occur at

$$\hat{H} = \frac{\mu}{\beta} \quad \text{and} \quad \hat{P} = \frac{\lambda}{\alpha} .$$

(2.5)

To examine small deviations from this point, introduce the transformations:

$$H(t) = \hat{H} + h(t)$$

$$P(t) = \hat{P} + p(t)$$

(2.6)

where h and p are small enough so that second order terms are negligible. Note that the quantities h and p are integers, and so take the values $h,p = 0,1,2,...$ This means that h^2 and p^2 have the values $h^2,p^2 = 0,1,4,9,...$ This would imply that h^2 and p^2 cannot be ignored except in the trivial case, when $h,p = 0$. However, consider the transformation

$$H(t) = \hat{H}(1 + h(t))$$

$$P(t) = \hat{P}(1 + p(t)) \ . \tag{2.7}$$

Because of dividing by $\hat{H}$ and $\hat{P}$, h and p are small enough so that second order terms are negligible. Strictly, when linearising the equations, we should use transformation 2.7 instead of 2.6. But, to the first order, both transformations lead to identical solutions for H and P. Because 2.6 is easier to work with, we shall generally use it to linearise equations.

Substituting 2.6 into 2.1, then, after linearising, the equations reduce to (see Pielou, 1977)

$$\dot{h} = -\alpha\hat{H}p$$

$$\dot{p} = \beta\hat{P}h \ , \tag{2.8}$$

where . denotes d/dt. These solve to give

$$h(t) = A \frac{\sqrt{\lambda\mu}}{(\beta\hat{P})} \cos (\sqrt{\lambda\mu}t + B)$$

$$p(t) = A \sin (\sqrt{\lambda\mu}t + B) \ , \tag{2.9}$$

where A and B are determined by the initial conditions. For example, suppose that at t=0

$$h(0) = 0 \quad \text{and} \quad p(0) = k \ , \tag{2.10}$$

then the solution 2.9 becomes

$$h(t) = -k \frac{\sqrt{\lambda\mu}}{(\beta\hat{P})} \sin \sqrt{\lambda\mu}t \tag{2.11}$$

$$p(t) = k \cos \sqrt{\lambda\mu}t \ .$$

From 2.9, we see that if the system is perturbed slightly from the equilibrium value, it will oscillate with constant amplitude, with the prey and predators $\pi/2$ out of phase with each other. These oscillations are not damped in time. This means that the system will not return to its equilibrium value, and so it is said to be unstable.

Volterra noticed (see Scudo, 1971) that the model followed a law of conservation, namely that the quantity

$$\beta H(t) + \alpha P(t) - \lambda\beta \int_0^t H(s)ds + \alpha\mu \int_0^t P(s)ds \qquad (2.12)$$

was constant for all time t. Because of this, the Lotka-Volterra model is called a conservative system.

2.3. Developments in Predator-Prey Modelling

2.3.1. More general growth rates

Since the introduction of the Lotka-Volterra model, many developments have been made in deterministic predator-prey modelling. These developments fall into three main categories: more general birth and death rates, which we will now discuss, the effect of age-structure or time delays, which will be considered in 2.3.2, and the introduction of spatial variation into the equations, which will be dealt with later.

The birth rate of the prey in the Lotka-Volterra model has been generalised to include a self-inhibiting factor (see Gause and Witt, 1935):

$$\dot{H} = (\lambda - cH)H - \alpha HP \qquad\qquad (2.13)$$

$$\dot{P} = \beta HP - \mu P \;.$$

The c term is called a Verhulst factor, and the model is known as the Volterra-Gause-Witt model. This will be discussed in more detail in Section 2.5.2, where it will be seen that when c is greater than zero the equilibrium value will be stable — that is, small perturbations from the equilibrium value will decay, and the system will return to equilibrium. Other density-dependent forms of the prey birth rate have been seen to have much the same effect. For example, instead of using the birth rate λH, Schoener (1973) considered

$$\lambda H \rightarrow \lambda H(K/H - 1) \;,$$

and Goel et al. (1971) considered

$$\lambda H \rightarrow \lambda H(1 - (H/K)^{g}) \;,$$

where K is constant, and $0 < g < 1$. In both of these cases, the birth rate of the prey is reduced when H is large, with K acting as an upper bound on the number of prey. This has the effect of stabilising the model.

The rate at which the prey are attacked by the predators is described in the Lotka-Volterra model as $-\alpha HP$, which means the attack capacity of the predators increases linearly with H, the number of prey. Other models in which the attack rates increase less fast than linearly with the number of prey have been considered, for example, by Ivlev (1961):

$$\alpha HP \rightarrow \alpha P(1 - e^{-cH}) \;,$$

or by Rosenwzeig (1971):

$$\alpha HP \rightarrow \alpha H^g P \ ,$$

where c is a positive constant and $0 < g \leqslant 1$. In both cases, as the number of prey increases, the death rate is reduced. This has the effect of destabilising the model. May (1974) commented that if the attack rate of the predators increases faster than linearly with the number of prey, this rate will have a stabilising effect, whereas if the rate increases less than linearly, a destabilising effect will be seen.

A reduction in the attack rate of the predators was also considered by Maynard Smith (1974), by allowing some of the prey, say H_0, to take cover or refuge and so be protected from the predators. The equations become

$$\dot{H} = \lambda H - \alpha P(H-H_0)$$

$$\dot{P} = \beta P(H-H_0) - \mu P \ . \tag{2.14}$$

Two types of cover are possible. First, the number of protected prey may be a fraction of the total number, that is

$$H_0 = kH$$

for some constant k. This does not alter the behaviour of the solution, but merely has the effect of decreasing α and β. However if the number of prey protected is constant, say

$$H_0 = k \ , \tag{2.15}$$

then the solution changes from one of constant amplitude oscillations

to damped oscillations. That is, prey cover of the form 2.15 stabil-
ises the model.

In the Lotka-Volterra model, the predator growth rate is given
as βHP. It has been suggested that this may be over-estimating the
contributory influence of the prey, and Gause (1934) considered this
growth rate may more reasonably be

$$\beta HP \rightarrow \beta H^{1/2} P .$$

This means that as the number of prey increases, the increase in the
predator birth rate is reduced, enabling the prey to increase faster
than the predators. The same conclusions found for the change in
attack rate apply here – that is, a less than linear growth rate has
a destabilising effect, and a faster than linear rate will be sta-
bilising (see May, 1974).

An alternative growth rate of the predators is considered by
Leslie and Gower (1960) in the model

$$\dot{H} = \lambda H - \alpha HP$$

$$\dot{P} = \beta P - \mu P^2 / H . \tag{2.16}$$

Here the growth rate of the predator depends on the relative sizes of
the populations, so that when the number of prey is small, the
increase in predators is small. The model has a stable equilibrium
value, and small deviations from it result in damped oscillations.

2.3.2. Time delays

Models so far have assumed that the growth rate of a species
will respond immediately to changes in population numbers. It is
often more realistic to assume there is a time lag in the system.

For example, a large predator population may be a result of abundance of prey in the past rather than the present, or alternatively animals may be required to mature before being able to reproduce. Although, in this thesis, we will not be studying systems incorporating time lags, it is interesting to outline here what the effects of these delays can be.

Models with potentially stabilising feedback mechanisms have often been used in engineering control theory, and it is known that a destablising influence may occur if the time delay is long compared with the natural response time of the system (Maynard Smith, 1974). This property also holds in ecology, as was first shown by Hutchinson (1948). He considered the growth of a species, $X(t)$, satisfying

$$\dot{X}(t) = X(t)[a - bX(t-T)] .$$

That is, as the number of individuals increases, the resources available to it decrease, but with a time lag T. If T is small compared with $1/a$, the system maintains its stable equilibrium point. If T is large compared with $1/a$, divergent oscillations result. May (1974) generalised this model so that the time delay does not depend on the population at a particular instant in the past, but on an average over past populations:

$$\dot{X}(t) = aX(t) - \int_{-\infty}^{t} X(u)Q(t-u)\,du$$

where $Q(t)$ is a weighting function. Not only is this equation a more realistic representation of time delay, it is also easier to solve, and can be solved using Laplace Transforms. The conclusion is the same — the system will become unstable if the delay factor is large.

Wangersky and Cunningham (1957) considered the model

$$\dot{H}(t) = \lambda H(t) - cH(t)^2 - \alpha H(t)P(t)$$

$$\dot{P}(t) = \beta H(t-T)P(t-T) - \mu P(t) , \qquad\qquad (2.17)$$

that is, a time T elapses between the killing of a prey and the sub-
sequent growth of predators. Using a computer to solve the equations
numerically, the authors noticed that, when c=0 and the equilibrium
is unstable, large amplitude oscillations occur. However, when c is
not zero (and the equilibrium stable), by including a time lag, the
system may be either stable or unstable, depending on the relative
sizes of damping, c, and destabilising, T. More general ecological
systems with delay in development time (as in 2.17) have been studied
by Caswell (1972). In these analyses, the effect of the time lag is
to destabilise the model.

Maynard Smith (1974) introduced the idea of discrete genera-
tions. If H_n and P_n are the prey and predator densities in year n,
the discrete generation model of the Lotka-Volterra process is

$$H_{n+1} = \lambda H_n - \alpha H_n P_n$$

$$P_{n+1} = \beta H_n P_n - \mu P_n .$$

The introduction of discrete generations changes the solution of the
model from constant amplitude oscillations to divergent oscillations.

Thus when time delay is considered, the predator prey model may
be stable or unstable, depending on a balance between damping in the
system and the size of the delay. In general a large time lag will

have a destabilising effect. However, Beddington and May (1975) have shown that in the neighbourhood of an unstable equilibrium point, time delays can slow down the rate at which the population diverges, and so in this case appear to have a stabilising influence.

2.4. Linear Solution to General Model

2.4.1. Solution

In Section 2.2, we examined the Lotka-Volterra model, and saw that small perturbations from the equilibrium value resulted in constant amplitude oscillations. In Section 2.3.1, we saw that by altering the parameters, the behaviour of the model could change, and in some cases become stable. In order to understand what type of behaviour we might expect in a predator-prey system, we now study the general two-species quadratic model.

The model we are considering is defined by

$$\frac{dH}{dt} = F(H,P)$$

$$\frac{dP}{dt} = G(H,P) \; , \tag{2.18}$$

where F and G are general quadratic functions of H and P. Assume that the equations have an equilibrium value at $\hat{H}, \hat{P}$ which satisfies

$$F(\hat{H},\hat{P}) = G(\hat{H},\hat{P}) = 0 \; . \tag{2.19}$$

When F and G are general functions, it may be possible to have more than one equilibrium. As we will only be dealing with linear approximations, the solution found will only be valid near the equilibrium. Thus, if more than one equilibrium exists, this method may be used to find the solution near each equilibrium point.

To approximate the behaviour of the system near the equilibrium point, use the transformation 2.6, that is

$$H(t) = \hat{H} + h(t)$$

$$P(t) = \hat{P} + p(t) \; ,$$

where (remembering the comments in Section 2.2.2) we may regard second order terms in h and p to be negligible. The functions F and G may be expanded about this point (see Nisbet and Gurney, 1982), as follows:

$$F(H,P) = F(\hat{H},\hat{P}) + \frac{\partial F}{\partial H}\bigg|_E h + \frac{\partial F}{\partial P}\bigg|_E p + o(h^2,p^2)$$

where $|_E$ denotes 'evaluation at the equilibrium point'. By ignoring higher order terms, system 2.18 may be written linearly as:

$$\dot{h} = C_1 h + C_2 p$$

$$\dot{p} = C_3 h + C_4 p \qquad\qquad (2.20)$$

where . denotes d/dt, and the C_i's are defined by

$$C_1 = \frac{\partial F}{\partial H}\bigg|_E \qquad C_2 = \frac{\partial F}{\partial P}\bigg|_E$$

$$C_3 = \frac{\partial G}{\partial H}\bigg|_E \qquad C_4 = \frac{\partial G}{\partial P}\bigg|_E \; . \qquad\qquad (2.21)$$

The equations 2.20 may be solved by substituting one into the other. There are four different cases of the solution to consider, depending on the values of the C_i's.

Case 1(a) $C_3 \neq 0$, $r \neq 0$.

$$h(t) = \frac{1}{C_3} e^{(C_1+C_4)t/2} \left[(\frac{(C_1-C_4)}{2} + r)Ae^{rt} \right.$$

$$\left. + (\frac{(C_1-C_4)}{2} - r)Be^{-rt} \right]$$

$$p(t) = e^{(C_1+C_4)t/2} (Ae^{rt} + Be^{-rt}) \qquad (2.22)$$

where $r = \frac{1}{2}\sqrt{(C_1-C_4)^2 + 4C_2C_3}$, and A and B are constants defined by initial conditions.

Case 1(b) $C_3 \neq 0$, $r = 0$.

$$h(t) = \frac{1}{C_3} e^{(C_1+C_4)t/2} [B(C_1-C_4)/2 + A(1 + (C_1-C_4)t/2)]$$

$$p(t) = (At + B)e^{(C_1+C_4)t/2} \qquad (2.23)$$

Case 2(a) $C_3 = 0$, $C_1 \neq C_4$.

$$h(t) = \frac{AC_2}{C_4-C_1} e^{C_4 t} + Be^{C_1 t}$$

$$p(t) = Ae^{C_4 t} \qquad (2.24)$$

Case 2(b) $C_3 = 0$, $C_1 = C_4$.

$$h(t) = (AC_2 t + B)e^{C_1 t}$$

$$p(t) = Ae^{C_1 t} . \qquad (2.25)$$

2.4.2. Analysis

We first notice that when $C_3 = 0$, the format of the solution changes. Recall from 2.21 that C_3 is a measure of the dependence of the predators on the prey. However, this change in the solution does not attach a strong significance to C_3. If C_2, the measure of dependence of prey on predators, equals zero, the Case 1 solutions will also simplify to the format of Case 2.

The solutions 2.22 - 2.25 represent four main types of behaviour.

(a) Damped exponential. The solution is a sum of exponential functions of time, but is governed by a damping exponential factor. It occurs in Case 1 when $(C_1 + C_4) < 0$, and r is real, $2r < |C_1 + C_4|$ (we are including 'damped linear' motion, Case 1(b), as a special case). This motion occurs in Case 2 when C_1 and C_4 are both negative. Examples of models displaying this type of behaviour will be given in the next section.

(b) Damped oscillatory. The solution is oscillatory but governed by a damping exponential factor. This occurs in Case 1 when $(C_1 + C_4) < 0$ and r is imaginary. Examples will be given later.

(c) Undamped oscillatory. The solution consists of oscillations of constant amplitude. It occurs in Case 1 when $(C_1 + C_4) = 0$ and r is imaginary. We have already had an example of this type of behaviour in the Lotka-Volterra model of Section 2.2.

(d) Divergent. This category covers any type of solution which tends to infinity as $t \to \infty$. It will happen in Case 1 when $(C_1 + C_4)$ is positive, or in Case 2 when C_1 or C_4 is positive.

Because the perturbations increase in magnitude, the linearisation assumption will be inappropriate here. The solutions 2.22 - 2.25 will not be a good approximation and should not be used.

Hence, we have seen that, in a general predator-prey system, small perturbations from the equilibrium value will behave in one of four different ways. In two of these types, (a) and (b), the solution is damped in time and the system will return to the equilibrium point - that is, the model is stable. When the system does not return to equilibrium, as in (c) and (d), the model is unstable (for example, the Lotka-Volterra model).

Because this approximation cannot be used for divergent solutions (type (d)), we will just look at solutions in the first three categories. In the next section, examples of predator-prey models which illustrate the different types of behaviour are discussed.

2.5. Examples of Predator-Prey Models

2.5.1. Immigration-death model

In order to give examples of models displaying behaviour patterns described in Section 2.4, we consider now an 'immigration-death' process. Suppose that the prey cannot be born into the system, but immigrate into it at a constant rate, λ. The equations of the model change to

$$\dot{H} = \lambda - \alpha HP$$

$$\dot{P} = \beta HP - \mu P \; . \tag{2.26}$$

The equilibrium value now occurs at

$$\hat{H} = \frac{\mu}{\beta} , \qquad \hat{P} = \frac{\lambda \beta}{\alpha \mu}. \qquad (2.27)$$

From 2.21 the C_i's may be calculated as:

$$C_1 = -\alpha \hat{P} \qquad C_3 = \beta \hat{P}$$

$$C_2 = -\alpha \hat{H} \qquad C_4 = 0 \qquad , \qquad (2.28)$$

and r is found to be

$$r = \frac{1}{2} \sqrt{(C_1 - C_4)^2 + 4C_2 C_3}$$

$$= \frac{1}{2} \sqrt{\alpha^2 \hat{P}^2 - 4\lambda \beta} .$$

This is a Case 1 solution, and so from 2.22 we see

$$h(t) = \frac{1}{\beta \hat{P}} e^{-\alpha \hat{P} t/2} [(-\alpha \hat{P} t/2 + r)Ae^{rt} + (-\alpha \hat{P} t/2 - r)Be^{-rt}]$$

$$p(t) = e^{-\alpha \hat{P} t/2} \left[Ae^{rt} + Be^{-rt} \right] \qquad (2.29)$$

(with similar modification of 2.23 when $r=0$).

From 2.29, we can see that the damping factor, $e^{-\alpha \hat{P} t/2}$, has been introduced. Because r may be real or imaginary, the motion may be exponential or oscillatory. Hence, on comparing 2.29 with the Lotka-Volterra solution, 2.9, we see that, by changing the birth rate to an immigration rate, the behaviour of the solution changes from type (c), undamped oscillatory, to types (a) or (b), damped exponential or oscillatory.

2.5.2. Density-dependent birth rate

Recall that the Volterra-Gause-Witt model, mentioned in Section 2.3, with a self-inhibiting factor in the birth rate of the prey, is defined by the equations (see 2.13)

$$\dot{H} = (\lambda - cH)H - \alpha HP$$

$$\dot{P} = \beta HP - \mu P , \qquad (2.30)$$

where all parameters, including c, are greater than zero. Because the prey birth rate is $(\lambda - cH)H$, this puts an upper bound of λ/c on the number of prey. This is often more realistic than the Lotka-Volterra model because, in general, a population cannot increase without limit, owing to finite constraints, for example, on the size of the habitat or the supply of resources.

The equilibrium value of this model is at

$$\hat{H} = \frac{\mu}{\beta} , \qquad \hat{P} = \frac{\lambda - c\hat{H}}{\alpha} . \qquad (2.31)$$

We calculate the C_i's and r to be

$$C_1 = -c\hat{H} \qquad C_3 = \beta\hat{P}$$

$$C_2 = -\alpha\hat{H} \qquad C_4 = 0$$

$$r = \frac{1}{2}\sqrt{c^2\hat{H}^2 - 4\alpha\beta\hat{H}\hat{P}} . \qquad (2.32)$$

Depending on the magnitude of c, r may be real or imaginary. The solution is in the Case 1 format, and when r is real is given by

$$h(t) = \frac{1}{\beta\hat{P}}e^{-c\hat{H}t/2}[(-c\hat{H}/2 + r)Ae^{rt} + (-c\hat{H}/2 - r)Be^{-rt}]$$

$$p(t) = e^{-c\hat{H}t/2}[Ae^{rt} + Be^{-rt}] .\tag{2.33}$$

When r is imaginary, this changes to

$$h(t) = \left[\frac{A}{\beta\hat{P}}\theta \cos(\theta t + B)\right] e^{-c\hat{H}t/2}$$

$$p(t) = \left[A \sin(\theta t + B)\right] e^{-c\hat{H}t/2}\tag{2.34}$$

where $\theta = \sqrt{\alpha\beta\hat{H}\hat{P} - c^2\hat{H}^2/4}$. (When r=0, the solution has the form of Case 1(b)).

To investigate the effect of including c in the model, first remember that, when c is zero, the model reduces to Lotka-Volterra and the solution is given by 2.9. That is, the solution oscillates with constant amplitude, and phase angle θ, where $\theta = \sqrt{\alpha\beta\hat{H}\hat{P}}$.

When c>0, but small, solution 2.34, the predators and prey still oscillate, and are $\pi/2$ out of phase with each other. However, these oscillations are now governed by a small damping factor

$$e^{-c\hat{H}t/2} ,$$

so that they eventually decay, and the system returns to equilibrium value. This may be illustrated using the phase diagram in Figure 2.2. When c=0 (Lotka-Volterra), the linear solution follows an elliptical path, whereas, when c>0 but small, the solution gradually spirals towards the equilibrium, E.

As c increases, the damping factor becomes stronger, the phase
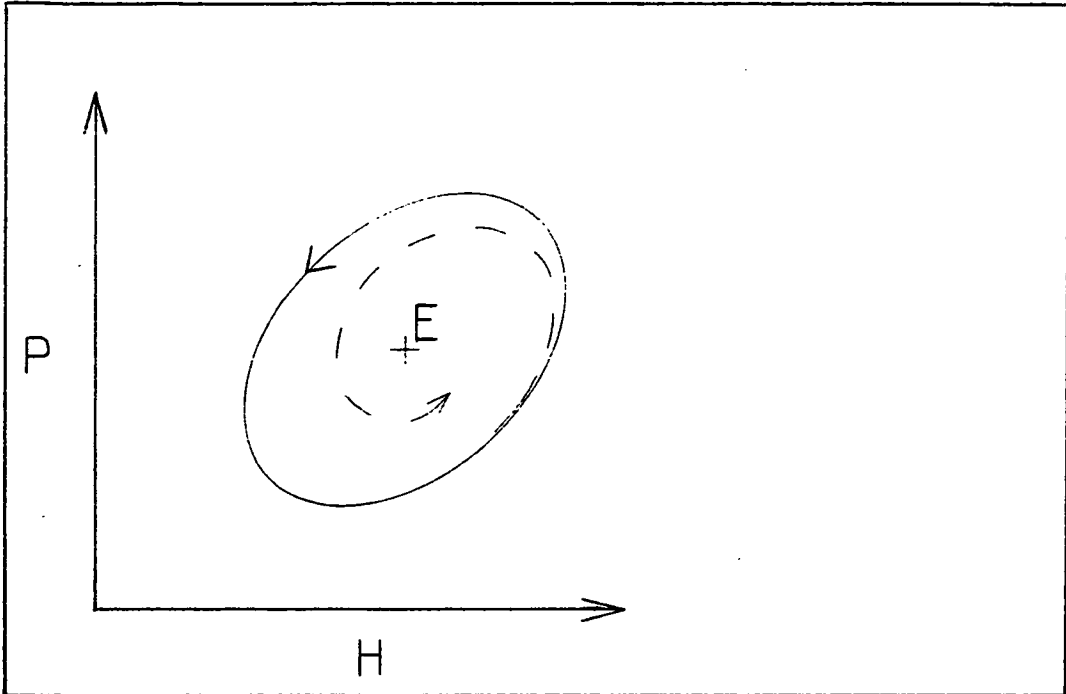
Figure 2.2. Typical phase diagram for Volterra-Gause-Witt model, with ——— showing linear solution for c=0, and - - - the solution when c>0, but small.

angle θ decreases, and the period of oscillation rises.

When

$$c \,>\, 2\beta[\,\sqrt{\tfrac{\lambda+\mu}{\mu}} - 1]\,\,, \qquad\qquad (2.35)$$

the solution is no longer oscillatory, but becomes damped exponential (solution 2.33). As c, the prey-inhibiting factor, increases, the damping force becomes stronger and the model returns to its equilibrium state faster. However as c gets larger, the predator equilibrium value, $\hat{P}$, decreases. In order to keep $\hat{P}$ positive, c must be subject to the constraint

$$c \,<\, \lambda/\hat{H}\,\,. \qquad\qquad (2.36)$$

Thus, while c increases to its upper limit of $\lambda/\hat{H}$, the solutions become more and more damped. Initially, the solutions are oscillatory, but when c reaches the value

$$2\beta[\sqrt{\frac{\lambda+\mu'}{\mu}} - 1] , \qquad (2.37)$$

the motion changes to exponential. (When c is equal to the quantity in 2.37, the solution is in a damped linear form which we treat as a special case of damped exponential). In particular, we have seen that introducing c stabilizes the model. Because the effect of stability in the system may be seen clearly (through c), we will in future use this system when we wish to consider an example of a stable model.

2.6. Other Population Models

2.6.1. Competition models

Of course, the general equation 2.18 does not just describe predator-prey models - it represents all two-species population models whose behaviour may be described by differential equations. The following system

$$\dot{X} = X(\alpha_1 - \beta_1 X - \gamma_1 Y)$$

$$\dot{Y} = Y(\alpha_2 - \beta_2 X - \gamma_2 Y) \qquad (2.38)$$

where all parameters are greater than zero, may be interpreted as a model of two species X,Y who are competing with each other for survival (see Maynard Smith, 1974). The equilibrium values are

$$\hat{X} = \frac{\alpha_2 \gamma_1 - \alpha_1 \gamma_2}{\beta_2 \gamma_1 - \beta_1 \gamma_2} , \qquad \hat{Y} = \frac{\alpha_1 \beta_2 - \alpha_2 \beta_1}{\beta_2 \gamma_1 - \beta_1 \gamma_2} \qquad (2.39)$$

assuming these exist and are non-negative. Applying the theory developed in Section 2.4, the C_i constants and r are

$$C_1 = -\beta_1 \hat{X} \qquad C_3 = -\beta_2 \hat{Y}$$

$$C_2 = -\gamma_1 \hat{X} \qquad C_4 = -\gamma_2 \hat{Y}$$

$$r = \frac{1}{2} \sqrt{(-\beta_1 \hat{X} + \gamma_2 \hat{Y})^2 + 4\gamma_1 \beta_2 \hat{X}\hat{Y}} \, . \qquad (2.40)$$

This is a Case 1(a) type solution, and, because r is real, will always be exponential. The equilibrium is stable if

$$\frac{1}{2} \left| C_1 + C_4 \right| > r$$

that is

$$\beta_1 \gamma_2 > \beta_2 \gamma_1 \, . \qquad (2.41)$$

In order that the equilibrium values in 2.39 be positive, the inequality 2.41 implies that

$$\alpha_2 \gamma_1 < \alpha_1 \gamma_2 \, .$$

$$\alpha_1 \beta_2 < \alpha_2 \beta_1 \, . \qquad (2.42)$$

Thus, using the theory developed for the solution of predator-prey models in Section 2.4, the conditions (2.41 and 2.42) may be found for the existence of a stable equilibrium in a competition model.

2.6.2. Epidemic models

Although, biologically, epidemic processes are different from predator-prey processes, algebraically, the models can be similar. Let $X(t)$ be the number of susceptibles at time t, and $Y(t)$ the number of infectives of a given disease. Consider the simple epidemic case (see Bailey, 1975) where the number of deaths or removals of susceptibles is ignored, and fresh susceptibles are supplied by immigration:

$$\dot{X} = \lambda - \beta XY$$

$$\dot{Y} = \beta XY - \mu Y .$$
(2.43)

This is merely a special case of the model studied in 2.5.1, (put $\alpha = \beta$ in equations 2.26), and the solution follows in the same way.

Because of this algebraic similarity, many of the results for epidemic models may be used in predator-prey theory. In Chapter 4, we will be discussing the simplified epidemic model by Dietz and Downton (1968):

$$\dot{X} = \lambda - \alpha XY$$

$$\dot{Y} = \beta - \mu Y ,$$
(2.44)

so it is useful here to describe its behaviour near equilibrium. The equilibrium is given by

$$\hat{X} = \frac{\lambda \mu}{\alpha \beta} , \qquad \hat{Y} = \frac{\beta}{\mu} .$$
(2.45)

The C_i constants are

$$C_1 = -\alpha\hat{Y} \qquad C_3 = 0$$

$$C_2 = -\alpha\hat{X} \qquad C_4 = -\mu \quad . \qquad\qquad\qquad (2.46)$$

The solution is in the form of Case 2(a) (or Case 2(b) when $\alpha\hat{Y}=\mu$), and so is a sum of negative exponentials (see 2.24 and 2.25). Thus, the model described by 2.44 is always stable.

2.7. Non-Linear Effects

In this chapter, a method has been developed for studying a general two-species system by linearising the equations about the equilibrium point, and thus examining the behaviour in the neighbourhood of that point. No account has been made so far for any non-linear effect which might influence the behaviour of the system. In a review article, May (1976) emphasised the danger of ignoring non-linear terms. He showed that even simple non-linear models can display a wide range of behaviour – such as, stable points, stable cycles, or 'chaos' which is similar to the sample function of a random process (though this is usually restricted to difference rather than differential equations). This type of behaviour may be unexpected if only linearised equations have been studied.

The non-linear Lotka-Volterra model has been examined by Frame (1974). By writing the population densities in terms of convergent trigonometric series, he found a close estimate for the sum of the series which gives the exact period, with the use of Bessel functions. Comparing his result with the linear approximation solution, he found that the periods of the linear solution depart increasingly from the true periods as the initial conditions depart from the equilibrium conditions. Biswas et al. (1977) investigated non-linearities in the Volterra-Gause-Witt model using a perturbation method developed by Ford and Waters (1963) to solve the energy

problem for a coupled oscillator system. This method gives corrections, order by order, to the linearised solution. Though this method does yield more accurate solutions than the linear approximations, the solutions found are in the form of complicated mathematical series, which do not give much indication of the general behaviour of the system. Another perturbation technique was used by Dutt and Ghosh (1975) to investigate non-linearity in the Lotka-Volterra equations. Solutions to the first order approximations are oscillatory with no overall damping. In the linear solution, the period of oscillation depends only on λ and μ, but the corrected periods include the effect of the interaction rates, α and β.

One technique which can sometimes be used to test global stability in systems is the use of Lyapunov functions (see Nisbet and Gurney, 1982). A Lyapunov function is a mathematical function similar to energy in physical systems. If the density of a species is denoted by X, with equilibrium at $\hat{X}$, then global stability is guaranteed if a function L(X) may be found such that

(i) $L(\hat{X}) = 0$

(ii) $L(X) > 0$, for all $X \neq \hat{X}$ (2.47)

(iii) $\frac{dL}{dt} < 0$, with equality only when $X = \hat{X}$.

The drawback of this method is that in ecological systems, choosing a Lyapunov function, L, to satisfy these conditions has turned out to be very difficult. A Lyapunov function has been found for some simple models (an example will be given at the end of this section), but these functions do not appear to have any obvious biological interpretation.

Subject to a few formal mathematical conditions, a general two-species non-linear differential equation model may result in a limit cycle (see Nisbet and Gurney, 1982). A limit cycle corresponds to a closed loop in the phase diagram. As with an equilibrium point, a limit cycle may be stable or unstable - stability implying that small deviations from the curve will return to the curve. Figure 2.3 represents a stable limit cycle, the dotted lines indicating the trajectories of the system.
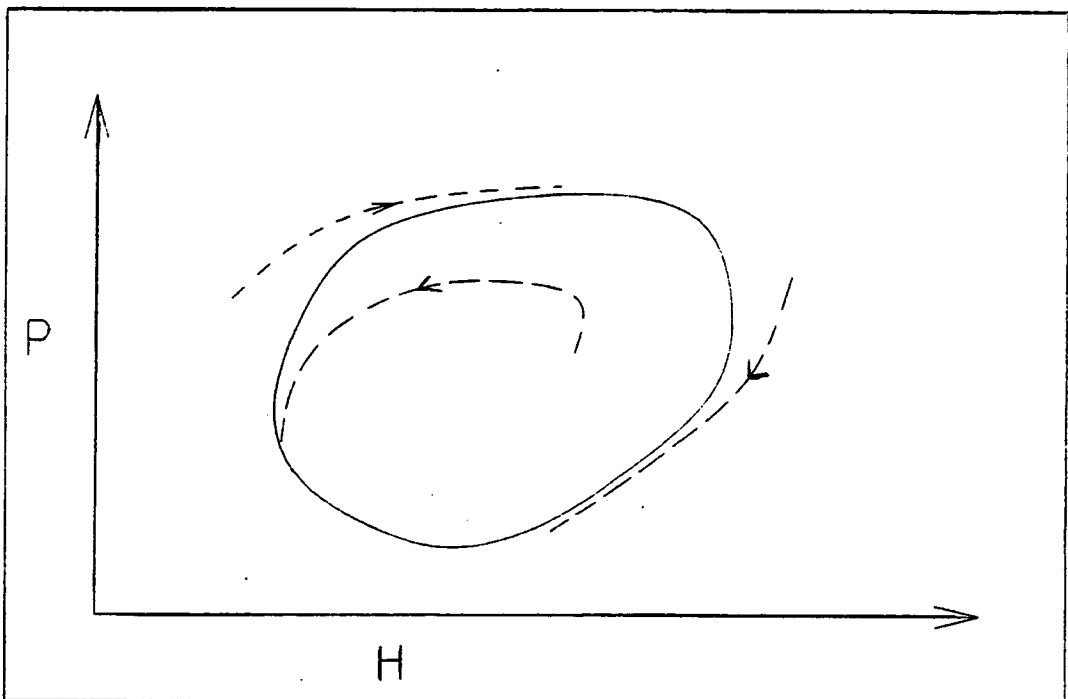
Figure 2.3. Phase diagram showing stable limit cycle, with trajectories marked by dotted lines.

By developing a theorem of Kolmogorov, May(1972) put forward a set of conditions whereby any two-species system satisfying these conditions was guaranteed to have either a single, globally stable equilibrium value, or a stable limit cycle. Further generalisations of these conditions were made by Bulmer (1976) and Brauer (1979). These conditions are essentially satisfied by all conventional

predator-prey models (May, 1974). Thus the non-linear solution of a predator-prey model will be be either a globally stable equilibrium, or a stable limit cycle.

Nisbet and Gurney (1982) stressed that a linear approximation near an equilibrium point may be a good indication of the behaviour of the non-linear model. Although a linear approximation may only prove local stability, they claim that this is usually a strong indicator of global stability. As an example to illustrate this, they consider the Volterra-Gause-Witt model of Section 2.5.2. Recall that the linearised equations indicated that the equilibrium point was stable. A Lyapunov function has been found for this model by Goel et al. (1971):

$$L(H',P') = P' - \hat{P}' - \hat{P}' \ln(P'/\hat{P}')$$

$$+ H' - \hat{H}' - \hat{H}' \ln(H'/\hat{H}') , \qquad (2.48)$$

where H', P' are scaled versions of H and P, such that

$$H' = H\frac{c}{\lambda} , \qquad P' = P\frac{\alpha c}{\lambda \beta} , \qquad (2.49)$$

and $\hat{H}'$ and $\hat{P}'$ are equilibria of the scaled equations, namely,

$$\hat{H}' = \frac{c\mu}{\lambda \beta} , \qquad \hat{P}' = (\lambda\beta - c\mu)\frac{c}{\lambda \beta^2} . \qquad (2.50)$$

It can be shown that L defined here fulfils all the conditions 2.47, and the model is globally stable.

To conclude, linear approximations appear to be good indications of the behaviour of the non-linear model. A stable equilibrium in the linear model seems to imply global stability, whereas persistent oscillations, as in the Lotka-Volterra model, may be an indication of

a stable limit cycle in the non-linear model.

CHAPTER 3

GENERAL STOCHASTIC METHODS

3.1. Introduction

In this chapter, the stochastic predator-prey model is intro-
duced, and several techniques, which have been used in stochastic
models and may be applicable to predator-prey processes, are exam-
ined.

We introduce the stochastic model (Section 3.2) by discussing
the stochastic analogue of the Lotka-Volterra model, and noting the
difficulties that arise. A brief outline of research done on sto-
chastic models is given in Section 3.3. We then consider three
methods which have been used successfully on single-species stochas-
tic models, and see if these can be extended to cover the predator-
prey process. In Section 3.4, a method of finding the stationary
probabilities of a birth-death process is discussed, and two possible
generalisations considered. Use of the cumulant generating function
has been suggested by Bailey (1964), and this is investigated in Sec-
tion 3.5. Bartlett (1978) has studied the growth of a single
species, and found its probability distribution to be approximately
Normal. In Section 3.6, we consider this theory in relation to
predator-prey models. Finally, in Section 3.7, in an attempt to sim-
plify the probability equation, we approximate the discrete state
space by one which is continuous, and a diffusion equation is found.

One method, which has been omitted from this chapter, is known
as Bartlett's stochastic linearisation. It is more suitable to

include this method in the next chapter.

3.2. Stochastic Analogue of the Lotka-Volterra Model

In stochastic models, we must regard $H(t)$ and $P(t)$ as random variables representing the numbers of prey and predators, respectively, at time t. By the notation (H,P), we mean that there are H prey and P predators present in the system. The stochastic process is defined by a set of transition probabilities. A transition probability is the probability that the system will be in state $(H+1,P)$, say, at time $t+\delta t$, conditional on being in state (H,P) at time t. This probability will be denoted by

$$\Pr\ [(H,P) \rightarrow (H+1,P)]\ \ .$$

The set of transition probabilities for the stochastic Lotka-Volterra model is

$$\Pr\ [(H,P) \rightarrow (H+1,P)] = \lambda H \delta t\ \ + o(\delta t)$$

$$\Pr\ [(H,P) \rightarrow (H-1,P)] = \alpha HP \delta t\ \ + o(\delta t)$$

$$\Pr\ [(H,P) \rightarrow (H,P+1)] = \beta HP \delta t\ \ + o(\delta t)$$

$$\Pr\ [(H,P) \rightarrow (H,P-1)] = \mu P \delta t\ \ + o(\delta t)$$

$$\Pr\ [\text{more than one event}] = o(\delta t) \tag{3.1}$$

where δt is a small time interval, and

$$\lim_{\delta t \to 0} \frac{o(\delta t)}{\delta t} = 0\ \ . \tag{3.2}$$

Notice from 3.1 that the probability of two or more changes to (H,P) in the time interval is negligible. Let $p_{ij}(t)$ denote the probability of having i prey and j predators at time t. Then using the transition probabilities from 3.1, we may form the forward equation (see, for example, Cox and Miller, 1965):

$$p_{ij}(t+\delta t) = p_{ij}(t) [1 - \delta t(\lambda i + \alpha i j + \beta i j + \mu j)]$$

$$+ \delta t [\lambda(i-1)p_{i-1,j}(t) + \alpha(i+1)jp_{i+1,j}(t)$$

$$+ \beta i(j-1)p_{i,j-1}(t) + \mu(j+1)p_{i,j+1}(t)] . \quad (3.3)$$

Taking the limit as $\delta t \to 0$, 3.3 becomes

$$p_{ij}' = -p_{ij} [\lambda i + (\alpha+\beta)ij + \mu j]$$

$$+ \lambda(i-1)p_{i-1,j} + \alpha(i+1)jp_{i+1,j}$$

$$+ \beta i(j-1)p_{i,j-1} + \mu(j+1)p_{i,j+1} \quad (3.4)$$

where $'$ denotes d/dt. Equation 3.4 is a difference-differential equation, and so we look for a solution by introducing a generating function. Let

$$G(z_1,z_2,t) \equiv \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} z_1^i z_2^j p_{ij}(t) \quad (3.5)$$

(assuming this converges in a suitably chosen domain where $|z_1| < 1$, $|z_2| < 1$). Multiplying equation 3.4 by $z_1^i z_2^j$ and summing over i and j, gives

$$\frac{\partial G}{\partial t} = \frac{\partial G}{\partial z_1} [-\lambda z_1 + \lambda z_1^2] + \frac{\partial G}{\partial z_2} [\mu - \mu z_2]$$

$$+ \frac{\partial^2 G}{\partial z_1 \partial z_2} [\alpha z_2 - (\alpha+\beta) z_1 z_2 + \beta z_1 z_2^2] \quad . \tag{3.6}$$

If equation 3.6 could be solved and expanded in terms of z_i, then we would have the solution for the probability distribution of the process. However, I could not find a solution to equation 3.6. Instead, we will look for the factorial moments of the distribution, through the derivatives of G. Using the notation $|_{(1)}$ to denote 'evaluated at $z_1 = z_2 = 1$', the first moments are given by

$$m_i(t) = \left[\frac{\partial G}{\partial z_i} \right]\Bigg|_{(1)} \qquad i=1,2 \quad , \tag{3.7}$$

and the second factorial moments are

$$V_{ii}(t) = \left[\frac{\partial^2 G}{\partial z_i^2} \right]\Bigg|_{(1)} \qquad i=1,2$$

$$V_{12}(t) = \left[\frac{\partial^2 G}{\partial z_1 \partial z_2} \right]\Bigg|_{(1)} = V_{21} \quad . \tag{3.8}$$

By differentiating equation 3.6 with respect to z_1 and z_2, the first moment equations are found to be

$$m_1'(t) = \lambda m_1(t) - \alpha V_{12}(t)$$

$$m_2'(t) = -\mu m_2(t) + \beta V_{12}(t) \quad . \tag{3.9}$$

Equations 3.9 cannot be solved simultaneously because of the V_{12} term. Similarly, second moment equations will involve third moments

- that is, the equations are not closed.

To conclude, we have introduced the stochastic analogue of the Lotka-Volterra model and derived the forward equation, 3.4, of its probability distribution. Because 3.4 is a difference-differential equation, a generating function is used, but I still could not solve the equation. The factorial moments of the distribution cannot be found because the moment equations are not closed.

The use of the probability generating function is just one technique which is commonly employed to solve difference-differential equations. During the rest of this chapter, we will consider other methods of finding the probability distribution of a stochastic process.

3.3. Developments in Stochastic Modelling

Having introduced the stochastic model, in the form of the stochastic analogue of the Lotka-Volterra model, we will now outline the main developments in stochastic modelling. Techniques used in studying other two-species models, such as stochastic competition and epidemic models, will also be discussed, because, algebraically, the same problems arise here as in the predator-prey case. When describing stochastic methods below, the models are given in the deterministic format because this is easier to read. The stochastic analogues of the models are obtained by changing the growth rates to transition probabilities, as in Section 3.2.

Chiang (1954) derived the generating function equation, 3.6, and the first moment equations, 3.9. By examining the deterministic structure of the process, he suggested that one might expect the moment equations to be

$$E'(H) = \lambda E(H) - \alpha E(HP)$$

$$E'(P) = \beta E(HP) - \mu E(P) \quad . \qquad\qquad (3.10)$$

These equations differ from 2.1 only in the interaction terms. Because the two species are dependent on each other,

$$E(HP) \neq E(H)E(P) \quad . \qquad\qquad (3.11)$$

Chiang suggested that this is an indication that the stochastic mean of a non-linear process will not follow directly along the deterministic path.

Weiss (1963) investigated a model of two antagonistic species ignoring birth rates, so that the deterministic model is

$$\dot{H} = -\alpha HP$$

$$\dot{P} = -\beta HP \quad . \qquad\qquad (3.12)$$

Rather than forming a probability equation, Weiss studied the stochastic model by considering the probabilities of the numbers of individuals left after each event. This he found to have a binomial distribution. Comparing the stochastic and deterministic results, Weiss found that the solutions agree qualitatively, and when the population sizes are large. However, the stochastic mean seemed to be always higher than the deterministic equilibrium.

Other interesting results arise from the use of different generating functions. Dietz and Downton (1968) considered the stochastic analogue of the epidemic model given, in 2.6.2, by the deterministic equations (2.44)

$$\dot{X} = \lambda - \alpha XY$$

$$\dot{Y} = \beta - \mu Y \quad . \tag{3.13}$$

The forward probability equation is formed, but the generating function used is

$$F_n(t,z) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} i^{(n)} z^j p_{ij}(t) \tag{3.14}$$

where $m^{(n)} = m(m-1)\ldots(m-n+1)$. A recursive expression for the solution of $F_n(t,z)$ is found, from which the means and variances may be calculated, for large t. Although the stochastic and deterministic means agree for Y, this is not the case for the X species. The stochastic mean, $E(X)$, is always greater than the deterministic mean, $\hat{X}$, though these values are close when numbers are large. Becker (1970) generalised the model of 3.13, by adding immigration and growth terms (though there is still only one non-linear interaction term). Solving in the same way, he found that $E(X)$ is always greater than $\hat{X}$, as before. As t becomes infinite, however, he showed it was possible for $E(X)$ to become infinite, while $\hat{X}$ goes to zero. Becker (1973) examined simple two-species population models with one non-linear interaction term which may be a death term (as in 3.13), or a growth term, such as

$$\dot{Y} = \beta XY \quad . \tag{3.15}$$

When this non-linear term represents death, Becker used the generating function described by 3.14. When it is a growth term (that is, positive), the generating function used is

$$F_n(t,z) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} j^{[n]} z^i p_{ij}(t) \tag{3.16}$$

where $m^{[n]} = m(m+1)\ldots(m+n-1)$. This enables the moments to be found, and compared with deterministic results. Discrepancies

between stochastic and deterministic results occur when the covariance is infinite - in this case, the stochastic mean may become infinite while the deterministic mean does not. Another problem occurs when the numbers are small - the stochastic probability of extinction may be small, while the deterministic values are zero.

Though the generating functions 3.14 and 3.16 have been useful in solving the models described above, they cannot be applied to a model, such as predator-prey, which has both birth and death quadratic terms.

In the late 1950's, computer simulation became an important tool in the study of stochastic models. Bartlett (1957) investigated the behaviour of the stochastic Lotka-Volterra model through simulation. He found that the model displays a cyclic pattern before extinction (of either species) occurs. A discrete-time competition model was simulated by Leslie and Gower (1958). Differences between stochastic and deterministic results are greater when the stationary state is unstable. Deterministically, the outcome is decided by the initial state, but, stochastically, only a probability can be associated with a particular outcome. When the stationary state is stable, the process settles to an approximately Normal distribution. Using Bartlett's 'stochastic linearisation' (to be described in Section 4.2), theoretical variances are calculated. Theoretical variances are found to be always smaller than variances calculated from simulations. Leslie and Gower (1960) performed a similar analysis of the discrete-time version (found by working in discrete time units - see Leslie, 1948) of the predator-prey model

$$\dot{H} = (\lambda - cH - \alpha P)H$$

$$\dot{P} = (\beta - \mu P/H)P \ . \qquad (3.17)$$

Good agreement is noticed between theoretical variances and those calculated from simulations, near the steady state, but again the theoretical variances are always smaller. A more detailed account of results using computer simulation is given by Holgate (1976).

A solution has been found for a special case of the stochastic Lotka-Volterra model by Billard (1977). The interactions are assumed to occur over a sufficiently short period of time so that no births occur. By using a new coordinate system developed by Severo (1969), the probability equation is transformed into a matrix equation:

$$\frac{dz(t)}{dt} = Bz(t) \ , \tag{3.18}$$

where $z(t)$ is a vector of the probabilities. The matrix B is a square matrix of order $(N_1+1)(N_2+1)$, where N_1 and N_2 are the initial sizes of the prey and predator populations. B is lower triangular and the solution to 3.18 is found using a recursion theorem of Severo (1969). This enables a series solution for the time-dependent state probabilities to be found.

3.4. Stationary Probabilities from Birth-Death Processes

3.4.1. Karlin and Taylor's results

Much work has been done on stochastic modelling of birth-death processes - for example, see Bailey (1964), Karlin and Taylor (1975) or Bartlett (1978). Although the birth-death process is simpler than the predator-prey process, it may be possible to extend the results to give an approximate solution for the predator-prey model. We consider here the method used by Karlin and Taylor (1975) for finding the stationary probabilities of a general birth-death process.

The transition probabilities are

$$Pr \, [i \rightarrow i+1] = \lambda_i \delta t + o(\delta t)$$

$$Pr \, [i \rightarrow i-1] = \mu_i \delta t + o(\delta t) \quad\quad\quad (3.19)$$

$$Pr \, [i \rightarrow i \;\;] = 1 - (\lambda_i + \mu_i) + o(\delta t)$$

in a small time interval δt. If p_j denotes the probability of being in state j (when t is large), then Karlin and Taylor showed, by induction, that

$$p_j = \pi_j / \sum_0^\infty \pi_k \quad\quad j=0,1,2,\ldots \quad\quad\quad (3.20)$$

provided that $\sum \pi_k < \infty$, where

$$\pi_0 = 1$$

$$\pi_j = \frac{\lambda_0 \lambda_1 \ldots \lambda_{j-1}}{\mu_1 \mu_2 \ldots \mu_j} \quad\quad j>0 \quad . \quad\quad\quad (3.21)$$

If $\sum \pi_k = \infty$, then no stationary distribution exists.

Two possible methods of extending this result will be considered - firstly, by approximating the predator-prey process by two separate birth-death processes, or secondly, by generalising the results to two dimensions.

3.4.2. Separate processes

Consider the predator-prey process whose transition probabilities, as shown by Figure 3.1, are
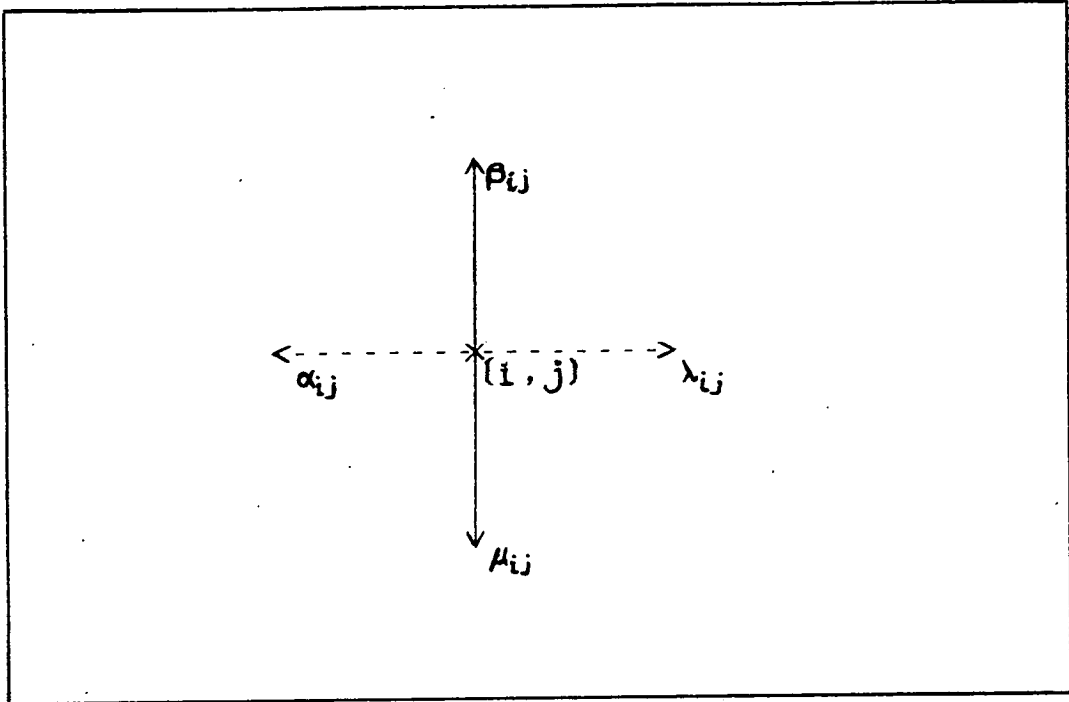
$$Pr[(i,j) \rightarrow (i+1,j)] = \lambda_{ij} \delta t + o(\delta t)$$

Figure 3.1. Transition probabilities for the predator-prey process defined by 3.22 at the point (i,j), where - - - represents prey and ———— predators.

$$Pr[(i,j) \rightarrow (i-1,j)] = \alpha_{ij}\delta t + o(\delta t)$$

$$Pr[(i,j) \rightarrow (i,j+1)] = \beta_{ij}\delta t + o(\delta t) \qquad (3.22)$$

$$Pr[(i,j) \rightarrow (i,j-1)] = \mu_{ij}\delta t + o(\delta t)$$

where

$$\lambda_{ij} = (\lambda - c_1 i)i$$

$$\alpha_{ij} = \alpha i j \qquad (3.23)$$

$$\beta_{ij} = (\beta i - c_2 j)j$$

$$\mu_{ij} = \mu j$$

and all parameters are constant. Note that c_1 and c_2 have been included so that both the predator and prey processes, when considered separately, will have a stationary distribution. In order to prevent extinction, we will not allow deaths to occur when only one member of a species remains. The deterministic equilibrium value of the system is at

$$\hat{H} = \frac{\alpha\mu + \lambda c_2}{\alpha\beta + c_1 c_2} \quad , \quad \hat{P} = \frac{\lambda\beta - \mu c_1}{\alpha\beta + c_1 c_2} \quad . \tag{3.24}$$

As an approximation to the predator-prey process, suppose we replace j in the prey transition probabilities by the deterministic equilibrium value for the predators, $\hat{P}$. Similarly, i is replaced in the predator transition probabilities by $\hat{H}$. The prey and predator processes may now be regarded as two separate birth-death processes. Let p_i denote the (stationary) probability of i prey, then, using Karlin and Taylor's method,

$$p_i = \frac{1}{Ti(\alpha\hat{P})^{i-1}} \prod_{j=1}^{i-1} (\lambda - c_1 j) \qquad 2 \leq i \leq M_1$$

$$p_1 = 1/T \tag{3.25}$$

where T is the normalising constant

$$T = 1 + \sum_{i=2}^{M_1} \prod_{j=1}^{i-1} \frac{(\lambda - c_1 j)}{i(\alpha\hat{P})^{i-1}} \quad , \tag{3.26}$$

and M_1 is the upper bound on the number of prey — that is, the smallest integer less than or equal to λ/c_1.

Similarly if q_i is the probability of having i predators, and

$$U = 1 + \sum_{i=2}^{M_2} \prod_{j=1}^{i-1} \frac{(\beta \hat{H} - c_2 j)}{i \mu^{i-1}} \qquad (3.27)$$

where M_2 is the upper bound on the predators, then

$$q_i = \frac{1}{U i \mu^{i-1}} \prod_{j=1}^{i-1} (\beta \hat{H} - c_2 j) \qquad 2 \leqslant i \leqslant M_2$$

$$q_1 = 1/U \quad . \qquad (3.28)$$

By assuming that the processes are independent, an approximation for $P(i,j)$, the stationary probability of having i prey and j predators, is given by

$$P(i,j) = p_i q_j \quad . \qquad (3.29)$$

We investigate the accuracy of this approximation using the following numerical example. Let the parameters of the model have the values

$$\alpha = 1.2 \qquad \lambda = 270$$

$$\beta = 0.5 \qquad \mu = 50 \qquad (3.30)$$

$$c_1 = 1.5 \qquad c_2 = 0.05 \quad .$$

The probability distribution of the original non-linear predator-prey process is calculated using the iteration procedure which will be described in detail in Section 4.7.1. Table 3.1 gives some values of the iterated probabilities, all probability values given being multiplied by 10^5. Because the deterministic equilibrium value is at

$$\hat{H} = 108.9, \quad \hat{P} = 88.9,$$

most of the $\overset{\text{larger}}{\underset{\wedge}{\text{non-zero}}}$ probability values are within the scope of the Table.

Table 3.1

Probability Values ($\times 10^5$) calculated using iteration method and parameters from 3.30.

		no. of predators					
		80	90	100	110	120	130
	80	1	8	22	26	15	4
no.	90	11	36	65	65	33	8
of	100	40	80	90	64	26	5
prey	110	68	80	52	22	6	1
	120	40	28	10	2	4	0
	130	6	2	1	0	0	0

Table 3.2

Probability vales ($\times 10^5$) calculated using birth-death approximation and parameters from 3.30.

		no. of predators					
		80	90	100	110	120	130
	80	0	0	0	0	0	0
no.	90	9	9	8	7	5	4
of	100	48	48	45	39	30	21
prey	110	79	80	74	63	49	35
	120	31	32	30	25	20	14
	130	2	2	2	2	2	1

Table 3.2 shows the corresponding probability values calculated using equation 3.29.

By comparing the Tables, we see that the general shapes of the distributions appear to be different. In Table 3.1, the probabilities seem to form an elliptical pattern, with the lowest probabilities occurring when the numbers of prey and predators are either both low or both high. In Table 3.2, the probabilities seem to have a stronger dependence on the prey numbers – high or low probabilities occur when the number of prey is high or low, with little regard for the number of predators. When the number of prey is at 110, and the predators at 90, denoted by (110,90), which is near the deterministic equilibrium, both Tables agree. However, following the elliptic shape in Table 3.1, as the prey decrease, and predators increase, large discrepancies occur – for example, at the points (100,100), (90,100), and (80,110).

Hence, with this set of parameter values (3.30), numerical results show that this method does not appear to give a good estimate of the probability distribution of a predator-prey process.

3.4.3. Two-dimensional birth-death processes

Let $P_{ij}(t)$ denote the probability of having i prey and j predators at time t. Then the two-dimensional equivalent of Karlin and Taylor's equations is

$$P_{11}' = -(\lambda_{11}+\beta_{11})P_{11} + \alpha_{21}P_{21} + \mu_{12}P_{12}$$

$$P_{1j}' = -(\lambda_{1j}+\beta_{1j}+\mu_{1j})P_{1j} + \alpha_{2j}P_{2j} + \beta_{1,j-1}P_{1,j-1} + \mu_{1,j+1}P_{1,j+1}$$

$$P_{i1}' = -(\lambda_{i1}+\alpha_{i1}+\beta_{i1})P_{i1} + \lambda_{i-1,1}P_{i-1,1} + \alpha_{i+1,1}P_{i+1,1} + \mu_{12}P_{12}$$

$$P_{ij}' = -(\lambda_{ij}+\alpha_{ij}+\beta_{ij}+\mu_{ij})P_{ij} + \lambda_{i-1,j}P_{i-1,j} + \alpha_{i+1,j}P_{i+1,j}$$

$$+ \beta_{i,j-1} P_{i,j-1} + \mu_{i,j+1} P_{i,j+1} \quad . \tag{3.31}$$

I tried to find a stationary solution to this by substituting in products of the parameters comparable with the one-dimensional case, but none were successful. To my knowledge, Karlin and Taylor's method has not been applied to a general birth-death process of more than one dimension.

However, results have been found for the two-dimensional birth-death process by Billard (1981). Using her method (mentioned in 3.3) of transforming the problem into a matrix equation, where the matrix is in lower triangular form, a solution may be calculated from a series of recursive equations. The transition probabilities of the predator-prey process may be found as a special case.

3.5. Cumulant Generating Function

Bailey (1964) suggested that it may be possible to find the solution to a one-dimensional non-linear process using the cumulant generating function. He proposed, without giving any justification, that the problem may be simplified by assuming that, for sufficiently large population numbers, cumulants of a higher order than j, say, may be ignored. If $K(\theta,t)$ is the cumulant generating function, then by equating powers of θ, a system of j differential equations in j unknowns is formed. Bailey suggested that it could be useful in a predator-prey context to form a system of equations for the cumulants k_{01}, k_{10}, k_{11}, k_{02}, k_{20}, where

$$K(\theta_1,\theta_2,t) = \sum_{i,j} \frac{1}{i!j!}\theta_1^i\theta_2^j k_{ij}(t) \quad . \tag{3.32}$$

Applying this method to the stochastic stable model (given deterministically by 2.30), we find the cumulant generating function satisfies

$$\frac{\partial K}{\partial t} = \frac{\partial K}{\partial \theta_1}[\lambda(e^{\theta_1}-1)] + \frac{\partial K}{\partial \theta_2}[\mu(e^{-\theta_2}-1)]$$

$$+ \left[\frac{\partial K}{\partial \theta_1}\right]^2 [c(1-e^{\theta_1})] + \frac{\partial^2 K}{\partial \theta_1^2}[c(1-e^{\theta_1})]$$

$$+ \frac{\partial K}{\partial \theta_1}\frac{\partial K}{\partial \theta_2}[\alpha(e^{-\theta_1}-1) + \beta(e^{\theta_2}-1)]$$

$$+ \frac{\partial^2 K}{\partial \theta_1 \partial \theta_2}[\alpha(e^{-\theta_1}-1) + \beta(e^{\theta_2}-1)] \quad . \tag{3.33}$$

(This is found from the probability generating equation by letting $K = \ln G$, and writing z_i as e^{θ_i}.) Let us assume that only the first five cumulants are non-zero, so that

$$K(\theta_1,\theta_2,t) = k_{10}\theta_1 + k_{01}\theta_2 + k_{11}\theta_1\theta_2$$

$$+ k_{20}\theta_1^2/2 + k_{02}\theta_2^2/2 \quad . \tag{3.34}$$

Then, equating the θ coefficients on both sides, we obtain

$$k_{10}' = \lambda k_{10} - ck_{10}^2 - ck_{20} - \alpha k_{10}k_{01} - \alpha k_{11}$$

$$k_{01}' = -\mu k_{01} + \beta k_{10}k_{01} + \beta k_{11}$$

$$k_{11}' = \lambda k_{11} - \mu k_{11} - 2ck_{10}k_{11} - \alpha k_{10}k_{11} + \beta k_{10}k_{02} \tag{3.35}$$

$$k_{20}' = \lambda k_{20} + 1/2\lambda k_{10} - 2ck_{10}k_{20} - ck_{10}^2/2$$

$$- 1/2ck_{20} - \alpha k_{10}k_{11} + 1/2\alpha k_{10}k_{01} + 1/2\alpha k_{11}$$

$$k_{02}' = 1/2\mu k_{01} - \mu k_{02} + \beta k_{10}k_{02} + 1/2\beta k_{11}k_{01} + 1/2\beta k_{11} \ .$$

However, this system of equations seems to be difficult to solve, even in the stationary case, so that using the cumulant generating function does not appear to simplify the problem.

3.6. Bartlett's Normal Approximation

Bartlett (1978) considered the stochastic behaviour of a single species undergoing a birth-death process. By using a transformation on the probability equation, he found that the probability distribution is approximately Normal.

We will illustrate this technique by applying it to the stable predator-prey model (Section 2.5.2). The forward probability equation of this model is

$$P_{ij}' = -p_{ij}[(\lambda-ci)i + (\alpha+\beta)ij + \mu j]$$

$$+ (\lambda-c(i-1))(i-1)p_{i-1,j} + \alpha(i+1)jp_{i+1,j}$$

$$+ \beta i(j-1)p_{i,j-1} + \mu(j+1)p_{i,j+1} \ . \tag{3.36}$$

Let us assume that a quasi-stationary state exists — that is, the population numbers are large enough so that extinction can be ignored, and the probability distribution is stationary. Let π_{ij} be the quasi-stationary probabilities of having i prey and j predators. Then, letting $t\to\infty$, equation 3.36 becomes

$$\pi_{ij}[(\lambda-ci)i + \mu j + (\alpha+\beta)ij] = (\lambda-c(i-1))(i-1)\pi_{i-1,j}$$

$$+ \alpha(i+1)j\pi_{i+1,j} + \beta i(j-1)\pi_{i,j-1} + \mu(j+1)\pi_{i,j+1} \quad . \quad (3.37)$$

Using Bartlett's transformation, write

$$x = \frac{(i-\hat{H})}{\sqrt{\hat{H}}} \quad , \quad y = \frac{(j-\hat{P})}{\sqrt{\hat{P}}} \quad . \quad (3.38)$$

Let

$$\pi_{ij} \equiv F(x,y)$$

$$\epsilon_x = \frac{1}{\sqrt{\hat{H}}} \quad , \quad \epsilon_y = \frac{1}{\sqrt{\hat{P}}} \quad . \quad (3.39)$$

Then equation 3.37 may be rewritten as

$$F(x,y)[(\lambda-cx)x + \mu y + (\alpha+\beta)xy]$$

$$= F(x-\epsilon_x,y)[(\lambda-c(x-\epsilon_x))(x-\epsilon_x)] + F(x+\epsilon_x,y)[\alpha(x+\epsilon_x)y]$$

$$+ F(x,y-\epsilon y)[\beta x(y-\epsilon y)] + F(x,y+\epsilon y)[\mu(y+\epsilon y)] \quad . \quad (3.40)$$

By a Taylor expansion of F, and ignoring terms higher than the first order of ϵ_x, ϵ_y, this becomes

$$F[(\lambda-2cx-\alpha y)/\sqrt{\hat{H}} + (\beta x-\mu)/\sqrt{\hat{P}}] \quad (3.41)$$

$$= \frac{\partial F}{\partial x}[-\lambda x+cx^2+\alpha xy]/\sqrt{\hat{H}} + \frac{\partial F}{\partial y}[-\beta xy+\mu y]/\sqrt{\hat{P}} \quad .$$

I could not find an approximating Normal solution for F in 3.41. However, in the next chapter, I will examine this model using a different method, and then will show that the probability distribution

may in fact be approximated by the Normal distribution.

3.7. Continuous Approximation

3.7.1. Kolmogorov equation

In the predator-prey process, the population numbers change by discrete unit steps (through birth or death). This leads to the difference-differential equation (such as 3.4), which is difficult to solve. By approximating the discrete state space by one in which only continuous changes occur, the forward equation is replaced by a well known partial differential equation.

In the continuous case, we use the notation that $x_1(t)$ represents the number of prey, and $x_2(t)$ the number of predators, at time t. The model we are studying is the stable predator-prey model, whose forward equation was given in 3.36. To derive the continuous approximation, first suppose that, instead of taking unit jumps, the populations change by discrete steps of size $\delta x_1, \delta x_2$. The transition probabilities for this process are

$$Pr[(x_1,x_2) \to (x_1+\delta x_1,x_2)] = (\tilde{\lambda}-\tilde{c}x_1)x_1\delta t + o(\delta t)$$

$$Pr[(x_1,x_2) \to (x_1-\delta x_1,x_2)] = \tilde{\alpha}x_1 x_2\delta t + o(\delta t)$$

$$Pr[(x_1,x_2) \to (x_1,x_2+\delta x_2)] = \tilde{\beta}x_1 x_2\delta t + o(\delta t)$$

$$Pr[(x_1,x_2) \to (x_1,x_2-\delta x_2)] = \tilde{\mu}x_2\delta t + o(\delta t)$$

$$Pr[\text{more than one event}] = o(\delta t) \tag{3.42}$$

in a small time interval δt, where $\bar{\lambda}, \tilde{\alpha}, \bar{\beta}, \bar{\mu}, \tilde{c}$ are suitably modified versions of the original parameters (we will explain, below, how these are to be modified). Let $p(x_1, x_2, t)$ be the probability of having x_1 prey, x_2 predators at time t. The forward equation now changes to

$$p(x_1, x_2, t+\delta t) = p(x_1, x_2, t)\{1 - \delta t[(\bar{\lambda}-\tilde{c}x_1)x_1 + (\tilde{\alpha}+\bar{\beta})x_1 x_2 + \bar{\mu}x_2]\}$$

$$+ \delta t[(\bar{\lambda}-\tilde{c}(x_1-\delta x_1))(x_1-\delta x_1)p(x_1-\delta x_1, x_2, t)$$

$$+ \tilde{\alpha}(x_1+\delta x_1)x_2 p(x_1+\delta x_1, x_2, t)$$

$$+ \bar{\beta}x_1(x_2-\delta x_2)p(x_1, x_2-\delta x_2, t)$$

$$+ \bar{\mu}(x_2+\delta x_2)p(x_1, x_2+\delta x_2, t)] \quad . \qquad (3.43)$$

By Taylor expansion (ignoring higher order terms), this becomes

$$\frac{\partial p}{\partial t} = p[\delta x_1(-\bar{\lambda}+2\tilde{c}x_1+\tilde{\alpha}x_2-\tilde{c}\delta x_1) + \delta x_2(-\bar{\beta}x_1+\bar{\mu})]$$

$$+ \frac{\partial p}{\partial x_1}[\delta x_1(-\bar{\lambda}x_1+\tilde{c}x_1^2+\tilde{\alpha}x_1 x_2) + \delta x_1^2(\bar{\lambda}-2\tilde{c}x_1+\tilde{\alpha}x_2)]$$

$$+ \frac{\partial p}{\partial x_2}[\delta x_2[(-\bar{\beta}x_1 x_2+\bar{\mu}x_2) + \delta x_2^2(\bar{\beta}x_1+\bar{\mu})]$$

$$+ \frac{\partial^2 p}{\partial x_1^2}[\delta x_1^2(\tilde{\lambda}x_1-\tilde{c}x_1^2+\tilde{\alpha}x_1 x_2)/2]$$

$$+ \frac{\partial^2 p}{\partial x_2^2}[\delta x_2^2 (\tilde{\beta} x_1 x_2 + \tilde{\mu} x_2)/2] \quad . \tag{3.44}$$

The system is made continuous by letting $\delta t, \delta x_i$ go to zero. In order that the continuous process be made consistent with the discrete one, we must impose constraints on the manner in which these quantities go to zero. The constraints we impose are that the infinitesimal means and variances remain unchanged (see Cox and Miller, 1965). To see what is meant by these constraints, we look at the instantaneous mean, for example, of the predators, which is

$$\lim_{\delta t \to 0} \frac{E[X_2(t+\delta t) - X_2(t)]}{\delta t} \quad .$$

To keep the instantaneous mean constant in the discrete and continuous cases, we must have

$$\lim_{\delta t \to 0} (\tilde{\beta} x_1 x_2 - \tilde{\mu} x_2) \delta x_2 = \beta x_1 x_2 - \mu x_2 \quad . \tag{3.45}$$

Similarly, keeping the variance unchanged, we have

$$\lim_{\delta t \to 0} (\tilde{\beta} x_1 x_2 + \tilde{\mu} x_2) \delta x_2^2 = \beta x_1 x_2 + \mu x_2 \quad . \tag{3.46}$$

The constraints 3.45 and 3.46 are compatible since it is possible, for example, to let

$$\tilde{\beta} x_1 x_2 = \frac{\beta x_1 x_2}{\delta x_2} + \frac{\beta x_1 x_2 + \mu x_2}{2 \delta x_2^2}$$

$$\tilde{\mu} x_2 = \frac{\mu x_2}{\delta x_2} + \frac{\beta x_1 x_2 + \mu x_2}{2 \delta x_2^2} \quad .$$

In the same way, keeping the prey mean and variance fixed, implies

$$\lim_{\delta t \to 0} (\tilde{\lambda} x_1 - \tilde{c} x_1^2 - \tilde{\alpha} x_1 x_2) \delta x_1 = \lambda x_1 - c x_1^2 - \alpha x_1 x_2 \qquad (3.47)$$

$$\lim_{\delta t \to 0} (\tilde{\lambda} x_1 - \tilde{c} x_1^2 + \tilde{\alpha} x_1 x_2) \delta x_1^2 = \lambda x_1 - c x_1^2 + \alpha x_1 x_2 \quad . \qquad (3.48)$$

Letting $\delta t, \delta x_i$ go to zero subject to the constraints 3.45 - 3.48, equation 3.44 becomes

$$\frac{\partial p}{\partial t} = \frac{1}{2} \sum_{\substack{i=1 \\ j=1}}^{2} \frac{\partial^2}{\partial x_i \partial x_j} (a_{ij} p) - \sum_{i=1}^{2} \frac{\partial}{\partial x_i} (b_i p) \quad , \qquad (3.49)$$

where the b_i are the instantaneous means, given in 3.47 and 3.45, the a_{ii} are the instantaneous variances, 3.48 and 3.46, and a_{ij} the covariances (which are zero here).

Equation 3.49 is known as the Kolmogorov or Fokker-Plank equation (written here in two dimensions). It appears very often in physics, in two forms. Firstly, it is a diffusion equation (see, Tychonov and Samarski, 1964) - it can describe any system in which particles can diffuse, for example, through air, or in a system in which particles are suspended in a fluid. Secondly, it appears as a heat conduction equation (Carslaw and Jaegar, 1959).

This continuous approximation was used to approximate simple discrete stochastic processes in genetics by Feller (1951) and Kimura (1957,1962). The Kolmogorov equation formed is just one-dimensional, and series solutions have been found for the probability function. The results appeared to be a good approximation when the population size (in this case the number of genes) was large. Many solutions to the one-dimensional equation have been found, with different boundary and initial conditions (Feller, 1954, Bharucha-Reid, 1960, and Cox and Miller, 1965). However, very little progress has been made in

finding the solution for second order partial differential equations with variable coefficients, and so the general Kolmogorov equation, in two or more variables, resists solution. Thus, to my knowledge, no approximations have been found for predator-prey models using the Kolmogorov equation.

3.7.2. Stochastic differential equation

By approximating the discrete process by a continuous one, we arrived at the Kolmogorov diffusion equation (Section 3.7.1). Using this Kolmogorov equation, we will now show that the process satisfies a stochastic differential equation, for which an approximate solution will later be found. Let $\underline{X}(t)$ denote the two-dimensional vector of the process with components $X_1(t), X_2(t)$, and let

$$\underline{B}(\underline{x}, t) = \begin{bmatrix} b_1(\underline{x}, t) \\ b_2(\underline{x}, t) \end{bmatrix} , \qquad (3.50)$$

and

$$\underline{A}(\underline{x}, t) = \begin{bmatrix} a_{11}(\underline{x}, t) & a_{12}(\underline{x}, t) \\ a_{21}(\underline{x}, t) & a_{22}(\underline{x}, t) \end{bmatrix} . \qquad (3.51)$$

Let $\underline{Z}(t)$, with components $Z_1(t), Z_2(t)$, be a vector of mutually independent purely random processes, with zero mean and unit variance. From the Kolmogorov equation (3.49), we deduce that the process, $X(t)$, satisfies the stochastic differential equation (see Gihman and Skorohod, 1972, or Arnold, 1974), given by

$$d\underline{X}(t) = \underline{B}(\underline{x}, t)dt + \underline{Z}(t)\underline{A}^{1/2}(\underline{x}, t) \sqrt{dt} , \qquad (3.52)$$

where $\underline{A}^{1/2}(\underline{x}, t)$ is the unique matrix satisfying

$$\underline{A}^{1/2} \cdot \underline{A}^{1/2} = \underline{A} . \qquad (3.53)$$

In the theory of stochastic differential equations, two types of equation are possible depending on what calculus is used in the derivation - one is an Ito equation (see Arnold, 1974), and the other a Stratonovich equation (Stratonovich, 1966). Arnold (1974) compared the two forms of calculus, and gave a conversion formula between the two types of equation. This is irrelevant to our discussion as we are considering differential equations in the sense of Ito, only. We study this type of equation because, although it is now intractable, by a suitable simplification of the a_{ij}'s and b_{ij}'s, an approximate solution for the process will be found in Chapter 4.

3.8. Conclusion

We have introduced the forward probability equation of a predator-prey process, using the Lotka-Volterra model as an example, but could not solve it. It was not possible either to find the moments of the distribution because these equations were not closed.

Attempts were made to find an approximate solution to the stochastic predator-prey process by generalising three single-species methods: Karlin and Taylor's method of finding stationary probabilities, Bartlett's Normal approximation, and Bailey's suggestion of using the cumulant generating function. Though stationary probabilities were found using the first method, these were seen to be a poor approximation to the predator-prey process. Otherwise these attempts were unsuccessful.

Finally, the discrete predator prey process was approximated by making the state-space continuous. The Kolmogorov diffusion equation was derived, and, from this, the stochastic differential equation. Though these equations cannot be solved now, they will be useful in the next chapter.

CHAPTER 4

STOCHASTIC METHODS USING LINEARISATION

4.1. Introduction

Approximate solutions for stochastic predator-prey models are found in this chapter using linearisation techniques.

In the next section, we introduce a method developed by Bartlett (1957), known as stochastic linearisation. This method can be applied to the (stochastic analogue of the) Volterra-Gause-Witt model to give approximate solutions for the moments of the distribution. Section 4.3 deals with probability linearisation: three methods of linearising probabilities are suggested and compared using a simple model. The most accurate method is applied to predator-prey models, both stable and unstable, in Sections 4.4 and 4.5. Using this probability linearisation technique, the diffusion equation, derived in Section 3.7, for the continuous approximation is simplified, so that a solution may be found (Section 4.6). As a test of the accuracy of this solution, a numerical example is considered in Section 4.7.

In Chapter 2, we saw that there were three types of (non-divergent) deterministic behaviour near the equilibrium value: unstable with constant amplitude oscillations; stable exponential; or, stable oscillatory. The Lotka-Volterra model was an example of the first type and the other two types of behaviour could be displayed by the Volterra-Gause-Witt model, depending on the value of c. Because these two models represent all possible behaviour types (in deterministic linear solutions), from now on we shall just use

these as examples, referring to Volterra-Gause-Witt model as the stable model, and the Lotka-Volterra model as the unstable model.

4.2. Bartlett's Stochastic Linearisation

4.2.1. Description of method

One method for approximating stochastic equations which has had some success in predator-prey models, was introduced by Bartlett (1957) and is known as 'stochastic linearisation'. The technique is to approximate the stochastic equations by adding small deviations to the deterministic equations. The method was used to find the means and variances in a competition model by Bartlett (1957), and Leslie and Gower (1958). Smith and Mead (1979) applied it to the stable predator-prey model (from Section 2.5.2). The technique will be explained here in the context of this model.

The stochastic equations of the model are approximated using deterministic equations, as follows:

$$dH = ((\lambda - cH)H - \alpha HP)dt + dZ_1$$

$$dP = (\beta HP - \mu P)dt + dZ_2 , \tag{4.1}$$

where dZ_1 and dZ_2 are independent random variables, modified so that the means are zero, and variances are

$$var (dZ_1) = ((\lambda - cH)H + \alpha HP)dt$$

$$var (dZ_2) = (\beta HP + \mu P)dt . \tag{4.2}$$

Let $\hat{H}$ and $\hat{P}$ be the equilibrium values for prey and predators, respectively. Then, we use the transformation

$$H(t) = \hat{H} + h(t)$$

$$P(t) = \hat{P} + p(t) \ ,$$

remembering the comments in Section 2.2.2 on how higher order terms in h and p may be negligible, to linearise the equations about the equilibrium:

$$dh = (-c\hat{H}h - \alpha\hat{H}p)dt + dZ_1$$

$$dp = \beta\hat{P}hdt + dZ_2 \ . \tag{4.3}$$

Because we are working with increments (such as dZ_1, dZ_2), we write

$$dh = h(t+dt) - h(t)$$

$$dp = p(t+dt) - p(t) \ , \tag{4.4}$$

so 4.3 may be rewritten as

$$h(t+dt) = h(t) + [-c\hat{H}h(t) - \alpha\hat{H}p(t)]dt + dZ_1$$

$$p(t+dt) = p(t) + [\beta\hat{P}h(t)]dt + dZ_2 \ . \tag{4.5}$$

Let us assume that the population sizes remain large relative to the standard deviations so that the chances of extinction by time t may be ignored, and a quasi-stationary distribution exists. Because of this stationarity assumption as t gets large

$$E[h(t+dt)^2] \approx E[h(t)^2] \equiv \sigma_h^2$$

$$E[p(t+dt)^2] \approx E[p(t)^2] \equiv \sigma^2_p \qquad (4.6)$$

$$E[h(t+dt)p(t+dt)] \approx E[h(t)p(t)] \equiv \sigma_{hp}$$

where $E[h]$ denotes the expected value of h, and σ^2_h the variance of h. Square and cross-multiply the equations in 4.5, and take expectations, ignoring terms of order dt^2

$$\sigma^2_h = \sigma^2_h + 2dt[-c\hat{H}\sigma^2_h - \alpha\hat{H}\sigma_{hp}] + ((\lambda - c\hat{H})\hat{H} + \alpha\hat{H}\hat{P})dt$$

$$\sigma^2_p = \sigma^2_p + 2\beta\hat{P}\sigma_{hp} + (\beta\hat{H}\hat{P} + \mu\hat{P})dt \qquad (4.7)$$

$$\sigma_{hp} = \sigma_{hp} + dt(-c\hat{H}\sigma_{hp} - \alpha\hat{H}\sigma^2_p + \beta\hat{P}\sigma^2_h) \ ,$$

which simplify to

$$-c\hat{H}\sigma^2_h - \alpha\hat{H}\sigma_{hp} + \alpha\hat{H}\hat{P} = 0$$

$$\beta\hat{P}\sigma_{hp} + \beta\hat{H}\hat{P} = 0 \qquad (4.8)$$

$$-c\hat{H}\sigma_{hp} - \alpha\hat{H}\sigma^2_p + \beta\hat{P}\sigma^2_h = 0 \ .$$

By solving equations 4.8 simultaneously, the variances and covariances of H and P (Smith and Mead, 1979) are found to be

$$\sigma^2_H = \alpha(\hat{P} + \hat{H})/c$$

$$\sigma^2_p = \beta\hat{P}(\hat{P} + \hat{H})/\{c\hat{H}\} + c\hat{H}/\alpha \qquad (4.9)$$

$$\sigma_{HP} = -\hat{H} \quad .$$

4.2.2. Analysis of results

The effects of the parameters of the process on the variance of the distribution can clearly be seen from 4.9. The variance of H may be decreased by lowering α or raising c. This will bring about an increase in σ_P^2 from the $c\hat{H}/\alpha$ term. The variance of P may be decreased without affecting σ_H^2 by lowering β.

Although, in deriving these variances, a quasi-stationary state was assumed, the results might give us some insight into the chances of extinction of the populations. Suppose that the equilibrium values are fixed. If the variance is large compared with the equilibrium value, it is likely that the species will experience large fluctuations, and will soon become extinct. Hence it appears that, for fixed equilibrium values, reducing the coefficient of variation, that is, the ratio of the standard deviation to the mean, should increase the chances of survival of a species. For the prey population, the coefficient of variation, CV(H), is given by

$$CV(H) = \sqrt{\alpha(\hat{P}+\hat{H})/c\hat{H}^2} \quad . \tag{4.10}$$

This quantity always decreases as c increases. The predator coefficient of variation, CV(P), is

$$CV(P) = \sqrt{\frac{\beta(\hat{P}+\hat{H})}{c\hat{H}\hat{P}} + \frac{c\hat{H}}{\alpha\hat{P}^2}} \quad . \tag{4.11}$$

Taking the first derivative of 4.11 with respect to c (keeping $\hat{P}$ fixed), we find that CV(P) reaches a minimum when

$$c = \sqrt{\frac{\alpha\beta\hat{P}(\hat{P}+\hat{H})}{\hat{H}}} \ . \qquad (4.12)$$

When $\hat{H}=\hat{P}$, this reduces to

$$c = \sqrt{2\alpha\beta\hat{H}}. \qquad (4.13)$$

Hence, the best chance of survival for the predators occurs when c satisfies 4.12. Increasing c beyond this, decreases the predator's chances but increases the chance of survival of prey. Of course, the probability of ultimate extinction is still one.

4.2.3. Disadvantages

This method relies on two main simplifying assumptions. First, the equations are linearised, so non-linear effects are ignored. Second, it assumes that the stochastic equations may be approximated by deviations from the deterministic equations. This means that the stochastic mean is assumed to coincide with the deterministic equilibrium. Although this may occur in linear equations, Chiang (1954) (see Section 3.3) pointed out that this will not be the case in a non-linear process. However, Becker (1973) (Section 3.3) suggested that the greatest discrepancies occur between the stochastic mean and deterministic equilibrium, when the covariance is infinite. Here the covariance, from 4.9, is $-\hat{H}$, so the difference should not be too great.

In deriving these variances, we also assumed that extinction could not occur, and that a quasi-stationary equilibrium existed. It is possible, as we shall see in Section 4.4.2, to relax this assumption and find time-dependent moments.

4.3. Probability Linearisation

4.3.1. Introduction

In Section 4.3.2, a method of linearising probabilities, developed by Jernigan and Tsokos (1980), is discussed. Using this technique, we develop two other ways in which probabilities may be linearised. All three methods are illustrated on the Dietz and Downton (1968) model, introduced in 2.6.2. The reason we have chosen this model is because exact stochastic solutions have been found for it, as mentioned in Section 3.3. These exact solutions are discussed in detail in Section 4.3.5. This will provide a test of accuracy of the linearisation methods. Comparing the results from all three linearised methods with the exact solutions (Section 4.3.6), we select the method which is most accurate.

4.3.2. Method A

Jernigan and Tsokos (1980) studied a stochastic model of the flow of a chemical nutrient through zones of plankton in a marine ecosystem. Although, biologically, this is unrelated to the predator-prey process, algebraically, the models are quite similar. In particular, the transition probabilities are non-linear and Jernigan and Tsokos encountered the same problems when trying to find the moments of the distributon - that is, the equations are not closed. They realised that this was due to the non-linear effects, and suggested a method for linearising the probabilties. We will illustrate this method using the Dietz and Downton (1968) model, described deterministically (see Section 2.6.2) as

$$\dot{X} = \lambda - \alpha XY$$

$$\dot{Y} = \beta - \mu Y \ . \tag{4.14}$$

To apply the Jernigan and Tsokos method, use the transformation

$$X = \hat{X} + u \ , \quad Y = \hat{Y} + v \ , \tag{4.15}$$

where $\hat{X}$ and $\hat{Y}$ are the deterministic equilibria, and u and v are small. Linearise the deterministic behaviour in the usual way:

$$\dot{X} = -\alpha\hat{X}v - \alpha\hat{Y}u$$

$$\dot{Y} = -\mu v \ . \tag{4.16}$$

Substituting back for u and v, from 4.15, and writing in matrix form, this becomes

$$\frac{d}{dt} \begin{bmatrix} X \\ Y \end{bmatrix} = \begin{bmatrix} -\alpha\hat{Y} & -\alpha\hat{X} \\ 0 & -\mu \end{bmatrix} \begin{bmatrix} X - \hat{X} \\ Y - \hat{Y} \end{bmatrix} \ . \tag{4.17}$$

Jernigan and Tsokos proposed that this linear deterministic system can be used to define linear transition probabilities in a stochastic model, just as the non-linear expressions were used to formulate the original non-linear model. They suggested that this is done by considering that whatever contributes positively to the change in a population in equation 4.17 should be regarded as a birth probability, with negative contributions representing a death probability. Using this theory, the linearised transition probabilities are

$$\Pr\ [(i,j) \to (i+1,j)] = 2\alpha\hat{X}\hat{Y}\delta t + o(\delta t)$$

$$\Pr\ [(i,j) \to (i-1,j)] = (\alpha\hat{Y}i + \alpha\hat{X}j)\delta t + o(\delta t)$$

$$\Pr\ [(i,j) \rightarrow (i,j+1)] = \mu\hat{Y}\delta t + o(\delta t) \tag{4.18}$$

$$\Pr\ [(i,j) \rightarrow (i,j-1)] = \mu j\delta t + o(\delta t)\ . $$

The probability generating function equation, using the new probabilities, is

$$\frac{\partial G}{\partial t} = G[-(2\alpha\hat{X}\hat{Y}+\mu\hat{Y}) + 2\alpha\hat{X}\hat{Y}z_1 + \mu\hat{Y}z_2]$$

$$+ \frac{\partial G}{\partial z_1}[\alpha\hat{Y}-z_1\alpha\hat{Y}] + \frac{\partial G}{\partial z_2}[\mu-z_2(\alpha\hat{X}+\mu)+\alpha\hat{X}z_2/z_1]\ , \tag{4.19}$$

where

$$G(z_1,z_2,t) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} z_1^i z_2^j P_{ij}(t)\ . \tag{4.20}$$

From 4.19, the equations for the factorial moments can be found – the first moment equations being

$$m_1{}'(t) = 2\alpha\hat{X}\hat{Y} - \alpha\hat{Y}m_1 - \alpha\hat{X}m_2$$

$$m_2{}'(t) = \mu\hat{Y} - \mu m_2\ . \tag{4.21}$$

The moment equations are now closed, and can be solved to give the means and variances of X and Y. The time-dependent solutions for the mean and variance of Y are given by

$$E_A(Y,t) = \beta/\mu + (k - \beta/\mu)e^{-\mu t} \tag{4.22}$$

$$Var_A(Y,t) = \beta/\mu + (k - \beta/\mu)e^{-\mu t} - ke^{-2\mu t}\ ,$$

where the initial conditions are X(0)=m, Y(0)=k. Using the exact

method of Dietz and Downton, the mean and variance of X could only be found in the stationary case. Thus, because the accuracy of the approximation can only be tested in this case, the mean and variance of X, and the covariance of X and Y, in the stationary case (using the Jernigan and Tsokos method), are

$$E_A(X) = \hat{X}$$

$$Var_A(X) = 2\hat{X} + \alpha\hat{X}^2/(\alpha\hat{Y}+\mu) \qquad (4.23)$$

$$Cov_A(X,Y) = -\alpha\hat{X}\hat{Y}/(\alpha\hat{Y}+\mu) \quad .$$

Jernigan and Tsokos claimed that numerical results show that this method produces good approximations to the original non-linear process. We will investigate this is Section 4.3.6.

This method of Jernigan and Tsokos is just one way of linearising probabilities. It is possible to do this in a number of ways. In the next two sections, we consider two more methods of linearisation, and will compare all methods in Section 4.3.6. From now on, we will refer to Jernigan and Tsokos' method as Method A.

4.3.3. Method B

Suppose, instead of looking at the effect of linearisation on the whole system, as above, we consider each probability individually. For example, the probability of a death in the X species is

$$Pr \,[death \; of \; X] = \alpha XY \delta t + o(\delta t)$$

$$= \alpha(\hat{X}+u)(\hat{Y}+v)\delta t + o(\delta t) \quad .$$

By linearising, this becomes

$$(\alpha\hat{X}\hat{Y}+\alpha\hat{Y}u+\alpha\hat{X}v)\delta t + o(\delta t) \ .$$

Replacing u and v, as in Method A, we get

$$[\alpha\hat{X}\hat{Y}+\alpha\hat{Y}(X-\hat{X})+\alpha\hat{X}(Y-\hat{Y})]\delta t + o(\delta t) \ ,$$

which simplifies to

$$(\alpha\hat{X}Y+\alpha\hat{Y}X-\alpha\hat{X}\hat{Y})\delta t + o(\delta t) \ .$$

That is, in the linearised case,

$$Pr \ [(i,j) \to (i-1,j)] = (\alpha\hat{Y}i+\alpha\hat{X}j-\alpha\hat{X}\hat{Y})\delta t + o(\delta t) \ . \qquad (4.24)$$

Notice that it is possible for this quantity to become negative when i and j are far from the equilibrium value. But, because of the linearity assumption, this approximation is only valid near the equilibrium. Hence, in deriving the equations, we will assume that no negative probabilities can occur.

This method appears to be a good approximation for three reasons. First, it does not rely on splitting the probabilities into positive and negative components, as in Method A. Second, the probabilities are accurate at the equilibrium point - this can be seen by replacing i and j by $\hat{X}$ and $\hat{Y}$, respectively, in 4.24. So the method should be a good approximation in the neighbourhood of the equilibrium. Third, transition probabilities which do not have a quadratic term are unchanged - for example

$$Pr \ [\text{death of } Y] = \mu Y\delta t + o(\delta t)$$

$$= \mu(\hat{Y}+v)\delta t + o(\delta t)$$

$$= [\mu\hat{Y}+\mu(Y-\hat{Y})]\delta t + o(\delta t)$$

$$= \mu Y\delta t + o(\delta t) \ . \tag{4.25}$$

Since these properties do not hold for Method A, this method appears to be a better approximation.

The equation for the probability generating function is formed using the new transition probabilities, and again the factorial moments may be found. The mean and variance for Y are identical to those found using Method A, given in 4.22. The stationary mean and variance of X, and covariance of X and Y, are:

$$E_B(X) = \hat{X}$$

$$Var_B(X) = \hat{X} + \alpha\hat{X}^2/\{\alpha\hat{Y}+\mu\} \tag{4.26}$$

$$Cov_B(X,Y) = -\alpha\hat{X}\hat{Y}/\{\alpha\hat{Y}+\mu\} \ .$$

These results will be discussed later.

4.3.4. Method C

Another possible form of linearisation would be to replace the quadratic XY term in the transition probabilities by

$$XY \approx 1/2 \ \hat{X}Y + 1/2 \ \hat{Y}X \ . \tag{4.27}$$

The probability of a death of an X individual will now be

$$\Pr\left[(i,j) \rightarrow (i-1,j)\right] = 1/2 \ (\alpha\hat{X}j + \alpha\hat{Y}i)\delta t + o(\delta t) \ , \qquad (4.28)$$

while all the other probabilities remain unchanged. This linearisation again seems to be a reasonable approximation because it possesses the properties of Method B — namely, no splitting into positive and negative components, accuracy at the equilibrium point, and linear terms are left unchanged.

Calculating the moments from the probability generating function equation, we again find that the mean and variance of Y are identical to those given in 4.22. The stationary mean and variance of X, and covariance of X and Y, for this method are

$$E_C(X) = \hat{X}$$

$$Var_C(X) = 2\hat{X} + \alpha\hat{X}^2/\{\alpha\hat{Y} + 2\mu\} \qquad (4.29)$$

$$Cov_C(X,Y) = -\alpha\hat{X}\hat{Y}/\{\alpha\hat{Y} + 2\mu\} \quad .$$

4.3.5. Dietz and Downton's results

As explained in 4.3.1, the reason for studying the model, given deterministically by

$$\dot{X} = \lambda - \alpha XY$$

$$\dot{Y} = \beta - \mu Y \ , \qquad (4.30)$$

is because Dietz and Downton (1968) found exact results for it. Although this model was proposed as an epidemic model, it is useful to study it here, because the effect of linearising the probability

(αXY) of a death of an X individual may clearly be seen.

Using the initial conditions

$$X(0) = m , \quad Y(0) = k , \tag{4.31}$$

Dietz and Downton found that the mean and variance for the Y species are obtained straightforwardly, and are given by

$$E_D(Y,t) = \beta/\mu + (k - \beta/\mu)e^{-\mu t}$$

$$Var_D(Y,t) = \beta/\mu + (k - \beta/\mu)e^{-\mu t} - ke^{-2\mu t} . \tag{4.32}$$

The behaviour of the X species is a lot more difficult to determine. Dietz and Downton obtained the solution for $E_D(X,t)$ in a very complicated integral form. Letting t become large, they found that the mean of X does not tend to the deterministic equilibrium, $\hat{X}$. The ratio of this mean to $\hat{X}$ is

$$\frac{1}{\hat{X}} \lim_{t \to \infty} [E_D(X,t)] = (1+\sigma)e^{-\eta}\Phi(\frac{\eta}{\sigma}, \frac{\eta}{\sigma}+1; \eta) , \tag{4.33}$$

where

$$\sigma = \alpha/\mu , \quad \eta = \alpha^2\beta/\{\mu(\alpha+\mu)^2\} , \tag{4.34}$$

and $\Phi(a\ c;x)$ is the confluent hypergeometric function defined by

$$\Phi(a,c;x) = \frac{\Gamma(c)}{\Gamma(a)\Gamma(c-a)} \int_0^1 e^{xu}u^{a-1}(1-u)^{c-a-1}du \tag{4.35}$$

(see Abramowitz and Stegun, 1965). Dietz and Downton showed that the stochastic mean is always greater than the deterministic equilibrium. By examining this ratio for various values of σ and η, see Table

4.1 they showed that the ratio tends to 1 when σ, the relative death rate, is small, and X is large.

An expression is found for the variance of X in the stationary case, which cannot be simplified analytically and requires numerical integration. Dietz and Downton gave numerical values (see Table 4.2) for the ratio, R_D, which is defined as

$$R_D = \lim_{t \to \infty} \left[\frac{E_D(X(X-1))}{E_D(X)^2} \right] - 1 \; . \tag{4.36}$$

This ratio is chosen because it may be written in terms of η and σ and explicit dependence on λ is eliminated. The coefficient of variation, CV(X), may easily be found from it:

$$CV(X) = \{R_D + 1/E_D(X)\}^{1/2} \; . \tag{4.37}$$

4.3.6. Comparison of results

We now test the accuracy of the linearisation methods by comparing the results with those of Dietz and Downton.

First, we look at the results for the Y species. The time-dependent mean and variance found by the linearised approximations are the same for all three methods (4.22), and are identical to those found by Dietz and Downton (4.32). Thus, none of the linearisation methods alters the solutions to equations which are already linear.

To examine the results for the X species, consider the mean of X for large t (that is, stationary). In all the linearised cases, this mean is $\hat{X}$, but this is not so with the non-linear method. However, Dietz and Downton showed that the stochastic mean is approximately $\hat{X}$ when σ, the relative death rate is small, and X is large.

Table 4.1

Ratio of stationary stochastic mean to deterministic equilibrium for X species, using different values of η and σ (defined in 4.34).

σ

η	0.2	0.6	1.0	2.0	3.0	4.0	5.0
0.2	1.088	1.379	1.695	2.503	3.318	4.135	4.952
0.6	1.040	1.203	1.398	1.919	2.456	2.999	3.543
1.0	1.025	1.134	1.264	1.614	1.975	2.338	2.704
2.0	1.013	1.070	1.135	1.297	1.451	1.600	1.745
3.0	1.009	1.047	1.089	1.185	1.267	1.340	1.408
4.0	1.007	1.035	1.066	1.132	1.184	1.227	1.264
5.0	1.005	1.028	1.052	1.102	1.139	1.168	1.192

Table 4.2

Stationary values of R_D (given in 4.36) for the X species, using different values of η and σ (4.34).

σ

η	0.2	0.6	1.0	2.0	3.0	4.0	5.0
0.2	0.093	0.371	0.579	0.870	1.016	1.102	1.160
0.6	0.042	0.242	0.486	0.999	1.338	1.566	1.728
1.0	0.026	0.160	0.352	0.895	1.374	1.759	2.065
2.0	0.014	0.079	0.172	0.493	0.904	1.358	1.824
3.0	0.009	0.051	0.106	0.277	0.499	0.771	1.085
4.0	0.007	0.038	0.075	0.179	0.298	0.438	0.600
5.0	0.006	0.030	0.058	0.129	0.200	0.276	0.358

Because Dietz and Downton's expression for the variance of X is so complicated, we will try to compare results using the numerical values (Table 4.2) they gave for the ratio R_D (4.36). In the linear cases, the ratios are given by

$$\text{Method A} : R_A = 1/\hat{X} + \alpha/\{\alpha\hat{Y}+\mu\}$$

$$\text{Method B} : R_B = \alpha/\{\alpha\hat{Y}+\mu\} \qquad\qquad (4.38)$$

$$\text{Method C} : R_C = 1/\hat{X} + \alpha/\{\alpha\hat{Y}+2\mu\} \quad .$$

In Methods A and C, the ratio involves λ, since (from equation 2.45)

$$\hat{X} = \lambda\mu/(\alpha\beta) \quad ,$$

so we cannot give a table of numerical values that will compare directly with Table 4.2. However, R_B does not involve λ, and a table of numerical values using Method B is given in Table 4.3. Comparing Tables 4.2 and 4.3, the values in 4.3 are all slightly smaller than those in 4.2, apart from the first row when

$$\eta = 0.2 \ , \quad \sigma \geqslant 2 \ , \qquad\qquad (4.39)$$

which is inaccurate due to inaccuracy of the means. When σ is small, and η large, the two Tables give very close results.

The other methods are compared using three numerical examples in Table 4.4. We saw from Table 4.1 that the stochastic mean is closest to $\hat{X}$ when $\sigma=0.2$, $\eta=5.0$. To obtain these values of σ, η, let $\mu=1$, $\alpha=0.2$ and $\beta=180$. Using these parameter values, the linearised methods should give a close approximation to the exact results. These values remain fixed for each example, only λ changes. From the

Table 4.3

Values of ratio R_B (4.38) calculated for the X species, using Method B, with different values of η and σ (4.34).

σ

η	0.2	0.6	1.0	2.0	3.0	4.0	5.0
0.2	0.082	0.324	0.556	1.053	1.452	1.778	2.049
0.6	0.038	0.169	0.294	0.541	0.714	0.842	0.940
1.0	0.024	0.114	0.200	0.364	0.474	0.552	0.610
2.0	0.013	0.063	0.111	0.200	0.257	0.296	0.325
3.0	0.009	0.043	0.077	0.138	0.176	0.203	0.221
4.0	0.007	0.033	0.059	0.105	0.134	0.154	0.168
5.0	0.005	0.027	0.048	0.085	0.108	0.124	0.135

Table, we can see that the standard deviation of X is considerably larger in Method A than the Dietz and Downton results, with Method C being higher again. The results using Method B are slightly smaller than the true solutions but appear to be very close.

Though this numerical analysis is only true for the parameter values given, we consider that this should be a good representation of the general pattern of results. Thus, because the solutions using Method B are closest to the true values, we will choose this method as the best form of probability linearisation. From now on, we will refer to Method B as the probability linearisation method.

4.3.7. Conclusion

To conclude, we have suggested a method (that is, Method B) of linearising transition probabilities, which gives approximate solutions for the stochastic moments of a non-linear process. By testing

Table 4.4

Three numerical examples showing mean and standard deviations of X and Y, calculated using each method. In all examples, $\alpha = 0.2$, $\mu = 1$, $\beta = 180$, while λ takes the values shown.

Example No.	Type of result (as $t \to \infty$)	Dietz + Downton	Method A	Method B	Method C
	E(X)	100.5	100.0	100.0	100.0
	E(Y)	180	180	180	180
1	Stan Dev(X)	12.69	15.94	12.41	15.89
($\lambda = 3600$)	Stan Dev(Y)	13.42	13.42	13.42	13.42
	CV(X)	0.1263	0.1594	0.1241	0.1589
	E(X)	150.75	150.0	150.0	150.0
	E(Y)	180	180	180	180
2	Stan Dev(X)	16.94	20.53	16.48	20.46
($\lambda = 5400$)	Stan Dev(Y)	13.42	13.42	13.42	13.42
	CV(X)	0.1124	0.1369	0.1099	0.1364
	E(X)	201	200	200	200
	E(Y)	180	180	180	180
3	Stan Dev(X)	21.05	24.82	20.40	24.71
($\lambda = 7200$)	Stan Dev(Y)	13.42	13.42	13.42	13.42
	CV(X)	0.1048	0.1240	0.1020	0.1235

it on the simple Dietz and Downton (1968) model, the linearisation method seems to be a good approximation when the death rate, α/μ, is small, and the prey population is large.

In the next section, we apply the probability linearisation method to the stable (Volterra-Gause-Witt) model, and compare the solutions with those found using Bartlett's stochastic linearisation.

4.4. Application to Stable Model

4.4.1. Moments using probability linearisation

The transition probabilities of the stochastic analogue of the stable model are

$$Pr\ [(H,P) \to (H+1,P)] = (\lambda H - cH^2)\delta t + o(\delta t)$$

$$Pr\ [(H,P) \to (H-1,P)] = \alpha HP\ \delta t + o(\delta t)$$

$$Pr\ [(H,P) \to (H,P+1)] = \beta HP\ \delta t + o(\delta t) \qquad (4.40)$$

$$Pr\ [(H,P) \to (H,P-1)] = \mu P\ \delta t + o(\delta t)\ .$$

We introduce the usual transformation

$$H = \hat{H} + h\ ,\quad P = \hat{P} + p\ , \qquad (4.41)$$

where $\hat{H}, \hat{P}$ are the deterministic equilibrium values, and h and p are small. We now linearise the transition probabilities by the method in Section 4.3.3 - for example

$$Pr\ [(H,P) \to (H+1,P)] = (\lambda H - cH^2)\delta t + o(\delta t)$$

$$= [\lambda(\hat{H}+h) - c(\hat{H}+h)^2]\delta t + o(\delta t)$$

$$= (\lambda\hat{H}+\lambda h - c\hat{H}^2 - 2c\hat{H}h)\delta t + o(\delta t) \qquad (4.42)$$

$$= [\lambda\hat{H}+\lambda(H-\hat{H})-c\hat{H}^2-2c\hat{H}(H-\hat{H})]\delta t + o(\delta t)$$

$$= [(\lambda-2c\hat{H})H + c\hat{H}^2]\ \delta t + o(\delta t)\quad.$$

The other probabilities are treated similarly, so that the new set of probabilities is

$$\Pr\ [(H,P) \rightarrow (H+1,P)] = [(\lambda-2c\hat{H})H + c\hat{H}^2]\ \delta t + o(\delta t)$$

$$\Pr\ [(H,P) \rightarrow (H-1,P)] = [\alpha\hat{P}H + \alpha\hat{H}P - \alpha\hat{H}\hat{P}]\ \delta t + o(\delta t)$$

$$\Pr\ [(H,P) \rightarrow (H,P+1)] = [\beta\hat{P}H + \beta\hat{H}P - \beta\hat{H}\hat{P}]\ \delta t + o(\delta t)\quad(4.43)$$

$$\Pr\ [(H,P) \rightarrow (H,P-1)] = \mu P\ \delta t + o(\delta t)$$

As in Section 4.3.3, using the linearity assumption, we consider that these probabilities are all greater than or equal to zero. We also assume that the population sizes remain large relative to the standard deviations, so that the chances of extinction in a finite time may be ignored (otherwise it would be possible, for example, when H is zero, to have a positive probability of a birth of H).

The forward probability equation is now formed using these transition probabilities, and the generating function equation (using the usual generating function, given in 3.5) is

$$\frac{\partial G}{\partial t} = G\ [\alpha\hat{H}\hat{P}+\beta\hat{H}\hat{P}-c\hat{H}^2+c\hat{H}^2 z_1-\alpha\hat{H}\hat{P}/z_1-\beta\hat{H}\hat{P}z_2]$$

$$+ \frac{\partial G}{\partial z_1}\ [\alpha\hat{P}-(\lambda-2c\hat{H}+\alpha\hat{P}+\beta\hat{P})z_1+(\lambda-2c\hat{H})z_1^2+\beta\hat{P}z_1 z_2]$$

$$+ \frac{\partial G}{\partial z_2} [\mu-(\alpha\hat{H}+\beta\hat{H}+\mu)z_2+\beta\hat{H}z_2^2+\alpha\hat{H}z_2/z_1] \; . \tag{4.44}$$

By differentiating equation 4.44 with respect to z_1 and z_2, and evaluating at $z_1=z_2=1$, the equations for the first two factorial moments may be found:

$$m_1'(t) = \lambda\hat{H}-c\hat{H}m_1(t)-\alpha\hat{H}m_2(t)$$

$$m_2'(t) = -\beta\hat{H}\hat{P}+\beta\hat{P}m_1(t)$$

$$V_{11}'(t) = -2\alpha\hat{H}\hat{P}+(2\lambda\hat{H}+2\lambda-4c\hat{H})m_1(t)+2\alpha\hat{H}m_2(t) \tag{4.45}$$

$$-2c\hat{H}V_{11}(t)-2\alpha\hat{H}V_{12}(t)$$

$$V_{22}'(t) = (2\beta\hat{H}-2\beta\hat{H}\hat{P})m_2(t)+2\beta\hat{P}V_{12}(t)$$

$$V_{12}'(t) = (\beta\hat{P}-\beta\hat{H}\hat{P})m_1(t)+(\lambda\hat{H}-\alpha\hat{H})m_2(t)+\beta\hat{P}V_{11}(t)$$

$$-\alpha\hat{H}V_{22}(t)-c\hat{H}V_{12}(t) \quad ,$$

where m_i and V_{ij} are the first and second factorial moments as defined in equation 3.7 and 3.8, respectively. By solving the equations in 4.45 simultaneously, time-dependent solutions may be found for the means and variances of H and P.

The means are given by

$$E(H,t) = (\beta\hat{P})^{-1} e^{-c\hat{H}t/2}[A(-c\hat{H}/2+r)e^{rt} + B(-c\hat{H}/2-r)e^{-rt}] + \hat{H}$$

$$E(P,t) = e^{-c\hat{H}t/2}[Ae^{rt} + Be^{-rt}] + \hat{P} \tag{4.46}$$

where

$$r = 1/2\sqrt{c^2\hat{H}^2 - 4\alpha\beta\hat{H}\hat{P}} \quad,$$

and A and B are constants to be determined by initial conditions. The variances and covariance of H and P are

$$\text{Var}(H,t) = \alpha\hat{H}/(\beta\hat{P})(N_1-2AB)e^{-c\hat{H}t} + (\beta\hat{P})^{-2}(-c\hat{H}/2+r)^2(N_2-A^2)e^{(-c\hat{H}+2r)t}$$

$$+ (\beta\hat{P})^{-2}(-c\hat{H}/2-r)^2(N_3-B^2)e^{(-c\hat{H}-2r)t}$$

$$+ e^{(-c\hat{H}/2+r)t}[M_1\alpha\hat{H}/(2\beta\hat{P}) + A(\beta\hat{P}^2)^{-1}(-c\hat{H}^2/2+\alpha\hat{H}\hat{P}(1-\hat{P})-r\hat{H})]$$

$$+ e^{(-c\hat{H}/2-r)t}[M_2\alpha\hat{H}/(2\beta\hat{P}) + B(\beta\hat{P}^2)^{-1}(-c\hat{H}^2/2+\alpha\hat{H}\hat{P}(1-\hat{P})+r\hat{H})]$$

$$+ \alpha(\hat{H}+\hat{P})/c \tag{4.47}$$

$$\text{Var}(P,t) = (N_1-2AB)e^{-c\hat{H}t} + (N_2-A^2)e^{(-c\hat{H}+2r)t}$$

$$+ (N_3-B^2)e^{(-c\hat{H}-2r)t}$$

$$+ [M_1 + A(1-2\hat{P})]e^{(-c\hat{H}/2+r)t} + [M_2 + B(1-2\hat{P})]e^{(-c\hat{H}/2-r)t}$$

$$+ c\hat{H}/\alpha + \beta\hat{P}(\hat{H}+\hat{P})/(c\hat{H}) \tag{4.48}$$

$$\text{Cov}(H,P,t) = -c\hat{H}(2\beta\hat{P})^{-1}(N_1-2AB)e^{-c\hat{H}t}$$

$$+ (-c\hat{H}+2r)(2\beta\hat{P})^{-1}(N_2-A^2)e^{(-c\hat{H}+2r)t}$$

$$+ (-c\hat{H}-2r)(2\beta\hat{P})^{-1}(N_3-B^2)e^{(-c\hat{H}-2r)t}$$

$$e^{(-c\hat{H}/2+r)t}[M_1(-c\hat{H}+2r)/(4\beta\hat{P}) - A(2\beta\hat{H}-c\hat{H}\hat{P}+2r\hat{P})/(2\beta\hat{P})]$$

$$+ e^{(-c\hat{H}/2-r)t}[M_2(-c\hat{H}-2r)/(4\beta\hat{P}) \tag{4.49}$$

$$+ B(-2\beta\hat{H} + c\hat{H}\hat{P} + 2r\hat{P})/2\beta\hat{P}]- \hat{H} ,$$

where

$$M_1 = 2A\{\alpha\beta\hat{H}\hat{P}(c\hat{H}+6r)\}^{-1}[c^2\hat{H}^2\beta(2\hat{H}+\hat{P}) + \alpha\beta\hat{H}\hat{P}c(\hat{P}\hat{H}-3\hat{H}-2\hat{P})$$

$$+ 2\alpha\beta^2\hat{H}\hat{P}(\hat{H}+\hat{P}) + 2\beta c\hat{H}r(2\hat{H}-\hat{P}) + 2\alpha\beta\hat{P}r(3\hat{H}\hat{P}-\hat{H}+2\hat{P})]$$

$$M_2 = 2B\{\alpha\beta\hat{H}\hat{P}(c\hat{H}-6r)\}^{-1}[c^2\hat{H}^2\beta(2\hat{H}+\hat{P}) + \alpha\beta\hat{H}\hat{P}c(\hat{P}\hat{H}-3\hat{H}-2\hat{P}) \tag{4.50}$$

$$+ 2\alpha\beta^2\hat{H}\hat{P}(\hat{H}+\hat{P}) - 2\alpha\beta c\hat{H}r(2\hat{H}-\hat{P}) - 2\alpha\beta\hat{P}r(3\hat{H}\hat{P}-\hat{H}+2\hat{P})] ,$$

and N_1, N_2, N_3 are constants of integration to be determined from the

initial conditions (of the second moments).

The solutions for the mean are identical to the results found earlier for the linearised deterministic equations (given by 2.33 and 2.34). That is, for all time t, the stochastic mean will follow the deterministic path. This path may be oscillatory or exponential depending on whether r is real or imaginary. As t gets large

$$E(H) \rightarrow \hat{H}$$

$$E(P) \rightarrow \hat{P} \ , \tag{4.51}$$

that is, the stochastic mean tends to the value of the deterministic equilibrium. On examining the results for the variance, we see that there exists at least a weakly stationary distribution – that is, stationary in the first two moments. The variances as $t \rightarrow \infty$ become

$$Var(H) \rightarrow \alpha(\hat{H} + \hat{P})/c$$

$$Var(P) \rightarrow c\hat{H}/\alpha + \beta\hat{P}(\hat{H} + \hat{P})/(c\hat{H})$$

$$Cov(H,P) \rightarrow -\hat{H} \ . \tag{4.52}$$

4.4.2 Comparison with Bartlett's results

The stationary means and variances given in 4.51 and 4.52 are identical to the stationary solutions found using Bartlett's stochastic linearisation in Section 4.2.

Although Bartlett's stochastic linearisation method has only been used to find results in the stationary case, it is possible to find time-dependent solutions. Consider, for example, the time-

dependent equation for the predators, from equation 4.5:

$$p(t+dt) = p(t) + \beta\hat{P}h(t)dt + dZ_2 \, , \tag{4.53}$$

where (from expression 4.2)

$$\text{var } dZ_2 = (\beta HP + \mu P)dt$$

$$\approx (2\beta\hat{H}\hat{P}+\beta\hat{P}h+\beta\hat{H}p+\mu p)dt \, . \tag{4.54}$$

By using the deterministic solutions for $h(t),p(t)$ (given by 2.33 and 2.34), time-dependent solutions may be found for the variances. These solutions are identical to the time-dependent solutions (4.47 - 4.49) found using the probability linearisation technique.

Hence the same results are found using probability linearisation and stochastic linearisation. However, the probability linearisation method relies on fewer assumptions. In the stochastic linearisation method, Bartlett assumed that the stochastic mean follows the equilibrium path, and that the stochastic equations can be approximated by the deterministic equations. No such assumption is made with the probability linearisation method - in this case the solutions for the moments are found using the forward probability equation. The equations using this method are also easier to solve. A further advantage of the probability linearisation technique will be seen when looking at the continuous approximation in Section 4.6.

4.5. Application to Unstable Model

As explained above, the probability linearisation method does not rely on the existence of a stationary distribution, and so can easily be applied to the unstable (Lotka-Volterra) model.

The moment equations are found by letting c equal zero in

equation 4.45. From this the means of the process are seen to be

$$E(H,t) = \hat{H} + A \sqrt{\lambda\mu} \, (\beta\hat{P})^{-1} \cos (\sqrt{\lambda\mu}t + B)$$

$$E(P,t) = \hat{P} + A \sin (\sqrt{\lambda\mu}t + B) \quad , \tag{4.55}$$

where A and B are constants to be determined by initial conditions. The variances and covariance of H and P are

$$Var(H,t) = N_1 \alpha\hat{H}(\beta\hat{P})^{-1} + \beta^{-1}(\alpha+\mu-\lambda)\hat{H} - \hat{H}^2 - \lambda\mu A^2(2\beta\hat{P}^2)^{-1}$$

$$- N_2 \alpha\hat{H}(\beta\hat{P})^{-1}\sin (2 \sqrt{\lambda\mu}t+N_3)$$

$$- \left[A^2\lambda\mu(\beta\hat{P})^{-2}/2\right] \cos (2 \sqrt{\lambda\mu}t+2B)$$

$$- A \sqrt{\lambda\mu}(3\beta\hat{P}^2)^{-1}(4\hat{H}+\hat{P})\cos (\sqrt{\lambda\mu}t+B)$$

$$+ A2\alpha\hat{H}(3\beta\hat{H}\hat{P})^{-1}(\hat{H}+\hat{P})\sin (\sqrt{\lambda\mu}t+B) + \alpha\hat{H}(\hat{P}+\hat{H})t \tag{4.56}$$

$$Var(P,t) = N_1 + \hat{P}(1-\hat{P}) - A^2/2 + N_2\sin (2 \sqrt{\lambda\mu}t+N_3)$$

$$+(A^2/2) \cos (2 \sqrt{\lambda\mu}t+2B)$$

$$- \left[A2\beta(\hat{P}+\hat{H})/(3 \sqrt{\lambda\mu})\right] \cos (\sqrt{\lambda\mu}t+B)$$

$$+\left[A(4\hat{P}+\hat{H})/(3\hat{H})\right] \sin (\sqrt{\lambda\mu}t+B) + \beta\hat{P}(\hat{P}+\hat{H})t \tag{4.57}$$

$$\text{Cov}(H,P,t) = (\hat{P}-\hat{H})/2 + \left[N_2 \sqrt{\lambda\mu}/(\beta\hat{P})\right] \cos (2 \sqrt{\lambda\mu}\,t+N_3)$$

$$- \left[A^2 \sqrt{\lambda\mu}/(2\beta\hat{P})\right] \sin (2 \sqrt{\lambda\mu}\,t+2B)$$

$$+ \left[A \sqrt{\lambda\mu}(2\hat{P}-\hat{H})/(3\beta\hat{H}\hat{P})\right] \cos (\sqrt{\lambda\mu}\,t+B)$$

$$+ \left[A(\hat{P}-2\hat{H})/(3\hat{P})\right] \sin (\sqrt{\lambda\mu}\,t+B) \quad , \tag{4.58}$$

where the N_i are constants of integration to be determined from initial conditions.

By comparing the solution for the means with expression 2.9, the solution for the linearised deterministic equations, we see that the stochastic means again follow the deterministic path. Thus the stochastic means follow cycles of constant amplitude oscillations, showing that no stationary probability distribution exists for this model. Because the stochastic means are periodic, we might expect that the probability distribution is periodic in time. On examining the variances, though, we see that they contain not only periodic terms, but also terms which are linear in t. This means that, as t goes to infinity, the variances become infinite, and so the probability distribution cannot be periodic.

This analysis, however, is based on the assumption that extinction can be ignored. In practice, extinction may occur very quickly - simulations performed by Bartlett (1957) showed that extinction of one or other species usually occurred after two or three cycles. If the time to extinction is short, these solutions might not give a good approximation to the behaviour of the system.

4.6. Continuous Approximation using Linearisation

4.6.1. Simplified stochastic differential equation

An important advantage of the probability linearisation technique is that the stochastic differential equation, introduced in Section 3.7.2, can be simplified. As we shall show in Section 4.6.2, the equation can now be solved using a solution from Arnold (1974), to give an approximate solution for the probability distribution of the stable model.

Consider the stable predator-prey model, and linearise in the usual way so that the new set of transition probabilities is given by 4.43. Recall, from equation 3.52, that the stochastic differential equation is given by

$$d\underline{X}(t) = \underline{B}(\underline{x},t)dt + \underline{A}^{1/2}(\underline{x},t)\underline{Z}(t)\sqrt{dt} \quad , \tag{4.59}$$

where $\underline{X}(t)$, $\underline{A}$, $\underline{B}$, $Z(t)$ are as defined in Section 3.7.2. The matrices $\underline{A}$ and $\underline{B}$ are matrices of the instantaneous means and variances (Section 3.7.1) of the process. When the transition probabilities of the process are linearised, the new instantaneous means and variances, calculated as in Section 3.7.1, but using the probabilities 4.43, are now

$$b_1 = -c\hat{H}x_1 - \alpha\hat{H}x_2 + \lambda\hat{H}$$

$$b_2 = \beta\hat{P}x_1 - \beta\hat{H}\hat{P}$$

$$a_{11} = (2\alpha\hat{P}-c\hat{H})x_1 + \alpha\hat{H}x_2 + c\hat{H}^2 - \alpha\hat{H}\hat{P} \tag{4.60}$$

$$a_{22} = \beta \hat{P} x_1 + 2\beta \hat{H} x_2 - \beta \hat{H} \hat{P}$$

$$a_{12} = a_{21} = 0 \quad .$$

4.6.2. Arnold's solution

The stochastic differential equation considered by Arnold (1974) was

$$d\underline{X}(t) = (C_1 \underline{X}(t) + C_2)dt + C_3 d\underline{W}(t) , \qquad (4.61)$$

with $\underline{X}(0) = \underline{x}_0$ and $0 < t < T$, and where $\underline{W}$ is a Wiener process (for the definition of a Wiener process, see Cox and Miller, 1965). The C_1's are matrices of constants, with C_1 and C_3 of order nxn, and C_2 of order nx1. Arnold found that the process, $\underline{X}(t)$, which satisfies equation 4.61, has an n-dimensional Normal distribution with mean and variance given by

$$m_t(\underline{x}_0) = e^{C_1 t} [\underline{x}_0 + (\int_0^t e^{-C_1 u} du)C_2]$$

$$V_t(\underline{x}_0) = \int_0^t e^{C_1(t-u)} C_3 C_3^T e^{C_1^T(t-u)} du , \qquad (4.62)$$

where C_3^T denotes the transpose of C_3.

To solve our equation (4.59), we rewrite it in the form used by Arnold. Let

$$C_1 = \begin{bmatrix} -c\hat{H} & -\alpha\hat{H} \\ \beta\hat{P} & 0 \end{bmatrix}$$

$$C_2 = (\lambda \hat{H} , -\beta \hat{H} \hat{P})^T . \tag{4.63}$$

As $\underline{Z}(t) \sqrt{dt}$ represents the increments of a Wiener process (see Cox and Miller, 1965), we may write this as $d\underline{W}$. Because C_3 (in 4.61) is a matrix of constants with no dependence on x_i, we must approximate the x_i in the elements of $\underline{A}$ (4.60) by the deterministic equilibrium. That is, we rewrite the a_{ij} using

$$x_1 \approx \hat{H} , \quad x_2 \approx \hat{P} . \tag{4.64}$$

C_3 can now be written as

$$C_3 = \text{Diag} \{(2\alpha \hat{H} \hat{P})^{1/2} , (2\beta \hat{H} \hat{P})^{1/2} \} \tag{4.65}$$

where

$$\text{Diag} \{a, b\} \equiv \begin{bmatrix} a & 0 \\ 0 & b \end{bmatrix} .$$

Thus, using the assumption that we may calculate the a_{ij}'s at the deterministic equilibrium, our equation (4.59) can be written in Arnold's form (4.61). Then, by Arnold, an approximate solution for the probability distribution of the stable model is the two-dimensional Normal distribution, with mean and variance given by 4.62. We will calculate this mean and variance in the next two sections.

4.6.3. Calculation of mean

To calculate the exponential of a matrix, we use the technique of expanding it in terms of the eigenvalues, and row and column eigenvectors (see Bartlett, 1978). In this way, we may write $e^{-C_1 t}$ as

$$e^{-C_1 t} = e^{-c\hat{H}t/2} [e^{rt}R_1 + e^{-rt}R_2] \qquad (4.66)$$

where

$$r^2 = c^2\hat{H}^2/4 - \alpha\beta\hat{H}\hat{P}$$

$$R_1 = \begin{bmatrix} (c\hat{H}+2r)/4r & [(c\hat{H}/2)^2 - r^2]/(\beta\hat{P}2r) \\ -\beta\hat{P}/2r & -(c\hat{H}-2r)/4r \end{bmatrix}$$

$$R_2 = \begin{bmatrix} -(c\hat{H}-2r)/4r & [(c\hat{H}/2)^2 - r^2]/(\beta\hat{P}2r) \\ \beta\hat{P}/2r & (c\hat{H}+2r)/4r \end{bmatrix} . \qquad (4.67)$$

Because R_1 and R_2 are constructed from row and column eigenvectors, respectively, they have the following properties:

$$R_1 R_2 = R_2 R_1 = 0 ,$$

$$R_1^2 = R_1 , \quad R_2^2 = R_2 . \qquad (4.68)$$

From 4.62, we can now write the mean as

$$m_t(\underline{x}_0) = e^{-c\hat{H}t/2}[e^{rt}R_2 + e^{-rt}R_1]$$

$$x \{\underline{x}_0 + (c\hat{H}/2+r)^{-1}[e^{(c\hat{H}/2+r)t} - 1]R_1 C_2 \qquad (4.69)$$

$$+ (c\hat{H}/2-r)^{-1}[e^{(c\hat{H}/2-r)t} - 1]R_2 C_2\} .$$

Because

$$|c\hat{H}/2| > |r| , \qquad (4.70)$$

when t gets very large, the terms which are exponentially damped become negligible. Then as t gets large, expression 4.69 tends to

$$\lim_{t \to \infty} m_t(\underline{x}_0) \to [(c\hat{H}/2-r)^{-1}R_2 + (c\hat{H}/2+r)^{-1}R_1]C_2$$

$$= (\hat{H}, \hat{P})^T \quad . \tag{4.71}$$

Note that, as t gets very large, the mean is no longer dependent on the initial value $\underline{x}_0$. Asymptotically, the stochastic mean of the continuous approximation is equal to the deterministic equilibrium.

4.6.4. Calculation of variance

Recall from 4.62, that the variance matrix is given by

$$V_t(\underline{x}_0) = \int_0^t e^{C_1(t-u)} C_3 C_3^T e^{C_1^T(t-u)} du \quad . \tag{4.72}$$

Using the expansion of the exponential from 4.66, this may be written as

$$V_t(\underline{x}_0) = \int_0^t e^{-c\hat{H}(t-u)} [e^{r(t-u)}R_2 + e^{-r(t-u)}R_1]$$

$$\times \, 2\hat{H}\hat{P} \, \text{Diag}\{\alpha, \beta\} [e^{r(t-u)}R_2^T + e^{-r(t-u)}R_1^T] du$$

$$= e^{-c\hat{H}t} \left[e^{2rt}(c\hat{H}-2r)^{-1} \{e^{(c\hat{H}-2r)t} - 1\} R_2 C_3 C_3^T R_2^T \right.$$

$$+ (c\hat{H})^{-1}(e^{c\hat{H}t}-1)R_2 C_3 C_3^T R_1^T + (c\hat{H})^{-1}(e^{c\hat{H}t}-1)R_1 C_3 C_3^T R_2^T$$

$$+ e^{-2rt}(c\hat{H}+2r)^{-1} \{e^{(c\hat{H}+2r)t}-1\}R_1 C_3 C_3^T R_1^T \Bigg] \quad . \qquad (4.73)$$

As t gets large, exponentially damped terms will become negligible, and the variance tends to

$$\lim_{t \to \infty} V_t(\underline{x}_0) = [(c\hat{H}-2r)^{-1}R_2 C_3 C_3^T R_2^T + (c\hat{H}+2r)^{-1}R_1 C_3 C_3^T R_1^T$$

$$+ (c\hat{H})^{-1}(R_1 C_3 C_3^T R_2^T + R_2 C_3 C_3^T R_1^T)] \quad , \qquad (4.74)$$

which is again independent of the initial values. The variance of H may be found from the (1,1) component of the variance matrix, which is

$$-\hat{H}\hat{P}/(2r^2)\Bigg[(c\hat{H}-2r)^{-1}\{\alpha(c\hat{H}/2-r)^2 + (\beta\hat{P}^2)^{-1}\{(c\hat{H}/2)^2-r^2\}^2\}$$

$$- 2(c\hat{H})^{-1}\{\alpha\{(c\hat{H}/2)^2-r^2\} + (\beta\hat{P}^2)^{-1}\{(c\hat{H}/2)^2-r^2\}^2\}$$

$$+ (c\hat{H}+2r)^{-1}\{\alpha(c\hat{H}/2+r)^2 + (\beta\hat{P}^2)^{-1}\{(c\hat{H}/2)^2-r^2\}^2\}\Bigg] \quad . \qquad (4.75)$$

This simplifies to

$$\alpha(\hat{H} + \hat{P})/c \quad .$$

The variance of P may be found similarly from the (2,2) component, and the covariance from the (1,2) or (2,1) component.

To summarise, in the limit as $t \to \infty$, the variances and covariances are given by

$$\text{Var (H)} = \alpha(\hat{H} + \hat{P})/c$$

$$\text{Var } (P) = \beta \hat{P}^2/(c\hat{H}) + \beta \hat{P}/c + c\hat{H}/\alpha \qquad\qquad (4.76)$$

$$\text{Cov } (H,P) = -\hat{H} \quad .$$

4.6.5. Conclusion

By approximating the discrete state space of the stable model by one which is continuous, a stochastic differential equation was formed. Using the probability linearisation technique, this was simplified to a form for which a solution could be found. From Arnold's results, we saw that an approximate soution for the probability distribution is the two-dimensional Normal distribution, for all time t, with the formulae for the mean and variance given by expression 4.62. Although it is possible to calculate time-dependent moments from these formulae, it is mathematically very tedious. The asymptotic moments found are identical to those previously calculated using stochastic linearisation (Section 4.2) and probability linearisation in the discrete state space (Section 4.4).

The main advantage to this approach is that it provides an approximate solution not only for the moments, but also the shape of the distribution – that is, two-dimensional Normal. Recall that, in Section 3.6, Bartlett (1978) approximated the stochastic behaviour of a single species undergoing a birth-death process by a Normal distribution, but, previously, no theoretical justification could be found for this in the two-species case. In the next section, we shall consider a numerical example in order to investigate how close the Normal approximation is to the exact distribution.

Another advantage of using this method is that the stochastic differential equation, 4.61, has been solved in n dimensions. As we shall see in Chapter 7, this will be useful when studying the multi-

colony spatial model.

4.7. Numerical Example

4.7.1. Iterated probability distribution

We now wish to test the accuracy of the approximate solution for the probability distribution of the stable model, which we found in the last section. We do this by calculating the distribution of the original, non-linear, discrete process for a given set of parameter values, using an iterative procedure. A comparison is made, in Section 4.7.3, between the computed distribution and the Normal distribution for these parameters.

The forward probability equation of the stable model (using non-linear transition probabilities), for large t, is

$$p_{ij}[(\lambda - ci)i + (\alpha + \beta)ij + \mu j] =$$

$$[\lambda - c(i-1)](i-1)p_{i-1,j} + \alpha(i+1)jp_{i+1,j} \qquad (4.77)$$

$$+ \beta i(j-1)p_{i,j-1} + \mu(j+1)p_{i,j+1} \quad .$$

Starting from a specified initial distribution, we will make successive approximations of the distribution using 4.77. Thus, if $p_{ij}^{(n)}$ denotes the n'th successive approximation, then $p_{ij}^{(n+1)}$ is calculated from

$$p_{ij}^{(n+1)} = \left[[\lambda - c(i-1)](i-1)p_{i-1,j}^{(n)} + \alpha(i+1)jp_{i+1,j}^{(n)} \right.$$

$$\left. + \beta i(j-1)p_{i,j-1}^{(n)} + \mu(j+1)p_{i,j+1}^{(n)} \right]$$

$$x \ [(\lambda - ci)i + (\alpha + \beta)ij + \mu j]^{-1} \ . \qquad (4.78)$$

By repeated use of 4.78, we can approximate the probability distribution for a given set of parameter values.

The parameters used in the example are

$$\alpha = 1.2, \qquad \lambda = 270,$$

$$\beta = 0.5, \qquad \mu = 50,$$

$$c = 1.5. \qquad (4.79)$$

These parameters were chosen, because, in order to have a good approximation, it was necessary to have fairly large equilibrium values, but relatively small standard deviations. The theoretical means and variances for these parameters (calculated from 4.71 and 4.76) are

$$E(H) = 100, \qquad E(P) = 100,$$

$$Var(H) = 160, \qquad Var(P) = 191.667,$$

$$Cov(H,P) = -100. \qquad (4.80)$$

In theory, the state space of the process is infinite. To calculate the probabilities using 4.78, it is necessary to put bounds on i and j. In our example, we constrain i and j to lie between 50 and 150, by allowing no births to occur at 150, and no deaths at 50. These bounds are 3.95 standard deviations from the equilibrium for the prey, and 3.61 standard deviations for the predators. If we assume

that most non-zero probabilities lie within three standard deviations on either side of the equilibrium, then these bounds should not greatly alter the probability distribution.

Successive approximations for the probability distribution are found until the distribution settles - that is, when the difference between the successive approximations is negligible. Figure 4.1 shows a contour map of the computed probability distribution. In order to avoid possible edge effects, the p_{ij} for i=51,150, j=51,60 and j=141,150 are set to zero (in the final approximation), and the probabilities are rescaled so that the remaining probabilities sum to one.

4.7.2. Normal distribution

The two-dimensional Normal distribution using the means and variances given in 4.80 is calculated, and a contour map drawn in the same way, shown in Figure 4.2. In order to keep the distributions on the same scale, the edge probabilities are set to zero as above, and the remaining probabilities rescaled. This made very little differ-ence to the graph in this case, as most non-zero probabilities lay between j=60, and j=140.

4.7.3. Comparison

The iterated distribution, Figure 4.1, and the Normal distribu-tion, Figure 4.2, appear to be quite similar in shape. The iterated distribution appears slightly flatter and more spread out. This is evident from the fact that the Normal graph has an extra contour and the ellipses appear a bit shorter than those in Figure 4.1. There also seems to be a slight skewness in Figure 4.1 - particularly when the number of prey is small and the number of predators large.

From the iterative solution, we calculated the first two moments
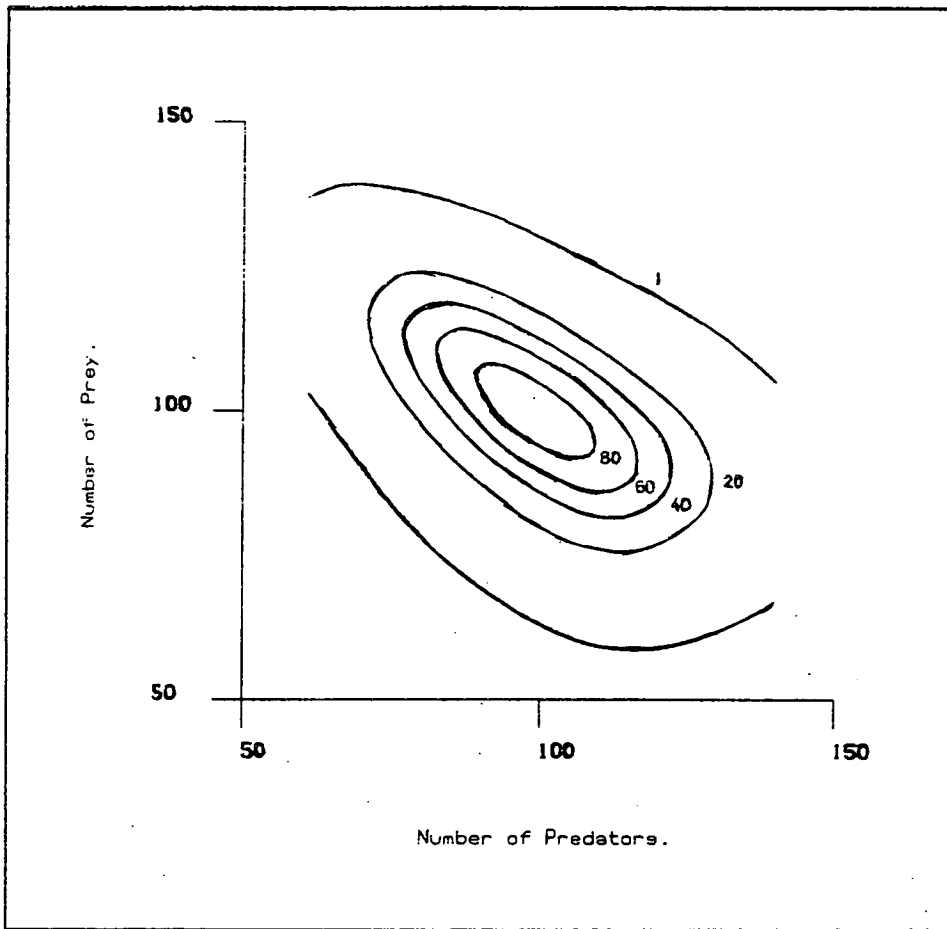
Figure 4.1. Contour map of the stationary distribution of the stable model, calculated through the iterative procedure described in 4.7.1, using the parameters given in 4.79. The figure on each curve is a probability value $\times 10^5$, showing the minimum probability value within the region enclosed by each contour.

to be

$$E(H) = 99.38, \qquad E(P) = 100.11,$$

$$\text{Var}(H) = 162.07, \qquad \text{Var}(P) = 231.96,$$

$$\text{Cov.}(H,P) = -114.44. \tag{4.81}$$

These appear to be very close to the theoretical calculations (4.80),

though the variance of P is somewhat larger. It is interesting to
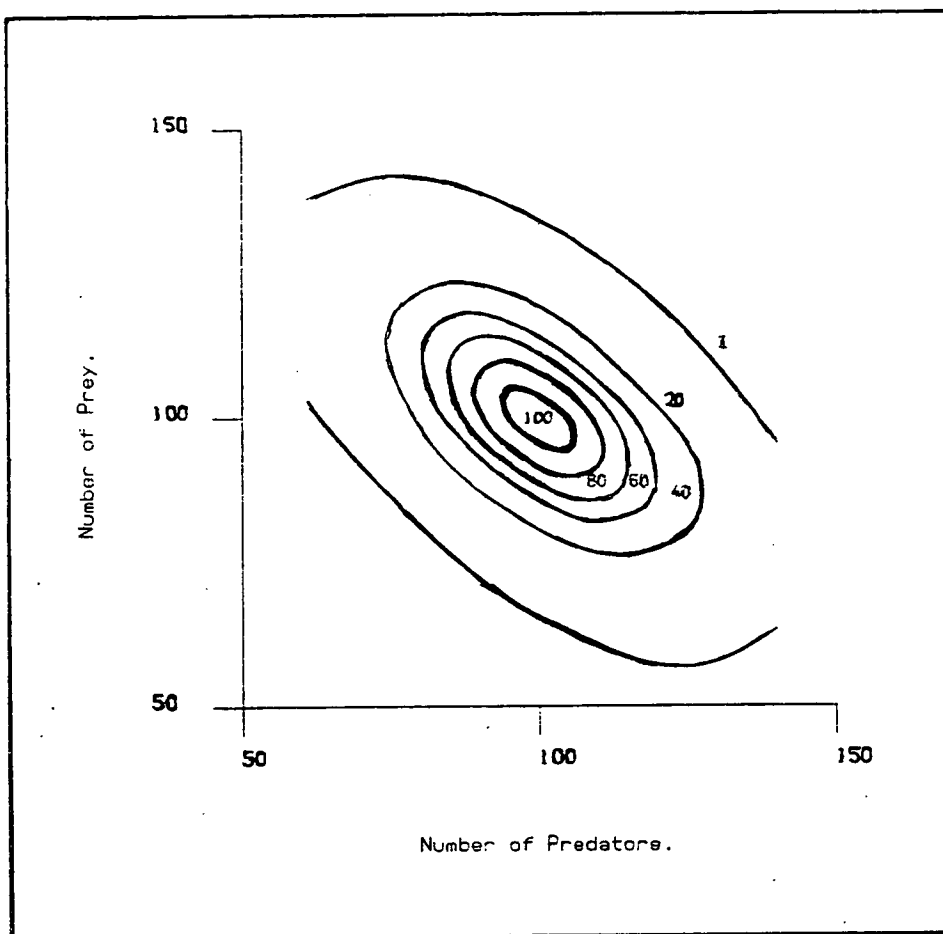
Figure 4.2. Contour map of Normal distribution using the means and variances given in 4.80. The figure on each curve is a probability value $x10^5$, showing the minimum probability value within the region enclosed by each contour.

note that Leslie and Gower (1958,1960) (see Section 3.3) calculated variances of competition processes by simulation, and also found that theoretical variances calculated using stochastic linearisation were always smaller than variances computed from simulations.

4.8. Conclusion

In this chapter, three methods of finding moments of the distributions of stochastic predator-prey processes were discussed.

The first method, known as Bartlett's stochastic linearisation, was described, and the stationary means and variances for the stable model found.

In the second method, the transition probabilities were linearised, thus simplifying the generating function equation so that time-dependent means and variances could be found. Three methods of linearising probabilities were discussed in relation to a simple model (Dietz and Downton, 1968), and the most accurate method chosen. This linearisation technique was applied to both the stable and unstable models and time-dependent moments found. The stable model solutions are identical to those found using Bartlett's method, but this technique makes fewer assumptions.

The third method used this probability linearisation technique in the continuous state space approximation. This enabled the stochastic differential equation to be simplified so that an approximate solution could be found for the distribution of the stable model. The solution showed that the process was the two-dimensional Normal distribution with asymptotic mean and variance identical to those previously found. To test the accuracy of this solution, a numerical example was given, in which the probability distribution of the original process was computed using an iterative procedure, and compared with the approximating Normal distribution. There was good agreement between the distributions, though the theoretical variances seemed to be smaller than the observed ones, especially in the predator case.

Of course, one major simplifying assumption used in all these methods is that of linearity. Nisbet and Gurney (1982) said that in practice they found that with stochastic models whose deterministic analogues have a single, stable equilibrium value, then locally linear approximations lead to a good estimate of the probability distribution (though I did not see any justification of this in their book). They claimed that it is only necessary to include non-linear effects when models have an unstable equilibrium, or two or more locally stable steady states. Our numerical results on stable models

(Sections 4.3 and 4.7) indicate that linearisation produces good approximations when population numbers are large.

CHAPTER 5

TWO-COLONY DETERMINISTIC MODELS

5.1. Introduction

In all the models considered in Chapters 2 - 4, no account has been made for spatial variability. The populations have been treated as though they were amassed at one point in space, with the same birth and death rates applying to all. In order to introduce the idea of allowing for variation through spatial separation, we consider here two-colony models - that is, the populations are divided into two interconnected colonies, each of which undergoes a predator-prey process. Later on, in Chapter 7, we will make this 'spatial' process less restrictive by extending the number of colonies.

The general two-colony model is introduced in Section 5.2. Because the linear solution to this model is too mathematically complicated to explain the behaviour of the populations, we shall examine some special cases of it by placing restrictions on migration. In Section 5.3, we demand that the individuals migrate at the same rate in both directions. A comparison is made between this model and the general one-colony (that is, non-spatial) model given in Section 2.4. Using the two-colony extensions of the stable and unstable models, we then study the effect of one-way migration of a species - first allowing prey to migrate (Section 5.4) and then predators (Section 5.5).

5.2. General Two-Colony Model

We introduce the deterministic two-colony model by looking at the linearised equations of the model with general migration rates.

Let $H_i(t)$ denote the number of prey at time t, and $P_i(t)$ the number of predators, in colony i, for $i=1,2$. Suppose that the prey (predators) can migrate from colony 1 to colony 2 at rate $\eta_1(\nu_1)$, and from colony 2 to colony 1 at rate $\eta_2(\nu_2)$. These migration rates are illustrated in Figure 5.1.
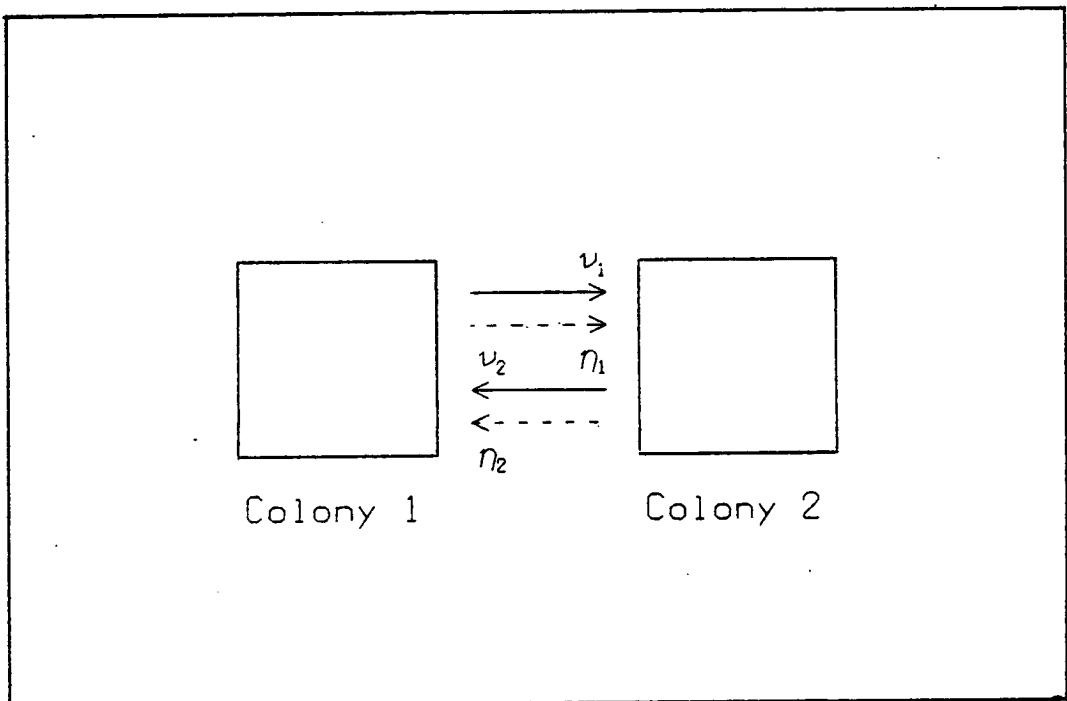
Figure 5.1. Diagram showing two prey migration rates, with - - - representing migration of the prey, and ——— the predators.

The deterministic equations of the two-colony model are

$$\dot{H}_1 = F(H_1,P_1) + \eta_2 H_2 - \eta_1 H_1$$

$$\dot{P}_1 = G(H_1,P_1) + \nu_2 P_2 - \nu_1 P_1$$

$$\dot{H}_2 = F(H_2, P_2) + \eta_1 H_1 - \eta_2 H_2 \qquad (5.1)$$

$$\dot{P}_2 = G(H_2, P_2) + \nu_1 P_1 - \nu_2 P_2 \quad,$$

where F and G are general quadratic functions of the H_i and P_i (as in the single-colony case, 2.18). Assume that the system 5.1 has an equilibrium value at

$$\hat{H}_1, \quad \hat{P}_1, \quad \hat{H}_2, \quad \hat{P}_2$$

(though, in the general model, these values may be difficult to determine). Using the transformation

$$H_i(t) = \hat{H}_i + h_i(t)$$

$$P_i(t) = \hat{P}_i + p_i(t) \quad, \qquad (5.2)$$

where h_i, p_i are small, we may write the equations in linear form:

$$\dot{h}_1 = a_1 h_1 + b_1 p_1 + \eta_2 h_2$$

$$\dot{p}_1 = e_1 h_1 + f_1 p_1 + \nu_2 p_2$$

$$\dot{h}_2 = a_2 h_2 + b_2 p_2 + \eta_1 h_1 \qquad (5.3)$$

$$\dot{p}_2 = e_2 h_2 + f_2 p_2 + \nu_1 p_1 \quad.$$

The coefficients in 5.3 are calculated in the same way as in Section 2.4.1 - for example

$$a_1 = \left. \frac{\partial F}{\partial H_1} \right|_E - \eta_1 \quad,$$

where by $|_E$ we mean evaluation at the equilibrium point. System 5.3 may be written in matrix form as

$$\dot{U} = A\, U \tag{5.4}$$

where

$$U = (h_1,\ p_1,\ h_2,\ p_2)^T$$

and

$$A = \begin{bmatrix} a_1 & b_1 & \eta_2 & 0 \\ e_1 & f_1 & 0 & \nu_2 \\ \eta_1 & 0 & a_2 & b_2 \\ 0 & \nu_1 & e_2 & f_2 \end{bmatrix} .$$

The solution to the equation 5.4 is given by

$$U(t) = e^{At}\, C , \tag{5.5}$$

where C is a 4x1 vector of initial values of h_i and p_i. Calculation of e^{At} in 5.5 may be simplified by finding the eigenvalues of A. From matrix algebra (see Liebeck, 1969), we know that, if the eigenvalues are all distinct, we may write

$$A = P\, N\, P^{-1} ,$$

where N is a diagonal matrix, so that

$$e^A = P\, e^N\, P^{-1} .$$

If two (say) eigenvalues are equal, using Jordan decomposition (see Lang, 1971), the problem of finding e^A is reduced to finding the exponential of a 2x2 matrix.

Thus, when an equilibrium exists, it is possible to find the linear solution to the general two-colony model. However, mathematically, this solution is very involved - to find the equilibrium values, we must solve four simultaneous quadratic equations, and the eigenvalues are the roots of a quartic polynomial. If we were to write the solution (5.5) in terms of the parameters of the model, owing to the mathematical complexity, it would give us no *ready* indication of the behaviour of the model. For this reason, we will look at special cases only of the two-colony process, by placing certain restrictions on the migration rates.

5.3. Equal Migration Parameters

5.3.1. Solution

Suppose in the two-colony model described by 5.1, we assume that the migration parameters are equal in both directions. That is, we assume that

$$\eta_1 = \eta_2 \equiv \eta \ , \qquad \nu_1 = \nu_2 \equiv \nu \ . \tag{5.6}$$

An equilibrium value occurs at

$$\hat{H}_1 = \hat{H}_2 \qquad , \qquad \hat{P}_1 = \hat{P}_2 \ .$$

We will solve the equations near this point. The equilibrium values are now solutions of the four equations

$$F(H_i, P_i) = 0$$

$$G(H_i, P_i) = 0 \qquad i=1,2. \tag{5.7}$$

Furthermore, these values satisfy the same equations as the one-colony equilibrium values (2.19). Then if $\hat{H}$ and $\hat{P}$ are the one-colony

equilibrium values, as a result of the constraint 5.6, we have

$$\hat{H}_1 = \hat{H}_2 = \hat{H}$$

$$\hat{P}_1 = \hat{P}_2 = \hat{P} \ . \tag{5.8}$$

Although we could find the solution of this model using the method previously considered (Section 5.2), it is easier to proceed in the following way.

The equations are linearised as before, using the transformation 5.2. But now write the linearised system as

(i) $\quad \dot{h}_1 = C_1 h_1 + C_2 p_1 + \eta(h_2 - h_1)$

(ii) $\quad \dot{p}_1 = C_3 h_1 + C_4 p_1 + \nu(p_2 - p_1)$

(iii) $\quad \dot{h}_2 = C_1 h_2 + C_2 p_2 + \eta(h_1 - h_2)$ $\tag{5.9}$

(iv) $\quad \dot{p}_2 = C_3 h_2 + C_4 p_2 + \nu(p_1 - p_2) \ ,$

where the C_i's are as defined in the one-colony situation (2.21), namely

$$C_1 = \left.\frac{\partial F}{\partial H_i}\right|_E \ , \qquad C_2 = \left.\frac{\partial F}{\partial P_i}\right|_E \ ,$$

$$C_3 = \left.\frac{\partial G}{\partial H_i}\right|_E \ , \qquad C_4 = \left.\frac{\partial G}{\partial P_i}\right|_E \ .$$

The equations are written in this form in order to separate the migration effects (governed by η and ν) from the interaction terms

(the C_i's). Because these C_i terms are the same as in the one-colony model, this should emphasise the effect of migration here.

Let

$$U(t) = h_1(t) + h_2(t)$$

$$V(t) = p_1(t) + p_2(t) . \qquad (5.10)$$

Then, by adding (i) to (iii), and (ii) to (iv) in equation 5.9, we get

$$\dot{U} = C_1 U + C_2 V$$

$$\dot{V} = C_3 U + C_4 V . \qquad (5.11)$$

These equations have the same form as the one-colony case, and so the solutions are the same, apart from the constants which are determined by initial conditions. For example, in the case where $r_1 \neq 0$ and $C_3 \neq 0$ (from 2.22)

$$U(t) = e^{(C_1 + C_4)t/2} (C_3)^{-1} [\{ (C_1 - C_4)/2 + r_1 \} A_T e^{r_1 t}$$

$$+ \{ (C_1 - C_4)/2 - r_1 \} B_T e^{-r_1 t}]$$

$$V(t) = e^{(C_1 + C_4)t/2} [A_T e^{r_1 t} + B_T e^{-r_1 t}] , \qquad (5.12)$$

where

$$r_1 = 1/2 \sqrt{(C_1 - C_4)^2 + 4 C_2 C_3} ,$$

and A_T and B_T are determined by initial conditions. (As in the one-colony model, this solution is only valid provided it is non-divergent, that is

$$C_1 + C_4 < 0 \quad \text{and} \quad 1/2 \left| C_1 + C_4 \right| > \left| r_1 \right| .$$

If these conditions do not hold, the solution to the model is divergent, and cannot be found in this way.) Other forms of the solution (as in 2.23 - 2.25) follow similarly.

We use the results for U and V to find the h_1 and p_1 solutions in the following way. From 5.10, we have

$$h_2 = U - h_1 , \qquad p_2 = V - p_1 . \tag{5.13}$$

Then, we may rewrite equations (i) and (ii) from 5.9 as

$$\text{(i)} \quad \dot{h}_1 = (C_1 - 2\eta)h_1 + C_2 p_1 + \eta U$$

$$\text{(ii)} \quad \dot{p}_1 = C_3 h_1 + (C_4 - 2\nu)p_1 + \nu V . \tag{5.14}$$

Substituting (ii) into (i), we form an equation for p_1 :

$$\ddot{p}_1 - \dot{p}_1[(C_4 - 2\nu) + (C_1 - 2\eta)] + p_1[(C_1 - 2\eta)(C_4 - 2\nu) - C_2 C_3]$$

$$= C_3 \eta U + \nu \dot{V} - \nu(C_1 - 2\eta)V . \tag{5.15}$$

From this equation, the solution for $p_1(t)$ may be calculated, and is given below. The solution for $h_1(t)$ is found from equation 5.14(i), and those for $h_2(t)$ and $p_2(t)$ from

$$h_2 = U - h_1 , \qquad p_2 = V - p_1 .$$

Thus, the full solution to the linearised equations (5.9) is

$$h_1(t) = e^{(C_1+C_4-\theta)t/2} [e^{r_2 t}\{(C_1-C_4)/2+(\nu-\eta)+r_2\}A_1/C_3$$

$$+ e^{-r_2 t}\{(C_1-C_4)/2+(\nu-\eta)-r_2\}B_1/C_3]$$

$$+ e^{(C_1+C_4)t/2} [e^{r_1 t}\{(C_1-C_4)/2+r_1\}A_T/(2C_3)$$

$$+ e^{-r_1 t}\{(C_1-C_4)/2-r_1\}B_T/(2C_3)] \qquad (5.16)$$

$$P_1(t) = e^{(C_1+C_4-\theta)t/2} [A_1 e^{r_2 t} + B_1 e^{-r_2 t}]$$

$$+ e^{(C_1+C_4)t/2} [e^{r_1 t}A_T/2 + e^{-r_1 t}B_T/2] \qquad (5.17)$$

$$h_2(t) = e^{(C_1+C_4-\theta)t/2} [e^{r_2 t}\{(C_1-C_4)/2+(\nu-\eta)+r_2\}(-A_1)/C_3$$

$$+ e^{-r_2 t}\{(C_1-C_4)/2+(\nu-\eta)-r_2\}(-B_1)/C_3]$$

$$+ e^{(C_1+C_4)t/2} [e^{r_1 t}\{(C_1-C_4)/2+r_1\}A_T/(2C_3)$$

$$+ e^{-r_1 t}\{(C_1-C_4)/2-r_1\}B_T/(2C_3)] \qquad (5.18)$$

$$P_2(t) = e^{(C_1+C_4-\theta)t/2} [-A_1 e^{r_2 t} - B_1 e^{-r_2 t}]$$

$$+ e^{(C_1+C_4)t/2} [e^{r_1 t} A_T/2 + e^{-r_1 t} B_T/2] \quad , \tag{5.19}$$

where

$$\theta = 2(\nu + \eta)$$

$$r_1 = 1/2 \sqrt{(C_1-C_4)^2 + 4C_2C_3} \tag{5.20}$$

$$r_2 = 1/2 \sqrt{[(C_1-2\eta)-(C_4-2\nu)]^2 + 4C_2C_3} \quad ,$$

and A_1, B_1, A_T, B_T are constants to be determined from initial conditions.

5.3.2. Analysis

By imposing the constraint that the migration rates are equal in both directions, we saw that the equilibrium values became equal, and identical to the one-colony equilibrium. Adding the equations for the prey perturbations, and the predator perturbations, we found solutions for the total fluctuations, U and V. The U and V solutions, for all time t, are identical to the one-colony result, except for the initial conditions. If the initial conditions are the same in both systems, the total prey, and predator, fluctuations in the two-colony model will be equal to the one-colony fluctuations.

Looking at the individual solutions in the two-colony model, the format is identical in both colonies. The solutions in both colonies have the same time-dependence, the only difference being in the constant coefficients. As t gets large, so that the first section, governed by $e^{(C_1+C_4-\theta)t/2}$, becomes negligible, the solutions become identical, and equal to the one-colony result (subject to the same initial conditions).

Hence, by splitting the populations into two colonies, and allowing individuals to migrate with equal rates in both directions, no long-term alteration is made to the non-spatial model. In particular, the one-colony solution is stable about the equilibrium point if, and only if, the two-colony solution is stable.

5.3.3. Predator-prey application

As with the one-colony case in Chapter 2, the solutions to this general two-species model may of course by applied to the simpler predator-prey models - in particular, to the stable model (both colonies undergoing a Volterra-Gause-Witt process) and the unstable model (two-colony Lotka-Volterra). In the stable model, all perturbations eventually decay to zero, whereas, in the unstable model, when t is large, the populations in each colony will oscillate in phase with each other with period $2\pi/\sqrt{\lambda\mu}$ and with the same amplitude.

5.4. One-Way Migration of Prey

5.4.1. Introduction

When migration between colonies is in one direction only, the equilibrium values are no longer equal, and the solution is more complicated than in the last section. So, instead of studying the effects of migration of prey on the general quadratic system, we will look at its effects first on the stable model (5.4.2) and then the unstable model (5.4.3). In Section 5.5, we will consider the effect of migration of predators.

5.4.2. Stable model

Let η be the migration rate of prey from colony 1 to colony 2. Then the model (represented by Figure 5.2) is defined by the deter-

ministic equations

$$\dot{H}_1 = \lambda H_1 - cH_1^2 - \alpha H_1 P_1 - \eta H_1$$

$$\dot{P}_1 = \beta H_1 P_1 - \mu P_1$$

$$\dot{H}_2 = \lambda H_2 - cH_2^2 - \alpha H_2 P_2 + \eta H_1 \qquad\qquad (5.21)$$

$$\dot{P}_2 = \beta H_2 P_2 - \mu P_2 \quad .$$
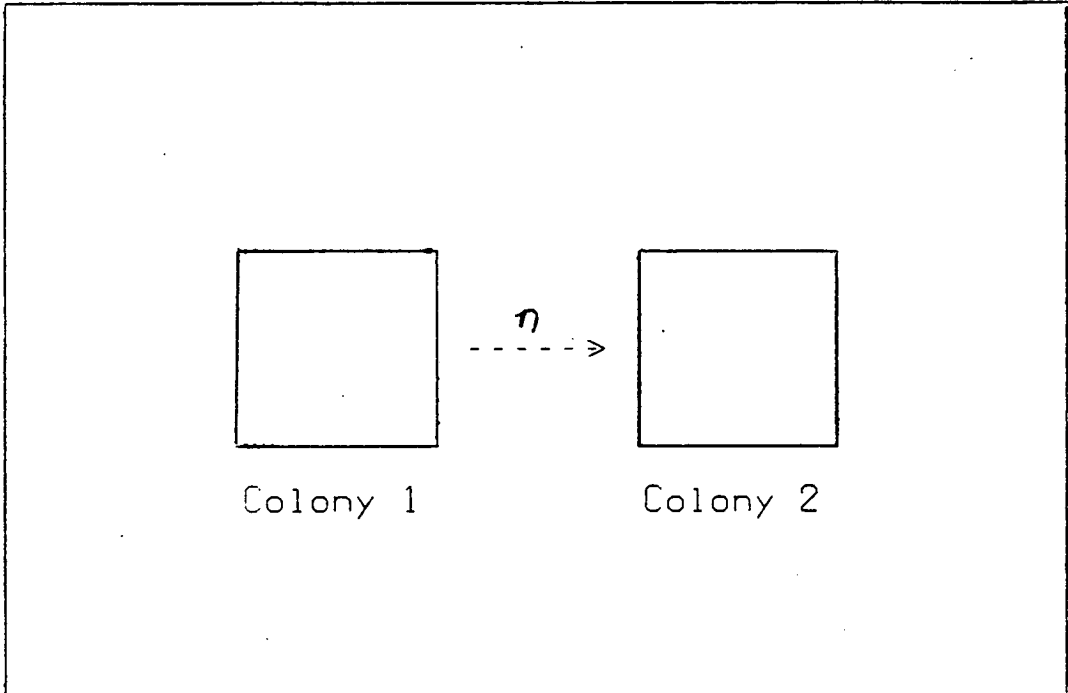
Figure 5.2. Two-colony model, with one-way migration of prey.

The deterministic equilibrium, found by setting these equations equal to zero, occurs at

$$\hat{H}_1 = \mu/\beta , \qquad\qquad \hat{H}_2 = \mu/\beta ,$$

$$\hat{P}_1 = (\lambda - c\hat{H}_1 - \eta)/\alpha , \qquad \hat{P}_2 = (\lambda - c\hat{H}_2 + \eta)/\alpha . \qquad (5.22)$$

In order that these equilibrium values remain greater than zero, it is necessary to impose the constraint on η that

$$\eta < \lambda - c\hat{H}_1 . \qquad (5.23)$$

Intuitively, a maximum value imposed on η is necessary, because, if η is very large, all the prey from colony 1 will soon migrate into colony 2, and then the predators in the first colony will become extinct.

By linearising the equations in the usual way, we have

$$\text{(i)} \quad \dot{h}_1 = -c\hat{H}_1 h_1 - \alpha\hat{H}_1 P_1$$

$$\text{(ii)} \quad \dot{p}_1 = \beta\hat{P}_1 h_1$$

$$\text{(iii)} \quad \dot{h}_2 = -c\hat{H}_2 h_2 - \alpha\hat{H}_2 P_2 + \eta(h_1 - h_2) \qquad (5.24)$$

$$\text{(iv)} \quad \dot{p}_2 = \beta\hat{P}_2 h_2 .$$

Equations (i) and (ii) from 5.24 are identical to the equations in the one-colony case, and hence the solution (2.33 and 2.34) is

$$h_1(t) = e^{-c\hat{H}_1 t/2}[A(-c\hat{H}_1/2 + r_1)e^{r_1 t}$$

$$+ B(-c\hat{H}_1/2 - r_1)e^{-r_1 t}]/(\beta\hat{P}_1)$$

$$p_1(t) = e^{-c\hat{H}_1 t/2}[Ae^{r_1 t} + Be^{-r_1 t}] , \qquad (5.25)$$

where

$$r_1 = 1/2 \sqrt{c^2\hat{H}_1^2 - 4\alpha\beta\hat{H}\hat{P}} ,$$

and A and B are determined by initial conditions. Using 5.25, the other two equations in 5.24 solve to give

$$h_2(t) = e^{-(c\hat{H}_2+\eta)t/2} (\beta\hat{P}_2)^{-1} [A_2(-c\hat{H}_2/2-\eta/2+r_2)e^{r_2 t}$$

$$+ B_2(-c\hat{H}_2/2-\eta/2-r_2)e^{-r_2 t}]$$

$$+ e^{-c\hat{H}_1 t/2} (\beta\hat{P}_2)^{-1} [(-c\hat{H}_1/2+r_1)X_1 e^{r_1 t}$$

$$+ (-c\hat{H}_1/2-r_1)X_2 e^{-r_1 t}]$$

$$p_2(t) = e^{-(c\hat{H}_2+\eta)t/2} [A_2 e^{r_2 t} + B_2 e^{-r_2 t}] \tag{5.26}$$

$$+ e^{-c\hat{H}_1 t/2} [X_1 e^{r_1 t} + X_2 e^{-r_2 t}] ,$$

where

$$X_1 = \frac{\hat{P}_2/\hat{P}_1 \; \eta A(-c\hat{H}_1/2+r_1)}{(-c\hat{H}_1/2+r_1)^2 + (c\hat{H}_2+\eta)(-c\hat{H}_1/2+r_1) + \alpha\beta\hat{H}_2\hat{P}_2}$$

$$X_2 = \frac{\hat{P}_2/\hat{P}_1 \; \eta B(-c\hat{H}_1/2-r_1)}{(-c\hat{H}_1/2-r_1)^2 + (c\hat{H}_2+\eta)(-c\hat{H}_1/2-r_1) + \alpha\beta\hat{H}_2\hat{P}_2} \tag{5.27}$$

and

$$r_2 = 1/2 \sqrt{(c\hat{H}_2+\eta)^2 - 4\alpha\beta\hat{H}_2\hat{P}_2} \; ,$$

and A_2, B_2 are constants.

Thus, migration of prey has the effect of reducing the predator equilibrium in colony 1, and increasing it in colony 2. Because of this (to stop $\hat{P}_1$ becoming zero), the migration parameter has an upper bound (given by 5.23). From equation 5.25, we see that the solution to the first colony has the same format as the single-colony solution (equations 2.33, 2.34) - except that $\hat{P}_1$ here is less than $\hat{P}$, the one-colony predator equilibrium. The h_2, p_2 solutions have an extra term, governed by the damping factor $e^{-(c\hat{H}_2+\eta)t/2}$. Because $\eta > 0$, this term decays first, and the solution is then in the single-colony format.

Migration of prey appears to have a stronger effect on the second colony than on the first. This we might expect, because migration out of the first colony is effectively increasing the death rate and should not drastically alter the solution. But migration into the second colony is exerting an extra force on the behaviour of the prey. This has no lasting effect, however, since, as t goes to ∞, the perturbations decay to zero, and the system returns to equilibrium.

5.4.3. Unstable model

A more interesting result appears in the model where both colonies undergo the Lotka-Volterra process. The solution to this model may be found by letting c equal zero in the model in 5.4.2. Thus, the equilibrium of the unstable model occurs at

$$\hat{H}_1 = \mu/\beta , \qquad \hat{H}_2 = \mu/\beta ,$$

$$\hat{P}_1 = (\lambda-\eta)/\alpha , \qquad \hat{P}_2 = (\lambda+\eta)/\alpha . \qquad (5.28)$$

The constraint 5.23 on η, changes to

$$\eta < \lambda .$$

It is easier to examine the effects of migration if we assume the initial conditions

$$h_1(0) = h_2(0) = p_2(0) = 0 , \quad p_1(0) = k , \qquad (5.29)$$

as these correspond to the initial conditions (2.10) which we assumed in the one-colony solution. Under conditions 5.29, the first colony solutions are

$$h_1(t) = -k\theta_1/(\beta\hat{P}_1) \sin \theta_1 t$$

$$p_1(t) = k \cos \theta_1 t , \qquad (5.30)$$

where

$$\theta_1 = \{\alpha\beta\hat{H}_1\hat{P}_1\}^{1/2} = \{\mu(\lambda-\eta)\}^{1/2} .$$

The second colony solution, which may be found from 5.26, has an additional term exponentially damped by $e^{-\eta t/2}$. As t increases, these solutions become

$$h_2(t) = \frac{-k\theta_1^2}{\beta\hat{P}_1(4\mu^2+\theta_1^2)} \sin (\theta_1 t+\delta)$$

$$P_2(t) \approx \frac{k\hat{P}_2 \theta_1}{\hat{P}_1(4\mu^2 + \theta_1^2)} \cos(\theta_1 t + \delta) , \qquad\qquad (5.31)$$

where

$$\delta = \tan^{-1} 2\sqrt{\mu/(\lambda - \eta)} .$$

As $t \to \infty$, both colonies experience constant amplitude oscillations of period $2\pi/\theta_1$. This period is greater than in the single-colony case, because $\hat{P}_1$ here is less than $\hat{P}$ in 2.11. However, the colonies are no longer oscillating in phase — colony 2 now leads colony 1 with a phase difference, given by δ. As η increases to its maximum λ, this phase difference increases.

Although this chapter is concerned with deterministic models, it seems more suitable to mention here, rather than in Chapter 6, what one possible consequence of these results might be for stochastic models. It may be possible that, in a stochastic environment, extinction of a species in a fixed time might be connected with the period of oscillation. We make this suggestion for the following reason. If two species are oscillating about a point, on every cycle each species will reach a minimum value. Allowing for statistical fluctuations, the chances of a species becoming extinct near this minimum value are high. The more cycles that occur in a fixed time t, the more often this minimum is reached, increasing the chances of extinction. If this is so, then allowing one-way migration of prey should increase the chances of survival of both species.

5.5. One-Way Migration of Predators

5.5.1. Stable model

Having looked at the effect of prey migration, we will now see

how these results are altered when predators migrate instead. Suppose the predators migrate from colony 1 to colony 2 at rate ν (see Figure 5.3).
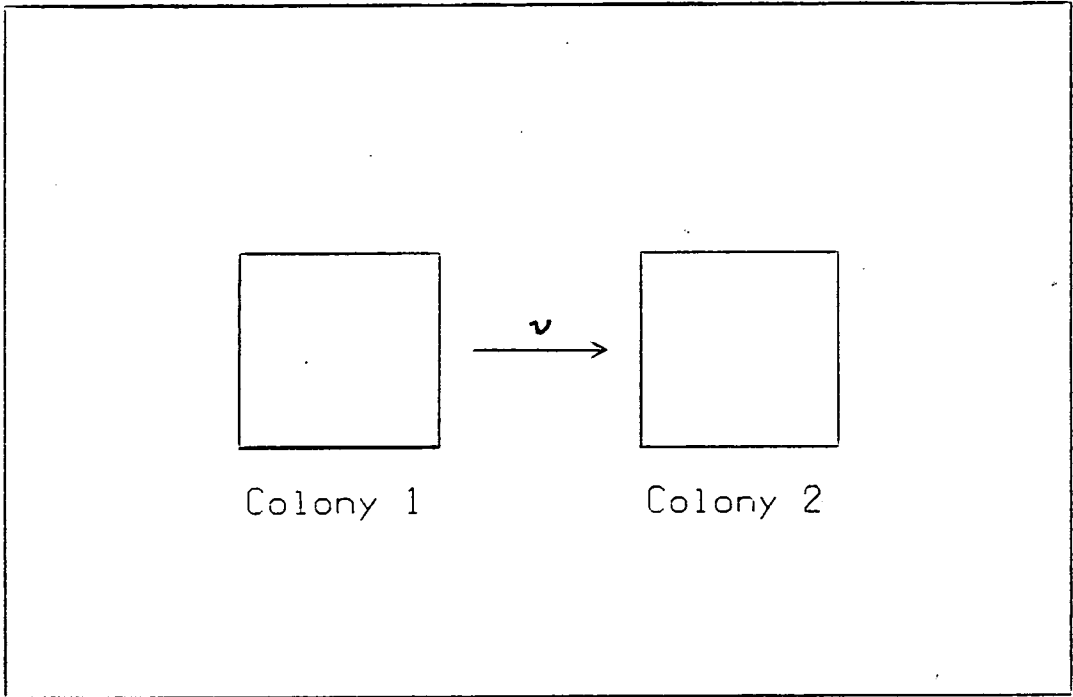
Figure 5.3. Two-colony model, with one-way migration of predators.

The model is then defined by the equations:

$$\dot{H}_1 = \lambda H_1 - c H_1^2 - \alpha H_1 P_1$$

$$\dot{P}_1 = \beta H_1 P_1 - \mu P_1 - \nu P_1$$

$$\dot{H}_2 = \lambda H_2 - c H_2^2 - \alpha H_2 P_2 \tag{5.32}$$

$$\dot{P}_2 = \beta H_2 P_2 - \mu P_2 + \nu P_1 \quad .$$

The equilibrium occurs at

$$\hat{H}_1 = (\mu + \nu)/\beta$$

$$\hat{P}_1 = (\lambda - c\hat{H}_1)/\alpha = (\lambda\beta - c\mu - c\nu)/(\alpha\beta)$$

$$\hat{H}_2 = (\lambda\beta + c\mu - a)/(2\beta c) \tag{5.33}$$

$$\hat{P}_2 = (\lambda\beta - c\mu + a)/(2\alpha\beta) \quad ,$$

where

$$a = \sqrt{(\lambda\beta + c\mu)^2 + 4\beta c(\alpha\nu\hat{P}_1 - \lambda\mu)} \quad .$$

We know that $\hat{H}_2$ and $\hat{P}_2$ are always real, because a may be written as

$$a = \sqrt{(\lambda\beta - c\mu)^2 + 4\alpha\beta c\nu\hat{P}_1} \quad .$$

In order that $\hat{P}_1, \hat{H}_2$ and $\hat{P}_2$ stay greater than zero, it is necessary to restrict ν to

$$0 < \nu < (\lambda\beta - c\mu - a_1)/(2c)$$

$$(\lambda\beta - c\mu + a_1)/(2c) < \nu < (\lambda\beta - c\mu)/c \quad ,$$

$$\text{where } a_1 = \sqrt{(\lambda\beta - c\mu)^2 - 4\lambda\beta c\mu} \quad , \tag{5.34}$$

that is, ν may only take values that lie within the shaded regions A and B of Figure 5.4. The constraints placed on ν are different from the upper bound found for η in the last section, for the following reason. In region A, an increase in ν raises $\hat{H}_1$ and lowers $\hat{H}_2$. To keep $\hat{H}_2$ greater than zero, an upper limit is put on ν, namely

$$\nu < (\lambda\beta - c\mu - a_1)/(2c) \quad .$$
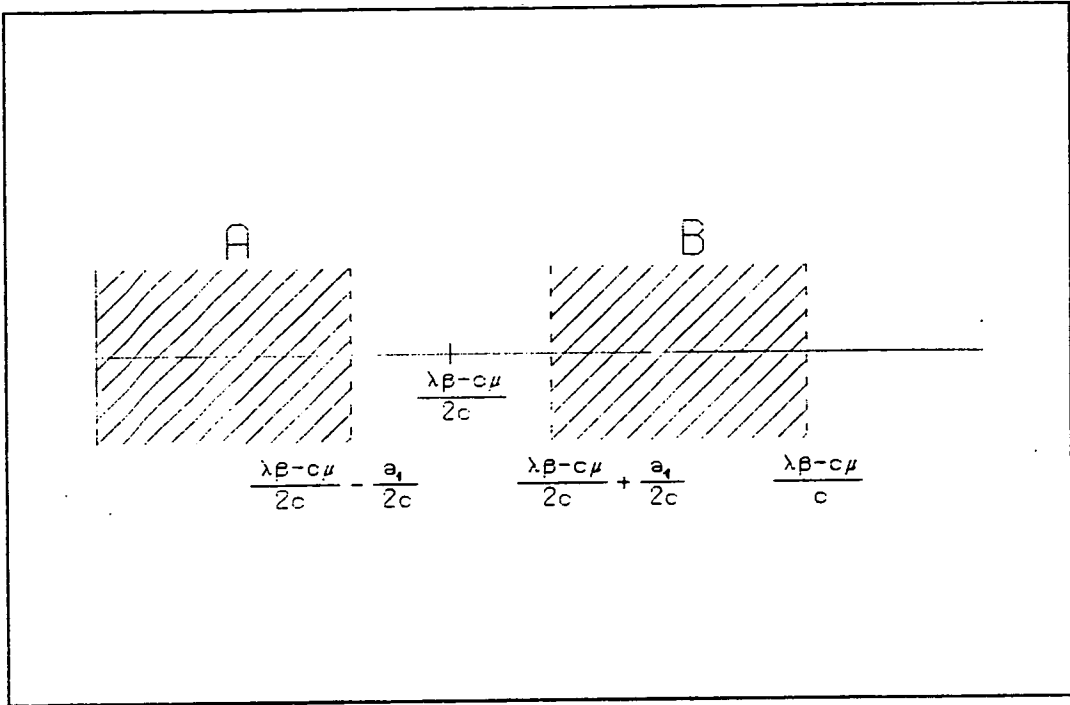
Figure 5.4. Shaded regions, A and B, show possible sections of the real line in which ν may lie, subject to the constraints in 5.34.

But, because $\hat{P}_1$ is dependent on $\hat{H}_1$, an increase in ν decreases $\hat{P}_1$. Thus, $\nu\hat{P}_1$ reaches a maximum when

$$\nu = (\lambda\beta - c\mu)/(2c) \ .$$

In region B, $\nu\hat{P}_1$ is decreasing, allowing $\hat{H}_2$ to increase.

The linearised equations are

$$\dot{h}_1 = -c\hat{H}_1 h_1 - \alpha\hat{H}_1 P_1$$

$$\dot{P}_1 = \beta\hat{P}h_1$$

$$\dot{h}_2 = -c\hat{H}_2 h_2 - \alpha\hat{H}_2 P_2 \qquad (5.35)$$

$$\dot{p}_2 = \beta \hat{P}_2 h_2 + (\beta \hat{H}_2 - \mu) p_2 + \nu p_1 ,$$

which solve to give

$$h_1(t) = e^{-c\hat{H}_1 t/2} (\beta \hat{P}_1)^{-1} [A_1(-c\hat{H}_1/2 + r_1) e^{r_1 t}$$

$$+ B_1(-c\hat{H}_1/2 - r_1) e^{-r_1 t}]$$

$$p_1(t) = e^{-c\hat{H}_1 t/2} [A_1 e^{r_1 t} + B_1 e^{-r_1 t}]$$

$$h_2(t) = e^{-(c\hat{H}_2 - \beta \hat{H}_2 + \mu)t/2} [A_T e^{r_2 t} + B_T e^{-r_2 t}] \qquad (5.36)$$

$$+ e^{-c\hat{H}_1 t/2} [X_1 e^{r_1 t} + X_2 e^{-r_2 t}]$$

$$p_2(t) = e^{-(c\hat{H}_2 - \beta \hat{H}_2 + \mu)t/2} [e^{r_2 t}(-c\hat{H}_2 - \beta \hat{H}_2 + \mu - 2r_2) A_T/(2\alpha \hat{H}_2)$$

$$+ e^{-r_2 t}(-c\hat{H}_2 - \beta \hat{H}_2 + \mu + 2r_2) B_T/(2\alpha \hat{H}_2)]$$

$$+ e^{-c\hat{H}_1 t/2} [e^{r_1 t}\{(-c\hat{H}_1/2 + r_1)(-X_1)/(\alpha \hat{H}_2) - cX_1/\alpha\}$$

$$+ e^{-r_1 t}\{(c\hat{H}_1/2 + r_1)X_2/(\alpha \hat{H}_2) - cX_2/\alpha\}] ,$$

where

$$r_1 = 1/2 \sqrt{(c\hat{H}_1)^2 - 4\alpha\beta\hat{H}_1\hat{P}_1}$$

$$r_2 = 1/2 \sqrt{(c\hat{H}_2+\beta\hat{H}_2-\mu)^2 - 4\alpha\beta\hat{H}_2\hat{P}_2}$$

$$X_1 = \frac{-\alpha\hat{H}_2\nu A_1}{(-c\hat{H}_1/2+r_1)^2+(c\hat{H}_2-\beta\hat{H}_2+\mu)(-c\hat{H}_1/2+r_1)+\alpha\beta\hat{H}_2\hat{P}_2-c\hat{H}_2(\beta\hat{H}_2-\mu)}$$

$$X_2 = \frac{-\alpha\hat{H}_2\nu B_1}{(-c\hat{H}_1/2-r_1)^2+(c\hat{H}_2-\beta\hat{H}_2+\mu)(-c\hat{H}_1/2-r_1)+\alpha\beta\hat{H}_2\hat{P}_2-c\hat{H}_2(\beta\hat{H}_2-\mu)} \quad (5.37)$$

and A_1, B_1, A_T, B_T are constants determined by initial conditions.

To check that these solutions converge, recall that ν is bounded by the constraints in 5.34, which ensures that $\hat{H}_2 < \mu/\beta$. This means that the factor

$$-(c\hat{H}_2-\beta\hat{H}_2+\mu) < 0 ,$$

and so, the exponential of this term acts as a damping factor for h_2 and p_2. We can see that

$$\frac{1}{2}\left|c\hat{H}_2-\beta\hat{H}_2+\mu\right| > \left|r_2\right| ,$$

$$\hat{H}_2 < (\lambda\beta + c\mu)/(2\beta c) ,$$

which is always true when ν is bounded. This shows that the first term in h_2 and p_2 is always damped and goes to zero as t goes to infinity.

Thus, as $t \to \infty$, the perturbations decay to zero and the system returns to equilibrium, showing that migration of predators has no

lasting effect on the model.

5.5.2. Unstable model

The effect of one-way migration of predators on the unstable (Lotka-Volterra) model may be seen by examining equations 5.32, and setting c equal to zero. Because the $\hat{P}_i$ do not depend on the $\hat{H}_i$, the equilibrium is in simpler form:

$$\hat{H}_1 = (\mu + \nu)/\beta , \qquad \hat{H}_2 = (\mu - \nu)/\beta ,$$

$$\hat{P}_1 = \lambda/\alpha , \qquad \hat{P}_2 = \lambda/\alpha . \qquad (5.38)$$

The constraint on ν is simplified to

$$\nu < \mu . \qquad (5.39)$$

The linearised solution to the model may be found from 5.36 by letting c equal zero. Subject to the initial conditions

$$h_1(0) = h_2(0) = p_2(0) = 0 , \quad p_1(0) = k ,$$

the solution, for large t, is

$$h_1(t) = -k(\beta \hat{P}_1)^{-1} \sqrt{\lambda(\mu + \nu)} \sin \sqrt{\lambda(\mu + \nu)}t$$

$$p_1(t) = k \cos \sqrt{\lambda(\mu + \nu)}t$$

$$h_2(t) \approx -k\alpha\hat{H}_2(4\lambda + \mu + \nu)^{-1} \sin (\sqrt{\lambda(\mu + \nu)}t - \delta) \qquad (5.40)$$

$$p_2(t) = k(4\lambda + \mu + \nu)^{-1} \sqrt{\lambda(\mu + \nu)} \cos (\sqrt{\lambda(\mu + \nu)}t - \delta)$$

where

$$\delta = \tan^{-1} 2 \sqrt{\lambda/(\mu+\nu)} \quad .$$

Thus, when t is large, the predators and prey in both colonies oscillate with constant amplitude, and period $2\pi/\sqrt{\lambda(\mu+\nu)}$. This period is shorter than in the single-colony case. If we again consider that, in a stochastic model, extinction of a species is related to the period of oscillation, then allowing predators to migrate appears to decrease the chances of survival of both species.

The colonies oscillate out of phase with each other, but this time the second colony lags the first with a phase lag given by δ. As ν increases, the phase lag decreases. This we might expect, since the larger the migration parameter becomes, the weaker is the effect of spatial separation.

5.6. Conclusion

When the populations are split into two colonies with equal migration rates between the colonies, the spatial separation has very little effect on the behaviour of the populations. As $t\to\infty$, the solutions reduce to the one-colony case, and, for t finite, the solutions sum together to give the one-colony result.

When migration is allowed in one direction only, a more pronounced effect may be seen. In the stable model, as $t\to\infty$, all perturbations from the equilibrium value decay to zero. In the unstable model, as $t\to\infty$, the solutions oscillate with constant amplitude, but the colonies are out of phase. When only migration of prey is possible, colony 2 leads colony 1, but when predators migrate, colony 2 lags colony 1. The period of oscillation is also altered - when prey migrate, the period is greater than that of the one-colony solution,

and when predators migrate, it is less. Though migration does not alter the deterministic stability of these models, it is possible that, in the stochastic situation, the chance of extinction by time t (assuming it is related to the period of oscillation) is increased by predators migrating, and decreased if prey migrate.

We have only considered the above special cases of the two-colony predator-prey process because of the mathematical complications involved in the more general model. In particular, we have always assumed equal birth and death rates in each colony. When conditions in the colonies are unequal, the equations become a lot more complicated, partly because of the difficulty of finding equilibrium values. One way of avoiding this problem was suggested by Chewning (1975). He examined the effect of migration between unequal colonies, subject to the constraint that the migration parameters are small. He calculated the equilibrium value which would occur in each colony if no migration were allowed, and then devised a method of linearising the equations (with migration) about this point. He derived a set of sufficient (but not necessary) conditions under which migration can stabilise a locally unstable system. In particular, he showed that it is possible for migration to stabilise a two-colony Lotka-Volterra system, if the parameters of the process are different in each colony.

CHAPTER 6

TWO-COLONY STOCHASTIC MODELS

6.1. Introduction

In Chapter 4, three different methods for studying stochastic models were developed - Bartlett's linearisation, probability linearisation and the continuous approximation. Here we will use these methods to examine the effect of migration on the stochastic model.

The model we study is the stable model where predators are allowed to migrate in both directions with the same migration rate, ν. We choose this model because the identical migration rates simplify the problem, as we will see later. Although it is also possible to study the effect of migration of prey using these methods, for mathematical convenience, this has been omitted. The model is investigated using Bartlett's linearisation in Section 6.2, probability linearisation in Section 6.3 and the continuous approximation in Section 6.4. The results using these methods are compared with the one-colony soution in Section 6.5, and the effect of the migration parameter ν, is analysed.

Finally, in Section 6.6, a less restrictive two-colony model is considered, and the general form of its stochastic behaviour is given.

6.2. Bartlett's Linearisation

As mentioned in Section 6.1, the model under investigation is

the two-colony stable model in which predators migrate in both directions at the same rate ν. This model (represented by Figure 6.1) is the stochastic analogue of the model defined deterministically as

$$\dot{H}_1 = (\lambda - cH_1)H_1 - \alpha H_1 P_1$$

$$\dot{P}_1 = \beta H_1 P_1 - \mu P_1 - \nu P_1 + \nu P_2$$

$$\dot{H}_2 = (\lambda - cH_2)H_2 - \alpha H_2 P_2 \tag{6.1}$$

$$\dot{P}_2 = \beta H_2 P_2 - \mu P_2 + \nu P_1 - \nu P_2 \ .$$
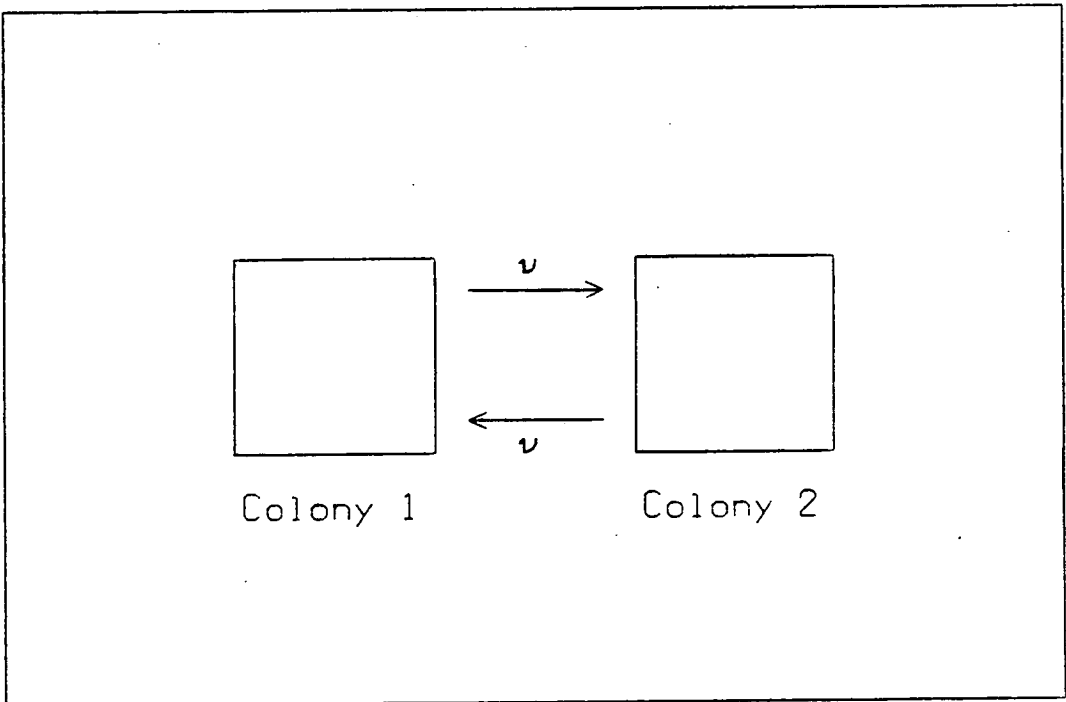
Figure 6.1. Two-colony model with migration of predators only.

The deterministic equilibrium values are equal in each colony (Section 5.3) and occur at

$$\hat{H}_1 = \hat{H}_2 = \frac{\mu}{\beta} \equiv \hat{H}$$

$$\hat{P}_1 = \hat{P}_2 = \frac{\lambda - c\hat{H}}{\alpha} \equiv \hat{P} \ . \tag{6.2}$$

To extend Bartlett's method, given in Section 4.2, approximate the stochastic behaviour of the system by adding small fluctuation terms to the deterministic equations:

$$dH_1 = [(\lambda - cH_1)H_1 - \alpha H_1 P_1]dt + dZ_1$$

$$dP_1 = [\beta H_1 P_1 - \mu P_1 + \nu(P_2 - P_1)]dt + dZ_2 - dZ_5 + dZ_6$$

$$dH_2 = [(\lambda - cH_2)H_2 - \alpha H_2 P_2]dt + dZ_3 \tag{6.3}$$

$$dP_2 = [\beta H_2 P_2 - \mu P_2 + \nu(P_1 - P_2)]dt + dZ_4 + dZ_5 - dZ_6$$

where the dZ_i are independent random variables, with zero means, and variances given by

$$\text{var}(dZ_1) = [(\lambda - cH_1)H_1 + \alpha H_1 P_1]dt$$

$$\text{var}(dZ_2) = [\beta H_1 P_1 + \mu P_1]dt$$

$$\text{var}(dZ_3) = [(\lambda - cH_2)H_2 + \alpha H_2 P_2]dt$$

$$\text{var}(dZ_4) = [\beta H_2 P_2 + \mu P_2]dt \tag{6.4}$$

$$\text{var}(dZ_5) = \nu P_1 dt$$

$$\text{var } (dZ_6) = \nu P_2 dt \text{ .}$$

Introduce the transformation

$$H_i = \hat{H} + h_i \text{ , } \qquad P_i = \hat{P} + p_i \text{ , } \tag{6.5}$$

where h_i and p_i are small, and linearise equations 6.3 to get

$$h_1(t+dt) = h_1(t) + dt[-c\hat{H}h_1 - \alpha\hat{H}p_1] + dZ_1$$

$$p_1(t+dt) = p_1(t) + dt[\beta\hat{P}h_1 + \nu(p_2-p_1)] + dZ_2 - dZ_5 + dZ_6$$

$$h_2(t+dt) = h_2(t) + dt[-c\hat{H}h_2 - \alpha\hat{H}p_2] + dZ_3 \tag{6.6}$$

$$p_2(t+dt) = p_2(t) + dt[\beta\hat{P}h_2 + \nu(p_1-p_2)] + dZ_4 + dZ_5 - dZ_6 \text{ .}$$

As in Section 4.2.1, assume that the chances of extinction by time t may be ignored and a quasi-stationary distribution exists. Then, as t gets large,

$$E[h_i(t+dt)^2] \approx E[h_i(t)^2] \equiv \sigma_{h_i}^2 \qquad i=1,2$$

$$E[p_i(t+dt)^2] \approx E[p_i(t)^2] \equiv \sigma_{p_i}^2 \qquad i=1,2$$

$$E[h_i(t+dt)p_j(t+dt)] \approx E[h_i(t)p_j(t)] \equiv \sigma_{h_ip_j} \qquad i,j=1,2$$

$$E[h_1(t+dt)h_2(t+dt)] \approx E[h_1(t)h_2(t)] \equiv \sigma_{h_1h_2}$$

$$E[p_1(t+dt)p_2(t+dt)] \approx E[p_1(t)p_2(t)] \equiv \sigma_{p_1 p_2}. \qquad (6.7)$$

To find the variances of the deviations, square and cross-multiply all the equations in 6.6 and take the expectations. This gives ten equations in the ten unknowns defined in 6.7. However, in our model, the migration parameters are identical, so that, when t is large, the influences on the behaviour of the populations are the same in both colonies. For this reason, we assume that the following identities should hold:

$$\sigma_{h_1}^2 = \sigma_{h_2}^2 \qquad \sigma_{p_1}^2 = \sigma_{p_2}^2$$

$$\sigma_{h_1 p_1} = \sigma_{h_2 p_2} \qquad \sigma_{h_1 p_2} = \sigma_{h_2 p_1}. \qquad (6.8)$$

(Using this assumption it is possible to find a solution, which has been checked by back substitution into the equations.) This reduces the set of simultaneous equations to the following six:

$$-c\hat{H}\sigma_{h_1}^2 - \alpha\hat{H}\sigma_{h_1 p_1} + \alpha\hat{H}\hat{P} = 0$$

$$\beta\hat{P}\sigma_{h_1 p_1} + \nu(\sigma_{p_1 p_2} - \sigma_{p_1}^2) + (\mu+\nu)\hat{P} = 0$$

$$\beta\hat{P}\sigma_{h_1}^2 + \nu\sigma_{h_1 p_2} - \alpha\hat{H}\sigma_{p_1}^2 - (c\hat{H}+\nu)\sigma_{h_1 p_1} = 0$$

$$\beta\hat{P}\sigma_{h_1 h_2} + \nu\sigma_{h_1 p_1} - (c\hat{H}+\nu)\sigma_{h_1 p_2} - \alpha\hat{H}\sigma_{p_1 p_2} = 0$$

$$-c\hat{H}\sigma_{h_1 h_2} - \alpha\hat{H}\sigma_{h_1 p_2} = 0 \qquad (6.9)$$

$$\beta \hat{P} \sigma_{h_1 P_2} + \nu(\sigma^2_{P_1} - \sigma_{P_1 P_2}) - \nu \hat{P} = 0 \ .$$

These equations are solved simultaneously to give the stationary variances of H_i and P_i:

$$\sigma_{H_1 P_1} = \frac{-\hat{H}\hat{P}[\frac{\alpha\beta}{c} + \frac{c\hat{H}+2\nu}{\hat{P}} + \alpha + \frac{\alpha\mu}{\nu} \frac{\alpha\beta\hat{P}}{c\hat{H}}]}{\frac{2\alpha\beta\hat{P}}{c} + 2c\hat{H} + 4\nu + \frac{\alpha\beta\hat{P}\hat{H}}{\nu}}$$

$$\sigma^2_{H_i} = \frac{\alpha\hat{P}}{c} + \frac{\frac{\alpha^2\beta\hat{P}\hat{H}}{c^2} + \alpha\hat{H}2 + \frac{2\alpha\nu\hat{H}}{c} + \frac{\alpha^2\hat{P}\hat{H}}{c}[1+\frac{\mu}{\nu}] - \frac{\alpha^2\beta\hat{P}^2}{c^2}}{\frac{2\alpha\beta\hat{P}}{c} + 2c\hat{H} + 4\nu + \frac{\alpha\beta\hat{P}\hat{H}}{\nu}}$$

$$\sigma_{P_i} = -\frac{1}{\alpha\hat{H}}\left[\frac{\alpha\beta}{c}\hat{P} + c\hat{H} + 2\nu\right]\sigma_{H_1 P_1} + \frac{\beta\hat{P}^2}{c\hat{H}} - \frac{\nu}{\alpha} \ . \qquad (6.10)$$

The solutions to $\sigma_{P_1 P_2}, \sigma_{H_1 H_2}, \sigma_{H_1 P_2}$ may be found similarly from equation 6.9. These results have been checked by substituting back into the original (ten) equations. In Section 6.5, these results will be analysed and compared with the one-colony results found previously in Section 4.2.

6.3. Probability Linearisation

We now examine the stochastic behaviour of the model using the two-colony extension of the probability linearisation method developed in Section 4.4.1. The probabilities are linearised in the same way as before (Section 4.4.1) so that, for example, the linearised transition probabilities for colony 1 are

$$\text{Pr}[(H_1,P_1) \rightarrow (H_1+1,P_1)] = [(\lambda-2c\hat{H})H_1 + c\hat{H}^2]\delta t + o(\delta t)$$

$$\Pr[(H_1,P_1) \to (H_1-1,P_1)] = [\alpha\hat{P}H_1+\alpha\hat{H}P_1-\alpha\hat{H}\hat{P}]\delta t + o(\delta t)$$

$$\Pr[(H_1,P_1) \to (H_1,P_1+1)] = [\beta\hat{H}P_1+\beta\hat{P}H_1-\beta\hat{H}\hat{P}]\delta t + o(\delta t)$$

$$\Pr[(H_1,P_1) \to (H_1,P_1-1)] = \mu P_1\delta t + o(\delta t) \qquad (6.11)$$

$$\Pr[(H_1,P_1) \to (H_1,P_1+1)] = \nu P_2\delta t + o(\delta t)$$

$$\Pr[(H_1,P_1) \to (H_1,P_1-1)] = \nu P_1\delta t + o(\delta t) \ ,$$

in a small time interval δt, where $\hat{H}$ and $\hat{P}$ are the deterministic equilibrium values (defined in expression 6.2). The last two probabilities in 6.11 represent the change in P_1 through migration, whereas the third and fourth probabilities represent change through birth and death. As in Section 4.4.1, we assume that these probabilities are non-negative (by not letting the populations deviate too far from the deterministic equilibrium), and also that the population sizes are large so that the chances of extinction, in a finite time t, may be ignored. Let

$$P_{ijkl}(t) = \text{probability of having i prey, j predators}$$

in colony 1, and k prey and l predators

in colony 2, at time t. $\qquad (6.12)$

The forward probability equation is now formed using the linearised transition probabilities. Let G be the generating function defined by

$$G(z_1, z_2, z_3, z_4 t) = \sum_{i,j,k,l=0}^{\infty} z_1^i z_2^j z_3^k z_4^l P_{ijkl}(t) , \tag{6.13}$$

(assuming this converges in a suitably chosen domain of the z_i's). Then the generating function equation is

$$\frac{\partial G}{\partial t} = G[-2c\hat{H}^2 + 2\alpha\hat{H}\hat{P} + 2\beta\hat{H}\hat{P} + c\hat{H}^2 z_1 + c\hat{H}^2 z_3$$

$$-\alpha\hat{H}\hat{P}/z_1 - \alpha\hat{H}\hat{P}/z_3 - \beta\hat{H}\hat{P}z_2 - \beta\hat{H}\hat{P}z_4]$$

$$+ \frac{\partial G}{\partial z_1}[\alpha\hat{P} - z_1(\lambda - 2c\hat{H} + \alpha\hat{P} + \beta\hat{P}) + z_1^2(\lambda - 2c\hat{H}) + \beta\hat{P}z_1 z_2]$$

$$+ \frac{\partial G}{\partial z_2}[\mu - z_2(\alpha\hat{H} + \beta\hat{H} + \mu + \nu) + \beta\hat{H}z_2^2 + \alpha\hat{H}z_2/z_1 + \nu z_4]$$

$$+ \frac{\partial G}{\partial z_3}[\alpha\hat{P} - z_3(\lambda - 2c\hat{H} + \alpha\hat{P} + \beta\hat{P}) + z_3^2(\lambda - 2c\hat{H}) + \beta\hat{P}z_3 z_4]$$

$$+ \frac{\partial G}{\partial z_4}[\mu - z_4(\alpha\hat{H} + \beta\hat{H} + \mu + \nu) + \beta\hat{H}z_4^2 + \alpha\hat{H}z_4/z_3 + \nu z_2]. \tag{6.14}$$

Let

$$m_i(t) \equiv \left[\frac{\partial G}{\partial z_i} \right] \Bigg|_{(1)} \qquad i=1,\ldots,4 \tag{6.15}$$

where $|_{(1)}$ denotes evaluation at $z_1 = z_2 = z_3 = z_4 = 1$. Then the first moment equations are easily obtained by differentiating 6.14

$$m_1'(t) = \lambda\hat{H} - c\hat{H}m_1(t) - \alpha\hat{H}m_2(t)$$

$$m_2'(t) = -\beta\hat{H}\hat{P} + \beta\hat{P}m_1(t) - \nu m_2(t) + \nu m_4(t)$$

$$m_3'(t) = \lambda\hat{H} - c\hat{H}m_3(t) - \alpha\hat{H}m_4(t) \qquad (6.16)$$

$$m_4'(t) = -\beta\hat{H}\hat{P} + \beta\hat{P}m_3(t) - \nu m_4(t) + \nu m_2(t) \ .$$

The time-dependent stochastic mean values are found by solving equations 6.16 simultaneously. These values are identical to the deterministic solutions of the linearised equations (found from 5.16 - 5.19). As $t \to \infty$, the stationary mean values are

$$m_1 = \hat{H} \qquad\qquad m_3 = \hat{H}$$

$$m_2 = \hat{P} \qquad\qquad m_4 = \hat{P} \ . \qquad (6.17)$$

The second factorial moments are defined by

$$V_{ii}(t) = \left[\frac{\partial^2 G}{\partial z_i^2}\right]\Bigg|_{(1)} \qquad i=1,\ldots,4$$

$$V_{ij}(t) = \left[\frac{\partial^2 G}{\partial z_i \partial z_j}\right]\Bigg|_{(1)} \qquad i,j=1,\ldots,4. \qquad (6.18)$$

This gives ten second moment equations. The time-dependent second moments could be found by solving simultaneously, but, as this is mathematically very tedious, we just look for stationary solutions. After a long time t, as in Section 6.2, both colonies experience the same influences, so the following identities may be assumed:

$$V_{11} = V_{33} \qquad\qquad V_{12} = V_{34}$$

$$V_{22} = V_{44} \qquad\qquad V_{14} = V_{23} \ . \qquad (6.19)$$

Using 6.19, the equations of the stationary second moments are

$$-2\alpha\hat{H}\hat{P}+m_1(2\lambda\hat{H}+2\lambda-4c\hat{H})+2\alpha\hat{H}m_2-2c\hat{H}V_{11}-2\alpha\hat{H}V_{12} = 0$$

$$m_2(2\beta\hat{H}-2\beta\hat{H}\hat{P})+2\beta\hat{P}V_{12}-2\nu V_{22}+2\nu V_{24} = 0$$

$$m_1(\beta\hat{P}-\beta\hat{H}\hat{P})+m_2(\lambda\hat{H}-\alpha\hat{H})+\beta\hat{P}V_{11}-(c\hat{H}+\nu)V_{12}-\alpha\hat{H}V_{22}+\nu V_{14} = 0$$

$$2\lambda\hat{H}m_1-2c\hat{H}V_{13}-2\alpha\hat{H}V_{14} = 0 \qquad\qquad (6.20)$$

$$-\beta\hat{H}\hat{P}m_1+\lambda\hat{H}m_2+\nu V_{12}-(c\hat{H}+\nu)V_{14}+\beta\hat{P}V_{13}-\alpha\hat{H}V_{24} = 0$$

$$-2\beta\hat{H}\hat{P}m_2+2\nu V_{22}-2\nu V_{24}+2\beta\hat{P}V_{14} = 0 \;.$$

We have solved equations 6.20 simultaneously, and found solutions for the V_{ii}'s and V_{ij}'s. From this, the variances and covariances are found by adding the appropriate constants, for example

$$\text{Var}(H_1) = V_{11} - m_1^2 + m_1 \;.$$

Although the methods are different, the results we have found for the variances using this method are identical to those found previously (6.10) using Bartlett's stochastic linearisation.

6.4. Continuous Approximation

6.4.1. Format of solution

Recall that, in Section 3.7, we approximated the discrete state space by a continuous state space, and found that the probability distribution of the process satisfied the Kolmogorov equation

(equation 3.49), and the equivalent stochastic differential equation (3.52). Although a solution to these equations could not be found in the general case, by linearising the transition probabilities, we saw, in Section 4.6, that the stochastic differential equation was simplified to a form for which a solution was known. We now extend the results from Section 4.6 to the two-colony case.

Let $p(x_1, x_2, x_3, x_4 t)$ be the probability of having x_1 prey in colony 1, x_2 predators in colony 1, x_3 prey in colony 2, and x_4 predators in colony 2. The forward Kolmogorov equation for two colonies (by extending 3.49) is

$$\frac{\partial p}{\partial t} = \frac{1}{2} \sum_{j=1}^{4} \sum_{i=1}^{4} \frac{\partial^2}{\partial x_i \partial x_j}(a_{ij}p) - \sum_{i=1}^{4} \frac{\partial}{\partial x_i}(b_i p) , \qquad (6.21)$$

where the coefficients, in the case where the transition probabilities are linearised (as in 6.11), are given by

$$b_1 = -c\hat{H}x_1 - \alpha\hat{H}x_2 + \lambda\hat{H}$$

$$b_2 = \beta\hat{P}x_1 - \beta\hat{H}\hat{P} + \nu(x_4 - x_2)$$

$$b_3 = -c\hat{H}x_3 - \alpha\hat{H}x_4 + \lambda\hat{H}$$

$$b_4 = \beta\hat{P}x_3 - \beta\hat{H}\hat{P} + \nu(x_2 - x_4)$$

$$a_{11} = (2\alpha\hat{P} - c\hat{H})x_1 + \alpha\hat{H}x_2 + c\hat{H}^2 - \alpha\hat{H}\hat{P} \qquad (6.22)$$

$$a_{22} = \beta\hat{P}x_1 + 2\beta\hat{H}x_2 - \beta\hat{H}\hat{P} + \nu(x_4 + x_2)$$

$$a_{33} = (2\alpha\hat{P} - c\hat{H})x_3 + \alpha\hat{H}x_4 + c\hat{H}^2 - \alpha\hat{H}\hat{P}$$

$$a_{44} = \beta\hat{P}x_3 + 2\beta\hat{H}x_4 - \beta\hat{H}\hat{P} + \nu(x_4 + x_2)$$

$$a_{24} = a_{42} = -\nu(x_2 + x_4)$$

$$a_{ij} = 0 , \quad \text{otherwise.}$$

The corresponding stochastic differential equation (see Section 3.7.2) is

$$d\underline{X}(t) = \underline{B}(\underline{x}, t) + \underline{A}^{1/2}(\underline{x}, t)\underline{Z}(t) \sqrt{dt} , \qquad (6.23)$$

as in the one-colony case, where now $\underline{X}(t)$ is a 4-dimensional vector of the X_i's, $\underline{B}$ is a 4-dimensional vector of the b_i's and $\underline{A}$ a 4x4 matrix of the a_{ij}'s.

This equation may be written in the form used by Arnold (Section 4.6.2), by defining the C_i's as

$$C_1 = \begin{bmatrix} -c\hat{H} & -\alpha\hat{H} & 0 & 0 \\ \beta\hat{P} & -\nu & 0 & \nu \\ 0 & 0 & -c\hat{H} & -\alpha\hat{H} \\ 0 & \nu & \beta\hat{P} & -\nu \end{bmatrix}$$

$$C_2 = (\lambda\hat{H}, -\beta\hat{H}\hat{P}, \lambda\hat{H}, -\beta\hat{H}\hat{P})^T \qquad (6.24)$$

$$
C_3^2 = \begin{bmatrix} 2_\alpha\hat{H}\hat{P} & 0 & 0 & 0 \\ 0 & 2_\beta\hat{H}\hat{P}+2_\nu\hat{P} & 0 & -2_\nu\hat{P} \\ 0 & 0 & 2_\alpha\hat{H}\hat{P} & 0 \\ 0 & -2_\nu\hat{P} & 0 & 2_\beta\hat{H}\hat{P}+2_\nu\hat{P} \end{bmatrix}.
$$

(As in 4.6.2, the x_i's in $\underline{A}$ are approximated by the deterministic equilibrium values). Then, from Arnold, the probability distribution of the process satisfying equation 6.23 is the 4-dimensional Normal distribution with mean vector and variance-covariance matrix given by

$$
m_t(\underline{x}_0) = e^{C_1 t}[x_0 + (\int_0^t e^{-C_1 u} du)C_2]
$$

$$
V_t(x_0) = \int_0^t e^{C_1(t-u)} C_3 C_3^T e^{C_1^T(t-u)} du , \tag{6.25}
$$

where $\underline{x}_0$ is the initial value of $\underline{X}$ (at t=0).

6.4.2. Calculation of mean

To calculate the mean, we can see from 6.25 that it is necessary to find the exponential of C_1, a 4x4 matrix. We will now see that by partitioning C_1 the problem is reduced to finding the exponential of two 2x2 matrices. The problem is further simplified when we discover that, as t→∞, one of the matrices has no effect on the solution.

The matrix C_1 is partitioned by writing

$$
C_1 = \left[\begin{array}{cc|cc} -c\hat{H} & -\alpha\hat{H} & 0 & 0 \\ \beta\hat{P} & -\nu & 0 & \nu \\ \hline 0 & 0 & -c\hat{H} & -\alpha\hat{H} \\ 0 & \nu & \beta\hat{P} & -\nu \end{array}\right]. \tag{6.26}
$$

In this way, we can see that C_1 may be written as

$$C_1 = PMP^{-1} , \tag{6.27}$$

where

$$P = \frac{1}{\sqrt{2}} \begin{bmatrix} 1 & 0 & -1 & 0 \\ 0 & 1 & 0 & -1 \\ 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \end{bmatrix} \tag{6.28}$$

and

$$M = \begin{bmatrix} -c\hat{H} & -\alpha\hat{H} & 0 & 0 \\ \beta\hat{P} & 0 & 0 & 0 \\ 0 & 0 & -c\hat{H} & -\alpha\hat{H} \\ 0 & 0 & \beta\hat{P} & -2\nu \end{bmatrix} . \tag{6.29}$$

Thus e^{C_1} is given by

$$e^{C_1} = Pe^{M}P^{-1} . \tag{6.30}$$

This simplifies the problem of calculating the exponential of C_1 because M has two zero blocks, and so to find e^{M} it is necessary only to calculate the exponential of two 2x2 matrices.

Let

$$M_1 = \begin{bmatrix} -c\hat{H} & -\alpha\hat{H} \\ \beta\hat{P} & 0 \end{bmatrix} \tag{6.31}$$

and

$$M_2 = \begin{bmatrix} -c\hat{H} & -\alpha\hat{H} \\ \beta\hat{P} & -2\nu \end{bmatrix} . \tag{6.32}$$

M_1 and M_2 act independently of each other, because M contains two blocks of zeros. M_1 is identical to the matrix referred to as C_1 in the one-colony case (see expression 4.63). From the results of Section 4.6.3, we may write the exponential of M_1 as

$$e^{M_1 t} = e^{r_1 t} R_1 + e^{r_2 t} R_2 , \qquad (6.33)$$

where

$$r_1 = -c\hat{H}/2 - \sqrt{c^2 \hat{H}^2/4 - \alpha\beta\hat{H}\hat{P}}$$

$$r_2 = -c\hat{H}/2 + \sqrt{c^2 \hat{H}^2/4 - \alpha\beta\hat{H}\hat{P}} , \qquad (6.34)$$

and R_1 and R_2 are the matrices defined in 4.67.

In the same way, by finding the eigenvalues of M_2, and calculating the row and column eigenvectors, we may write

$$e^{M_2 t} = e^{r_3 t} R_3 + e^{r_4 t} R_4 , \qquad (6.35)$$

where

$$r_3 = -(\frac{c\hat{H}}{2}+\nu) + \frac{1}{2}\sqrt{(c\hat{H}-2\nu)^2 - 4\alpha\beta\hat{H}\hat{P}}$$

$$r_4 = -(\frac{c\hat{H}}{2}+\nu) - \frac{1}{2}\sqrt{(c\hat{H}-2\nu)^2 - 4\alpha\beta\hat{H}\hat{P}} .$$

As we shall see, the stationary mean is not affected by M_2, and so, there is no need to calculate R_3 and R_4.

Using this decomposition of C_1, the mean is now given by the expression

$$m_t(\underline{x}_0) = Pe^{Mt}P^{-1}\underline{x}_0 + Pe^{Mt}\int_0^t e^{-Mu}du \, P^{-1}C_2 \; . \qquad (6.36)$$

Although it is possible to find the time-dependent mean from this, to avoid too much mathematical tedium, we will just calculate the mean for the stationary case. In the limiting case, as $t \to \infty$,

$$\lim_{t \to \infty} m_t(\underline{x}_0) = \lim_{t \to \infty} (Pe^{Mt}\int_0^t e^{-Mu}du \, P^{-1}C_2). \qquad (6.37)$$

From expression 4.71, we know that as $t \to \infty$

$$e^{M_1 t}\int_0^t e^{-M_1 u}du \to -\frac{1}{r_1}R_1 - \frac{1}{r_2}R_2 \; . \qquad (6.38)$$

Treating the M_2 partition similarly

$$e^{M_2 t}\int_0^t e^{-M_2 u}du \to -\frac{1}{r_3}R_3 - \frac{1}{r_4}R_4 \; , \qquad (6.39)$$

as $t \to \infty$. However, if we calculate $P^{-1}C_2$:

$$P^{-1}C_2 = \frac{1}{\sqrt{2}}
\begin{bmatrix}
1 & 0 & 1 & 0 \\
0 & 1 & 0 & 1 \\
-1 & 0 & 1 & 0 \\
0 & -1 & 0 & 1
\end{bmatrix}
\begin{bmatrix}
\lambda\hat{H} \\
-\beta\hat{H}\hat{P} \\
\lambda\hat{H} \\
-\beta\hat{H}\hat{P}
\end{bmatrix}$$

$$= 1/\sqrt{2} \; (2\lambda\hat{H}, \, -2\beta\hat{H}\hat{P}, \, 0, \, 0)^T \; . \qquad (6.40)$$

Because the last two components of $P^{-1}C_2$ are zero, then, as $t \to \infty$, M_2 has no effect on the mean. Thus, 6.37 may be written as

$$\lim_{t \to \infty} m_t(\underline{x}_0) = \frac{1}{2}
\begin{bmatrix}
1 & 0 & -1 & 0 \\
0 & 1 & 0 & -1 \\
1 & 0 & 1 & 0 \\
0 & 1 & 0 & 1
\end{bmatrix}
\begin{bmatrix}
0 & \dfrac{-1}{\beta \hat{P}} & 0 & 0 \\
\dfrac{1}{\alpha \hat{H}} & \dfrac{c\hat{H}}{\alpha\beta\hat{H}\hat{P}} & 0 & 0 \\
0 & 0 & * & * \\
0 & 0 & * & *
\end{bmatrix}
\begin{bmatrix}
2\lambda\hat{H} \\
-2\beta\hat{H}\hat{P} \\
0 \\
0
\end{bmatrix}$$

(where * denotes elements from expression 6.39, which need not be calculated)

$$= (\hat{H}, \hat{P}, \hat{H}, \hat{P})^T . \qquad (6.41)$$

Therefore, the mean, as t gets large, tends to the deterministic equilibrium.

6.4.3. The exponential of M_2

Although the matrix M_2 had no effect on the stationary mean, we will find it necessary to know e^{M_2} when calculating the variance. We will, therefore, calculate e^{M_2} before investigating the variance equation in 6.4.4.

The exponential of M_2 can be found in the same way as before, using eigenvalue decomposition. However, we find that the calculations are simpler, and the elements in a better format, if we proceed in the following way. From 6.32,

$$M_2 = \begin{bmatrix} -c\hat{H} & -\alpha\hat{H} \\ \beta\hat{P} & -2\nu \end{bmatrix}.$$

This may be written as

$$M_2 = (-c\hat{H}/2 - \nu)I + S \tag{6.42}$$

where I is the 2x2 identity matrix, and

$$S = \begin{bmatrix} -c\hat{H}/2+\nu & -\alpha\hat{H} \\ \beta\hat{P} & -c\hat{H}/2-\nu \end{bmatrix}. \tag{6.43}$$

Because I and S commute,

$$e^{M_2} = e^{-c\hat{H}/2-\nu}e^{S}. \tag{6.44}$$

e^{S} is simpler to find, when we notice that

$$S^2 = aI \tag{6.45}$$

where

$$a = (c\hat{H}/2 - \nu)^2 - \alpha\beta\hat{H}\hat{P}.$$

The (1,1) component of e^{S} is

$$= 1 + (\frac{-c\hat{H}}{2}+\nu) + \frac{a}{2!} + (\frac{-c\hat{H}}{2}+\nu)\frac{a}{3!} + \frac{a^2}{4!} + \ldots$$

which, by adding alternate terms, simplifies to

$$\frac{(e^{\sqrt{a}}+e^{-\sqrt{a}})}{2} - (c\hat{H}/2-\nu)\frac{(e^{\sqrt{a}}-e^{-\sqrt{a}})}{(2\sqrt{a})}$$

which becomes

$$\frac{1}{2}\left[1-\frac{c\hat{H}-2\nu}{2\sqrt{a}}\right]e^{\sqrt{a}} + \frac{1}{2}\left[1+\frac{c\hat{H}-2\nu}{2\sqrt{a}}\right]e^{-\sqrt{a}} .$$

The other components are calculated similarly. Let

$$b_1 = 1 - \frac{c\hat{H}-2\nu}{2\sqrt{a}} \quad , \quad b_2 = 1 + \frac{c\hat{H}-2\nu}{2\sqrt{a}}$$

Therefore

$$e^{M_2 t} = \frac{1}{2}e^{-\left(\frac{c\hat{H}}{2}+\nu\right)t}\begin{bmatrix} b_1 e^{\sqrt{a}}+b_2 e^{-\sqrt{a}} & -\frac{\alpha\hat{H}}{\sqrt{a}}[e^{\sqrt{a}}-e^{-\sqrt{a}}] \\ \frac{\beta\hat{P}}{\sqrt{a}}[e^{\sqrt{a}}-e^{-\sqrt{a}}] & b_2 e^{\sqrt{a}}+b_1 e^{-\sqrt{a}} \end{bmatrix} \qquad (6.46)$$

6.4.4. Calculation of variance

Recall, from 6.25, that the expression for the variance-covariance matrix is

$$V_t(\underline{x}_0) = \int_0^t e^{C_1(t-u)} C_3 C_3^T e^{C_1^T(t-u)} du .$$

In 6.24, an expression was given for the matrix C_3^2. We may easily calculate C_3 from this by diagonalising C_3^2. We notice that

$$C_3^2 = P \; \text{Diag}\{2\alpha\hat{H}\hat{P}, \; 2\beta\hat{H}\hat{P}, \; 2\alpha\hat{H}\hat{P}, \; 2\beta\hat{H}\hat{P}+4\nu\hat{P}\}P^{-1}$$

where P is the matrix which was used to diagonalise C_1 (6.28). Let the diagonal matrix be denoted by N, so that

$$\sqrt{N} = \text{Diag}\{\sqrt{2\alpha\hat{H}\hat{P}}, \; \sqrt{2\beta\hat{H}\hat{P}}, \; \sqrt{2\alpha\hat{H}\hat{P}}, \; \sqrt{2\beta\hat{H}\hat{P}+4\nu\hat{P}}\} . \qquad (6.47)$$

Then

$$C_3 = P \sqrt{N}P^{-1} \; . \tag{6.48}$$

To find the transpose of C_3:

$$C_3^T = (P \sqrt{N}P^{-1})^T$$

$$= (P^{-1})^T \sqrt{N}^T P^T$$

$$= P \sqrt{N}P^{-1}$$

$$= C_3 \; ,$$

and so

$$C_3 C_3^T = PNP^{-1} \; . \tag{6.49}$$

The expression for the variance is now simplified to

$$V_t(\underline{x}_0) = P\int_0^t e^{M(t-u)} N \, e^{M^T(t-u)} du \; P^{-1} \; . \tag{6.50}$$

Because N is diagonal, we are again dealing with the two 2x2 matrices, M_1 and M_2 (6.31 and 6.32). If M_1 is used in expression 6.50, then the problem is identical to that of the one-colony variance, Section 4.6.4, ignoring the P and P^{-1} matrices. Thus, we need only evaluate 6.50 in the case of M_2.

Let

$$n_1 = 2\alpha\hat{H}\hat{P}$$

$$\hat{n}_2 = 2\beta\hat{H}\hat{P} + 4\nu\hat{P} \; . \tag{6.51}$$

We need to calculate

$$\int_0^t e^{M_2(t-u)} \begin{bmatrix} n_1 & 0 \\ 0 & n_2 \end{bmatrix} e^{M_2^T(t-u)} \, du \; . \tag{6.52}$$

As before, mathematical complications simplify greatly when we consider the limit as $t \to \infty$. Using the expression for e^{M_2} from 6.46, after integration, the $(1,1)$ component of the limit (as $t \to \infty$) of (6.52) is

$$\frac{n_1}{4}\left[1 - \frac{c\hat{H}-2\nu}{2\sqrt{a}}\right]^2 \frac{1}{c\hat{H}+2\nu-2\sqrt{a}} + \frac{n_1}{4}\left[1 + \frac{c\hat{H}-2\nu}{2\sqrt{a}}\right]^2 \frac{1}{c\hat{H}+2\nu+2\sqrt{a}}$$

$$+ \frac{n_1}{2}\left[1 - \frac{(c\hat{H}-2\nu)^2}{4a}\right]\frac{1}{c\hat{H}+2\nu}$$

$$+ \frac{n_2}{4}\frac{(\alpha\hat{H})^2}{a}\left[\frac{1}{c\hat{H}+2\nu-2\sqrt{a}} + \frac{1}{c\hat{H}+2\nu+2\sqrt{a}} - \frac{2}{c\hat{H}+2\nu}\right] \; .$$

This simplifies to

$$B_1 \equiv \frac{\alpha\hat{H}\hat{P}}{c\hat{H}+2\nu} + \frac{\alpha\hat{P}[4\nu^2+\alpha\beta\hat{H}^2+2\alpha\nu\hat{H}]}{(2\nu c+\alpha\beta\hat{P})(c\hat{H}+2\nu)} \; . \tag{6.53}$$

Similarly, the $(2,2)$ component simplifies to

$$B_2 \equiv \frac{\beta\hat{H}\hat{P}}{c\hat{H}+2\nu} + \frac{\hat{P}[\alpha\beta\hat{P}(\beta\hat{P}+2\nu)+\beta c^2\hat{H}^2+2\nu c^2\hat{H}+4\nu^2 c]}{(2\nu c+\alpha\beta\hat{P})(c\hat{H}+2\nu)} \; . \tag{6.54}$$

The $(1,2)$ and $(2,1)$ components are identical, and equal to

$$B_3 \equiv \frac{\alpha\hat{P}}{(2_\nu c + \alpha\beta\hat{P})(c\hat{H} + 2_\nu)} . \qquad (6.55)$$

The B_i's are the solutions as $t \to \infty$ for the M_2 section of the variance (6.52). As mentioned, the M_1 section of the variance is known from the one-colony solution. As t gets large, the components of the solution, from 4.76, are

$$A_1 \equiv (1,1) \text{ comp} = \alpha(\hat{H} + \hat{P})/c$$

$$A_2 \equiv (2,2) \text{ comp} = \frac{\beta\hat{P}^2}{c\hat{H}} + \frac{\beta\hat{P}}{c} + \frac{c\hat{H}}{\alpha} \qquad (6.56)$$

$$A_3 \equiv (1,2) \text{ comp} = -\hat{H}$$

$$= (2,1) \text{ comp} .$$

From 6.50, the variance, for t large, is found from the A_i's and B_i's as follows:

$$\lim_{t \to \infty} V_t(\underline{x}_0) = P \begin{bmatrix} A_1 & A_3 & 0 & 0 \\ A_3 & A_2 & 0 & 0 \\ 0 & 0 & B_1 & B_3 \\ 0 & 0 & B_3 & B_2 \end{bmatrix} P^{-1}$$

which is

$$= \frac{1}{2} \begin{bmatrix} A_1+B_1 & A_3+B_3 & A_1-B_1 & A_3-B_3 \\ A_3+B_3 & A_2+B_2 & A_3-B_3 & A_2-B_2 \\ A_1-B_1 & A_3-B_3 & A_1+B_1 & A_3+B_3 \\ A_3-B_3 & A_2-B_2 & A_3+B_3 & A_2+B_2 \end{bmatrix} . \qquad (6.57)$$

These stationary variances and covariances are identical to those previously found using Bartlett's stochastic linearisation.

6.5. Effect of Migration on Moments

6.5.1. Introduction

In the last three sections, the means and variances of a stochastic model were found using three different methods. It is possible to find time-dependent solutions using the methods, but to avoid too many mathematically tedious calculations, only stationary solutions were given. Although the format of the results differ, the means and variances calculated using the three methods can be shown to be equal. These methods appear to be different, and we cannot offer an explanation for the equality of the results.

The most general method is the continuous approximation (Section 6.4), because this method tells us that an approximate solution for the probability distribution is the 4-dimensional Normal distribution. In the other two methods, we assumed that, because the parameters were equal, after a time t, the variances were equal in both colonies (6.8 and 6.19). Using the continuous approximation method, we did not need to make this assumption, but it can be seen (from 6.57) that the variances are, in fact, equal.

To examine the effect of migration on the variance, it is most convenient to use the format of the results from the third method, given in 6.57. In the one-colony case, the prey variance is A_1 and the predator variance A_2. In the two-colony situation, the prey variance is $(A_1+B_1)/2$ and the predator variance is $(A_2+B_2)/2$. Thus, by comparing the A_i's and B_i's, we will, in Sections 6.5.3 and 6.5.4 be able to see how migration affects the variance. These results will be analysed from a biological point of view in Section 6.5.6.

6.5.2. The mean of the predators and prey

In Section 6.3, we saw that the time-dependent means of H_i and P_i were identical to the deterministic solution. Hence, for finite time t, migration affects the stochastic mean in exactly the same way as it affects the deterministic solution (see Section 5.3). As $t \to \infty$, the mean of H_i goes to $\hat{H}$, and the mean of P_i goes to $\hat{P}$. That is, for large values of t, migration (when the parameters are equal in both directions) has no effect on the means.

6.5.3. The prey variance

As mentioned in 6.5.1, the prey variance in the one-colony case is A_1, and in the two-colony case is $(A_1+B_1)/2$. Let

$$x = B_1 - A_1 . \tag{6.58}$$

Then x is a measure of the change in variance with migration. If x is positive, migration increases the prey variance; if x is negative, the variance is decreased; if x is zero, the variance remains the same. In this section, we will give a mathematical analysis of x to see what factors will increase or decrease variance. A biological interpretation will be given in Section 6.5.6.

Using the expressions for A_1 and B_1 from 6.56 and 6.53, respectively, we see that

$$x = \{c(2\nu c+\alpha\beta\hat{P})(c\hat{H}+2\nu)\}^{-1}[\alpha c\hat{H}\hat{P}(2\nu c+\alpha\beta\hat{P})+\alpha c\hat{P}(4\nu^2+\alpha\beta\hat{H}^2+2\alpha\nu\hat{H})$$

$$-\alpha(\hat{H}+\hat{P})(2\nu c+\alpha\beta\hat{P})(c\hat{H}+2\nu)]$$

which simplifies to

$$x = \frac{2\alpha\nu[\alpha\hat{P}(c\hat{H}-\beta\hat{P}-\beta\hat{H})-c^2\hat{H}^2-2\nu c\hat{H}]}{c(2\nu c+\alpha\beta\hat{P})(c\hat{H}+2\nu)} . \tag{6.59}$$

Thus

$$x < 0$$

$$\Leftrightarrow \alpha\hat{P}[c\hat{H}-\beta\hat{P}-\beta\hat{H}]-c^2\hat{H}^2-2\nu c\hat{H} < 0$$

$$\Leftrightarrow \nu > \frac{\alpha\hat{P}[c\hat{H}-\beta\hat{P}-\beta\hat{H}]-c^2\hat{H}^2}{2c\hat{H}} \tag{6.60}$$

and the variance is decreased. If this inequality does not hold, and

$$\nu < \frac{\alpha\hat{P}[c\hat{H}-\beta\hat{P}-\beta\hat{H}]-c^2\hat{H}^2}{2c\hat{H}} , \tag{6.61}$$

then the variance is increased (or unchanged when the equality holds).

The inequality in 6.60 shows that the change in variance depends on the quantity

$$c\hat{H}-\beta\hat{P}-\beta\hat{H} . \tag{6.62}$$

If this quantity is negative, then the right hand side of 6.60 is negative. This means that the variance will decrease for all $\nu > 0$ (when $\nu = 0$, then $x = 0$ and we have the single colony solution). Similarly, if

$$c\hat{H}-\beta\hat{P}-\beta\hat{H} < c^2\hat{H}^2/(\alpha\hat{P}) , \tag{6.63}$$

the variance will automatically decrease for all $\nu > 0$. When the

inequality in 6.63 is reversed, then migration between colonies will only decrease the variance when the migration parameter is large enough.

In the limit as $\nu \to \infty$, the variance of H_1 becomes

$$\lim_{\nu \to \infty} \text{var } H_1 = \frac{\alpha}{c}(\hat{P} + \frac{\hat{H}}{2}) \, , \tag{6.64}$$

which shows an ultimate decrease in the variance of the prey by a factor of $\alpha\hat{H}/(2c)$. A summary of these results will be given (Section 6.5.5) which will clarify the change in prey variance with ν.

6.5.4. The predator variance

The single-colony predator variance is A_2 (6.56) and the two-colony predator variance is $(A_2+B_2)/2$ (for B_2, see 6.54). Let

$$y = B_2 - A_2 \, . \tag{6.65}$$

As in the last section:

if $y > 0$, the predator variance is increased,

if $y < 0$, the predator variance is decreased,

if $y = 0$, the predator variance is unchanged.

Substituting for A_2 and B_2 in 6.65,

$$y = 2\nu\{\alpha c\hat{H}^2(2\nu c + \alpha\beta\hat{P})(c\hat{H}+2\nu)\}^{-1}[2\nu\{\alpha c\hat{H}\hat{P}(c\hat{H}-\beta\hat{P}-\beta\hat{H})-c^3\hat{H}^3\}$$

$$+\alpha\hat{P}(\alpha\beta\hat{H}\hat{P}+c^2\hat{H}^2)(c\hat{H}-\beta\hat{P}-\beta\hat{H})-c^4\hat{H}^4] \, . \tag{6.66}$$

Then the predator variance is decreased

$$\Longleftrightarrow y < 0$$

$$\Longleftrightarrow 2\nu c\hat{H}[\alpha\hat{P}(c\hat{H}-\beta\hat{P}-\beta\hat{H})-c^2\hat{H}^2]$$

$$+\alpha\hat{P}[\alpha\beta\hat{H}\hat{P}c^2\hat{H}^2][c\hat{H}-\beta\hat{P}-\beta\hat{H}]-c^4\hat{H}^4 < 0 . \qquad (6.67)$$

The following three situations arise, depending on the value of $(c\hat{H}-\beta\hat{P}-\beta\hat{H})$:

(a) if $c\hat{H}-\beta\hat{P}-\beta\hat{H} < 0$,

then the variance is always decreased, for all $\nu > 0$.

(b) if $0 < c\hat{H}-\beta\hat{P}-\beta\hat{H} < c^2\hat{H}^2/(\alpha\hat{P})$,

then the variance is decreased if

$$\nu > \frac{-\alpha\hat{P}(\alpha\beta\hat{H}\hat{P}+c^2\hat{H}^2)(c\hat{H}-\beta\hat{P}-\beta\hat{H})+c^4\hat{H}^4}{2c\hat{H}[\alpha\hat{P}(c\hat{H}-\beta\hat{P}-\beta\hat{H})-c^2\hat{H}^2]}$$

$$= -\frac{c\hat{H}}{2} + \frac{\alpha^2\beta\hat{H}\hat{P}^2(c\hat{H}-\beta\hat{P}-\beta\hat{H})}{2c\hat{H}[c^2\hat{H}^2-\alpha\hat{P}(c\hat{H}-\beta\hat{P}-\beta\hat{H})]} .$$

(c) if $c\hat{H}-\beta\hat{P}-\beta\hat{H} > c^2\hat{H}^2/(\alpha\hat{P})$,

then the variance is decreased if

$$\nu < -\frac{c\hat{H}}{2} - \frac{\alpha^2\beta\hat{H}\hat{P}^2(c\hat{H}-\beta\hat{P}-\beta\hat{H})}{2c\hat{H}[\alpha\hat{P}(c\hat{H}-\beta\hat{P}-\beta\hat{H})-c^2\hat{H}^2]} .$$

Since the right hand side here is negative, in this case, migration always increases the variance.

If we look at the limiting case of the variance, as $\nu \to \infty$, we see that

$$\lim_{\nu \to \infty} \text{var } P_1 = \lim_{\nu \to \infty} (A_2 + B_2)/2$$

$$= \frac{\hat{P}}{2} + \frac{\beta \hat{P}^2}{2c\hat{H}} + \frac{\beta \hat{P}}{2c} + \frac{c\hat{H}}{2\alpha} . \tag{6.68}$$

We compare this with A_2, the single-colony variance:

$$A_2 - \lim_{\nu \to \infty} \text{var } P_1 = \{2\alpha c\hat{H}\}^{-1} [\alpha \hat{P}(\beta \hat{P} + \beta \hat{H} - c\hat{H}) + c^2 \hat{H}^2] . \tag{6.69}$$

This confirms the results given above, that, in the limit as $\nu \to \infty$, migration decreases the variance of the predators, if and only if

$$c\hat{H} - \beta \hat{P} - \beta \hat{H} < c^2 \hat{H}^2 / (\alpha \hat{P}) .$$

6.5.5. Summary of effect

The effect of migration on the prey and predator variance falls into three distinct categories:

(a) $c\hat{H} - \beta \hat{P} - \beta \hat{H} < 0$.

Var (H_1) is decreased for all $\nu > 0$.

Var (P_1) is decreased for all $\nu > 0$.

(c) $0 < c\hat{H} - \beta \hat{P} - \beta \hat{H} < c^2 \hat{H}^2 / (\alpha \hat{P})$.

Var (H_1) is decreased for all $\nu > 0$.

Var (P_1) is decreased only when ν is sufficiently large, that is,

$$\nu > -\frac{c\hat{H}}{2} + \frac{\alpha^2 \beta \hat{H} \hat{P}^2 [c\hat{H} - \beta \hat{P} - \beta \hat{H}]}{2c\hat{H}[c^2 \hat{H}^2 - \alpha \hat{P}(c\hat{H} - \beta \hat{P} - \beta \hat{H})]} .$$

(c) $c\hat{H}-\beta\hat{P}-\beta\hat{H} \geqslant c^2\hat{H}^2/(\alpha\hat{P})$.

Var (H_1) is decreased only when ν is sufficiently large, that is,

$$\nu > \frac{\alpha\hat{P}[c\hat{H}-\beta\hat{P}-\beta\hat{H}]-c^2\hat{H}^2}{2c\hat{H}} .$$

Var (P_1) always increases.

6.5.6. Analysis of results

For notational convenience, let

$$Q = c\hat{H}-\beta\hat{P}-\beta\hat{H} . \qquad (6.70)$$

Recall that, under linearisation,

$$\text{Pr [birth of } H_1] = [(\lambda-2c\hat{H})H_1+c\hat{H}^2]\delta t$$

and

$$\text{Pr [death of } P_1] = [\beta\hat{P}H_1+\beta\hat{H}P_1-\beta\hat{H}\hat{P}]\delta t .$$

The quantity Q then represents the restricting influence on the birth of H_1, and the contributing influence on the birth of P_1.

When Q is very small, or negative, the birth rates of both the prey and predators are strong (through c being small and β large). In this case (type (a) from 6.5.5), migration reduces the variance of both the predators and prey. This is what we might expect, because allowing predators to migrate between the colonies should even out the variations in fluctuations of the predators, and hence of the prey.

As Q gets larger, the birth rates of both the predators and prey

get smaller. In order to keep $\hat{P}$ and $\hat{H}$ constant, the death rates also decrease, so that the predator and prey activity is slowed down. In this case ((b) from 6.5.5), it is necessary to have a fairly large migration parameter in order to reduce the predator variance.

When Q gets very large (case (c)), very little activity is experienced by both populations. Allowing migration can only increase the predator variance, though it can decrease the prey variance when ν is sufficiently large. In order to keep $\hat{P}$ positive, an upper limit must be placed on c, namely

$$c < \lambda/\hat{H} .$$

This means that Q has a maximum of λ. Even though Q is bounded above, it is possible to have

$$Q > c^2 \hat{H}^2/(\alpha \hat{P}) .$$

A numerical example of this is when $\hat{H} = \hat{P} = 100$, $\alpha = 5$, $\beta = 1/2$, $c = 3$.

The results for the limiting case as $\nu \to \infty$ are surprising. We might expect that as $\nu \to \infty$, the effects from the spatial segregation of the colonies would become negligible. Instead, as $\nu \to \infty$, the prey variance always shows a decrease, and the predator variance is decreased if and only if

$$Q < c^2 \hat{H}^2/(\alpha \hat{P}) .$$

6.6. General Model

Although Bartlett's stochastic linearisation and the probability linearisation methods can only be used on very simplified models, the continuous approximation method may by used to find moments for more

general models.

Suppose that both predators and prey are allowed to migrate in both directions with different probabilities (as in Figure 6.2).
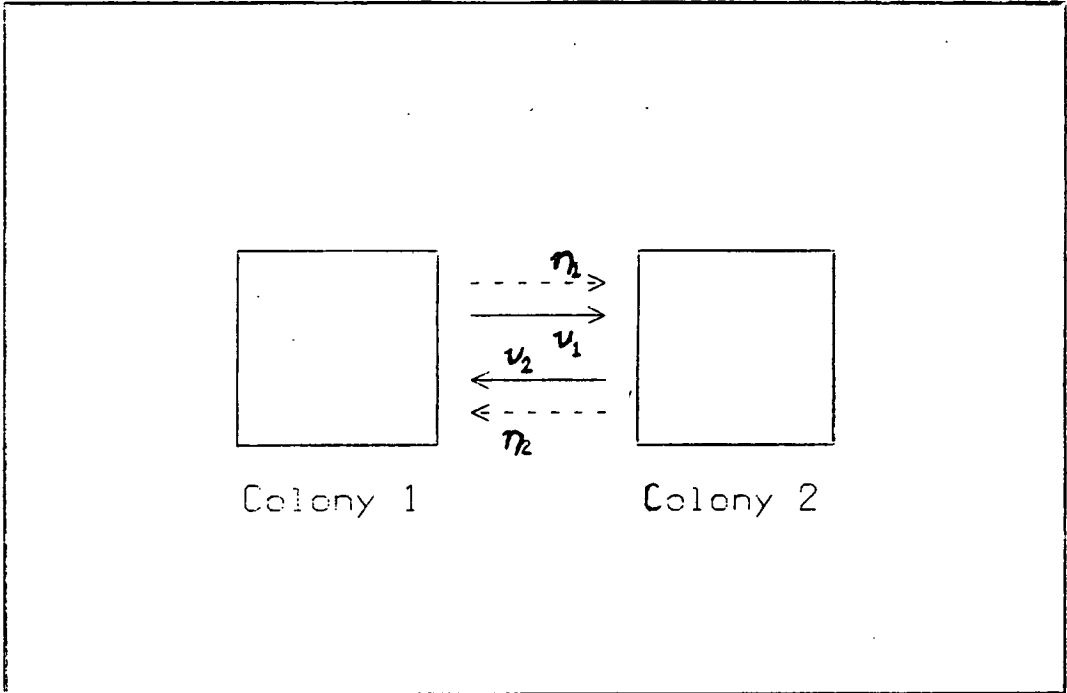
Figure 6.2. Two-colony model showing general two-way migration, with - - - representing prey, and ——— predators.

In deterministic terms, the equations of the model are:

$$\dot{H}_1 = \lambda H_1 - c H_1^2 - \alpha H_1 P_1 - \eta_1 H_1 + \eta_2 H_2$$

$$\dot{P}_1 = \beta H_1 P_1 - \mu P_1 - \nu_1 P_1 + \nu_2 P_2$$

$$\dot{H}_2 = \lambda H_2 - c H_2^2 - \alpha H_2 P_2 - \eta_2 H_2 + \eta_1 H_1 \qquad (6.71)$$

$$\dot{P}_2 = \beta H_2 P_2 - \mu P_2 - \nu P_2 + \nu_1 P_1 \ .$$

Suppose a deterministic equilibrium exists at

$$\hat{H}_1, \hat{P}_1, \hat{H}_2, \hat{P}_2.$$

Using this equilibrium, the probabilities are linearised in the same way as before, for example,

$$\text{Pr (birth of } H_1) = [(\lambda - 2c\hat{H}_1)H_1 + c\hat{H}_1^2]\delta t + o(\delta t) .$$

Approximating the discrete state space by a continuous state space, the forward Kolmogorov equation is

$$\frac{\partial p}{\partial t} = \frac{1}{2}\sum_{j=1}^{4}\sum_{i=1}^{4}\frac{\partial^2}{\partial x_i \partial x_j}(a_{ij}p) - \sum_{i=1}^{4}\frac{\partial}{\partial x_i}(b_i p) , \qquad (6.72)$$

where now the coefficients are given by

$$b_1 = (\lambda - 2c\hat{H}_1 - \alpha\hat{P}_1 - \eta_1)x_1 - \alpha\hat{H}_1 x_2 + \eta_2 x_3 + c\hat{H}_1^2 + \alpha\hat{H}_1\hat{P}_1$$

$$b_2 = \beta\hat{P}_1 x_1 + (\beta\hat{H}_1 - \mu - \nu_1)x_2 + \nu_2 x_4 - \beta\hat{H}_1\hat{P}_1$$

$$b_3 = (\lambda - 2c\hat{H}_2 - \alpha\hat{P}_2 - \eta_2)x_3 - \alpha\hat{H}_2 x_4 + \eta_1 x_1 + c\hat{H}_2^2 + \alpha\hat{H}_2\hat{P}_2$$

$$b_4 = \beta\hat{P}_2 x_3 + (\beta\hat{H}_2 - \mu - \nu_2)x_4 + \nu_1 x_2 - \beta\hat{H}_2\hat{P}_2$$

$$a_{11} = (\lambda - 2c\hat{H}_1 + \alpha\hat{P}_1 + \eta_1)x_1 + \alpha\hat{H}_1 x_2 + \eta_2 x_3 + c\hat{H}_1^2 - \alpha\hat{H}_1\hat{P}_1 \qquad (6.73)$$

$$a_{22} = \beta\hat{P}_1 x_1 + (\beta\hat{H}_1 + \mu + \nu_1)x_2 + \nu_2 x_4 - \beta\hat{H}_1\hat{P}_1$$

$$a_{33} = (\lambda - 2c\hat{H}_2 + \alpha\hat{P}_2 + \eta_2)x_3 + \alpha\hat{H}_2 x_4 + \eta_1 x_1 + c\hat{H}_2^2 - \alpha\hat{H}_2\hat{P}_2$$

$$a_{44} = \beta\hat{P}_2 x_3 + (\beta\hat{H}_2 + \mu + \nu_2)x_4 + \nu_1 x_2 - \beta\hat{H}_2\hat{P}_2$$

$$a_{24} = -(\nu_1 x_2 + \nu_2 x_4) = a_{42}$$

$$a_{13} = -(\eta_1 x_1 + \eta_2 x_3) = a_{31}$$

$$a_{ij} = 0 \quad \text{otherwise.}$$

Using Arnold's solution, the probability distribution is the 4-dimensional Normal distribution with mean and variance

$$m_t(\underline{x}_0) = e^{C_1 t}[\underline{x}_0 + (\int_0^t e^{-C_1 u} du)C_2]$$

$$V_t(\underline{x}_0) = \int_0^t e^{C_1(t-u)} C_3 C_3^T e^{C_1^T(t-u)} du , \tag{6.74}$$

where $\underline{x}_0$ is the initial value of $\underline{X}$ at $t=0$, and

$$
C_1 = \begin{bmatrix}
\lambda - 2c\hat{H}_1 - \alpha\hat{P}_1 - \eta_1 & -\alpha\hat{H}_1 & \eta_2 & 0 \\[2em]
\beta\hat{P}_1 & \beta\hat{H}_1 - \mu - \nu_1 & 0 & \nu_2 \\[2em]
\eta_1 & 0 & \lambda - 2c\hat{H}_2 - \alpha\hat{P}_2 - \eta_2 & -\alpha\hat{H}_2 \\[2em]
0 & \nu_1 & \beta\hat{P}_2 & \beta\hat{H}_2 - \mu - \nu_2
\end{bmatrix}
$$

$$
C_2 = (c\hat{H}_1^2 + \alpha\hat{H}_1\hat{P}_1,\ -\beta\hat{H}_1\hat{P}_1,\ c\hat{H}_2^2 + \alpha\hat{H}_2\hat{P}_2,\ -\beta\hat{H}_2\hat{P}_2)^T
$$

$$
C_3 = \begin{bmatrix}
2\alpha\hat{H}_1\hat{P}_1 + 2\eta_1\hat{H}_1 & 0 & -(\nu_1\hat{H}_1 + \eta_2\hat{H}_2) & 0 \\[2em]
0 & 2\mu\hat{P}_1 + 2\nu_1\hat{P}_1 & 0 & -(\nu_1\hat{P}_1 + \nu_2\hat{P}_2) \\[2em]
-(\eta_1\hat{H}_1 + \eta_2\hat{H}_2) & 0 & 2\alpha\hat{H}_2\hat{P}_2 + 2\eta_2\hat{H}_2 & 0 \\[2em]
0 & -(\nu_1\hat{P}_1 + \nu_2\hat{P}_2) & 0 & 2\mu\hat{P}_2 + 2\nu_2\hat{P}_2
\end{bmatrix}
$$

Thus, the continuous approximation method can be applied to other more general models. In more complicated models, the general expression (as in 6.74) may be found for the moments, though these are too mathematically complicated to evaluate.

CHAPTER 7

MULTI-COLONY MODELS

7.1. Introduction

In the last two chapters, a spatial element was introduced into predator-prey modelling by splitting the population between two distinct colonies. Now we develop this idea of allowing for spatial variability by partitioning the population into a large or infinite number of colonies, with a limited form of migration between them.

When the colonies may be represented by the integer points on a single coordinate axis and migration occurs between nearest neighbours only, the model is known as the one-dimensional stepping-stone model. This is described in detail in Section 7.2. Stepping-stone models have been used in studying processes in genetics, and in birth-death-migration processes. These results, and other methods of studying interconnected predator-prey systems, are summarised in Section 7.3. The general solution for the unstable model (Lotka-Volterra) extended over infinite colonies has been found by Renshaw (1982). In Section 7.4. this solution is generalised to cover the stable model, where c, the density-dependent birth factor, is non-zero.

In the next two sections, results previously found for deterministic two-colony models are extended. In Section 7.5, we see that when the populations are split into any finite number of colonies, with equal migration rates between colonies, the total predator and prey movement is unaltered. However, this is not so when the number

of colonies is infinite. The effects of one-way migration of predators and prey on the Lotka-Volterra model are examined in Section 7.6.

In Section 7.7, we investigate the general stochastic N-colony model. Using the probability linearisation technique, an approximate solution for the probability structure of the stable model is found.

The effects of spatial separation of the prey and predator populations are further discussed in the next chapter, when we consider a spatially continuous approximation to the discrete stepping-stone model.

7.2. Description of the Stepping-Stone Model

Consider the predator and prey populations divided into an infinite number of colonies situated at the integer points of a single coordinate axis, represented by $-\infty < i < \infty$. Each colony undergoes a predator-prey process. Both the prey and predators may migrate to neighbouring colonies. The migration rates for the prey from colony i to $i+1, i-1$ are n_+, n_-, and for the predators are ν_+, ν_- (as illustrated in Figure 7.1). Let $H_i(t)$ denote the number of prey in colony i at time t, and $P_i(t)$ the number of predators. If, for example, the predator-prey process in each colony is the Volterra-Gause-Witt process, then the equations of the model are

$$\dot{H}_i = \lambda H_i - cH_i^2 - \alpha H_i P_i - (n_+ + n_-)H_i + n_+ H_{i-1} + n_- H_{i+1}$$

$$\dot{P}_i = \beta H_i P_i - \mu P_i - (\nu_+ + \nu_-)P_i + \nu_+ P_{i-1} + \nu_- P_{i+1} \qquad (7.1)$$

where $-\infty < i < \infty$.

The model described by equation 7.1 is a one-dimensional stepping-stone model. The model may be made more general by relaxing
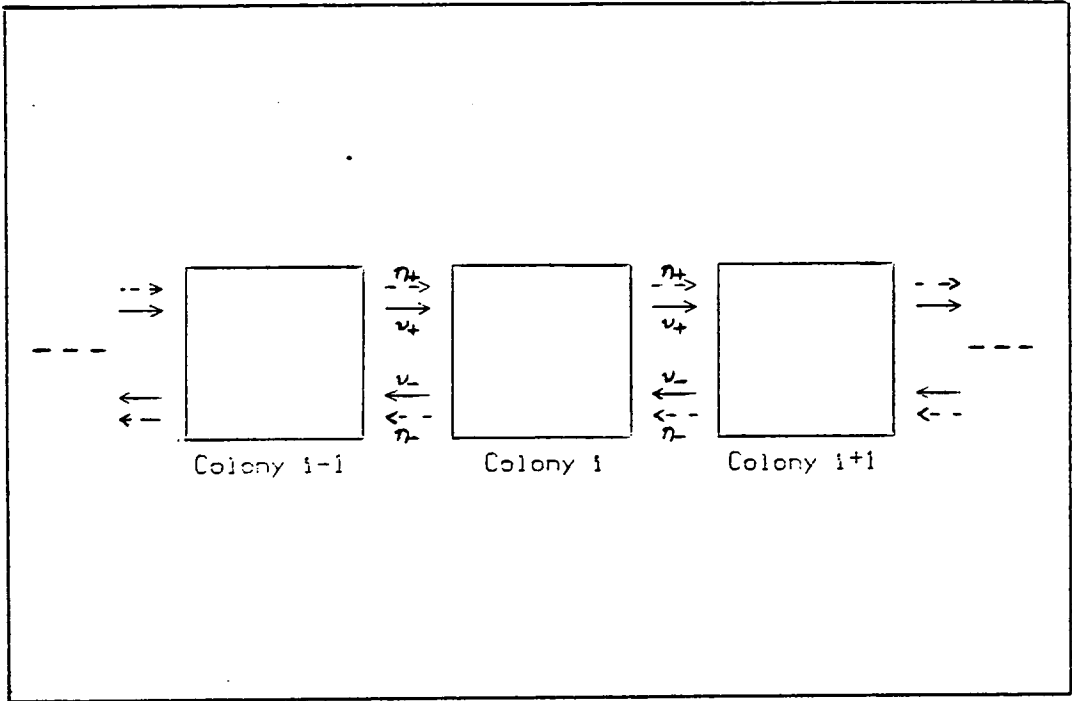
Figure 7.1. Diagram illustrating stepping-stone model with
- - - representing prey and ——— predators.

the migration restrictions, that is, by allowing the rates of migration between colonies to differ or by considering the predator-prey process in each colony to be different. The number of colonies in a stepping-stone model may also be finite ($1 \leqslant i \leqslant N$, where N is a fixed integer) or semi-infinite ($0 \leqslant i \leqslant \infty$).

When the arrangement of the colonies is linear the model is one-dimensional. Higher dimensional stepping-stone models are also possible. A two-dimensional model, for example, is formed by considering the colonies situated at the integer points of a two-dimensional lattice and allowing migration between nearest neighbours.

Because of the mathematical difficulty involved in more general models, throughout this chapter we shall only be looking at the one-dimensional model described by equations 7.1, with either a finite or

infinite number of colonies.

7.3. Recent Research

The stepping-stone model was originally introduced in the study of genetics, then applied to birth-death processes, and later to predator-prey processes. A survey of these developments is given here. We also include other results found when studying spatial separation in two-species population models, which do not rely on the stepping-stone arrangements.

The stepping-stone model was first proposed by Kimura (1953) to study the genetic structure of a population. Kimura assumed that the population was divided into infinitely many colonies located at the grid points of an n-dimensional lattice. Migration of individuals occurs between neighbouring colonies in each generation. Each colony also receives immigrants as random samples from the whole population. The first type of migration he called 'short range migration', and the second type 'long range migration'. Biological discussions of this model were given by Kimura and Weiss (1964), and Crow and Kimura (1970). Formulae for the genetic correlation and variance between colonies were obtained by Weiss and Kimura (1965) for more general cases of the model, but subject to the restriction that the short range migration is symmetrical in each fixed direction. Maruyama (1969) extended these results to cover situations where the restriction of symmetry of short range migration is removed. Stepping-stone models of finite length were considered by Maruyama (1970).

Stepping-stone models were used to study the effect of geographical separation of a population by Bailey (1968). The population is divided into an infinite number of colonies along a single dimension. Each colony undergoes a stochastic birth-death process with identical birth and death rates. Migration is allowed between neighbouring

colonies, with all migration rates equal. Bailey formed the forward probability equation and by using a generating function, calculated the first- and second-order moments. An approximate solution for the probability structure was found by Renshaw (1974). Adke (1969) generalised Bailey's model to include time-dependent birth and death rates. Adke and Moyal (1963) considered an analogous situation to Bailey's model by allowing individuals to diffuse continuously along a line, instead of migrating between discrete integer points. They developed an iterative procedure for evaluating the generating function of the colony sizes and found asymptotic properties when the population size is fixed. This model is extended to include time-dependent birth and death rates by Adke (1964). Stepping-stone models of finite length have been investigated for the general birth-death-migration process by Renshaw (1972).

The predator-prey process has been considered in the stepping-stone arrangement by Renshaw (1982) The process involved is the Volterra-Gause-Witt process in the infinite domain. Renshaw examined the effect of introducing predators into a previously predator-free environment. Expressions are given to describe the manner in which the predators advance through the system. Renshaw also found the general solution to the linearised equations of the infinite-colony Lotka-Volterra model. He showed that this solution ultimately decays to zero. However by altering the spatial arrangement, so that the colonies are represented by the non-negative integers ($0 \leqslant i < \infty$), and migration occurs to the right only, then a stable cycle will persist in colony 0 which will also affect the behaviour in the other colonies. The result, for large t, is a series of linked elliptical cycles around the equilibrium values. The amplitude of these cycles decreases geometrically with i, and the phase lag increases linearly.

The effect of spatial separation in competition models was stu-

died by Levins and Culver (1971) and Horn and Mac Arthur (1972) by looking at the proportion of habitats, or colonies, occupied by a given species. It was shown that stabilisation is possible even for potentially unstable competitive interactions. This procedure was used with predator-prey models by Vandermeer (1973). He examined the proportion of habitats occupied by prey or predators only, both prey and predators, or neither. He found that an approximate balance between interhabitat migration and local population extinction is capable of stabilising an otherwise unstable model. The system becomes stable as the rate of predator migration becomes large relative to prey migration, or the extinction rate of the predators becomes large relative to the extinction rate of the prey.

Another method of studying the spatial separation effect in predator-prey models is that investigated by Chewning (1975), and mentioned in Section 5.6. Keeping the migration parameters small, Chewning linearised the equations of the model about the equilibrium point which would occur if no migration were present. General conditions under which limited migration can have a stabilising influence on locally unstable predator-prey dynamics are given when the number of colonies is finite.

7.4. Solution for Stable Model

7.4.1. Solution

The linear solution for the infinite colony ($-\infty < i < \infty$) system, in which each colony undergoes a Lotka Volterra process, and migration of both predators and prey is possible, was found by Renshaw (1982). Here we extend this technique to cover the stable system (given by equations 7.1) where c, the self-inhibiting factor in the prey birth rate, is non-zero.

Recall (from 7.1) that the deterministic equations of the model are

$$\dot{H}_i = (\lambda - cH_i)H_i - \alpha H_i P_i - \eta_+(H_i - H_{i-1}) - \eta_-(H_i - H_{i+1})$$

$$\dot{P}_i = \beta H_i P_i - \mu P_i - \nu_+(P_i - P_{i-1}) - \nu_-(P_i - P_{i+1}) \qquad (7.2)$$

for $-\infty < i < \infty$. The deterministic eqilulibrium occurs at

$$\hat{H} = \frac{\mu}{\beta} \qquad \hat{P} = \frac{\lambda - c\hat{H}}{\alpha} \, ,$$

in all colonies, and the equations linearised around these are

$$\dot{h}_i = -c\hat{H}h_i - \alpha\hat{H}p_i - \eta_+(h_i - h_{i-1}) - \eta_-(h_i - h_{i+1})$$

$$\dot{p}_i = \beta\hat{P}h_i - \nu_+(p_i - p_{i-1}) - \nu_-(p_i - p_{i+1}) \, . \qquad (7.3)$$

Define the generating functions

$$U(z,t) = \sum_{i=-\infty}^{\infty} h_i(t) z^i$$

$$V(z,t) = \sum_{i=-\infty}^{\infty} p_i(t) z^i \, , \qquad (7.4)$$

assuming they exist in some suitably chosen domain of z. Multiplying equations 7.3 by z^i and summing over i, we can solve to find U and V:

$$U(z,t) = A(z)e^{\omega_1 t} + B(z)e^{\omega_2 t}$$

$$V(z,t) = \frac{-1}{\alpha\hat{H}}[A(z)\omega_1 e^{\omega_1 t} + B(z)\omega_2 e^{\omega_2 t}] \qquad (7.5)$$

$$+\{c\hat{H}+\eta_+(1-z)+\eta_-(1-z^{-1})\}(A(z)e^{\omega_1 t}+B(z)e^{\omega_2 t})\}\ ,$$

where

$$\omega_{1,2} = [-c\hat{H}-(\eta_++\nu_+)(1-z)-(\eta_-+\nu_-)(1-z^{-1}) \pm \Delta]/2$$

$$\Delta^2 = [c\hat{H}+(\nu_+-\eta_+)(1-z)+(\nu_--\eta_-)(1-z^{-1})]^2-4\alpha\beta\hat{H}\hat{P}, \qquad (7.6)$$

and the constants A and B are

$$A(z)(\omega_2-\omega_1) = \alpha\hat{H}V(z,0)+[\omega_2+c\hat{H}+\eta_+(1-z)+\eta_-(1-z^{-1})]U(z,0)$$

$$B(z)(\omega_1-\omega_2) = \alpha\hat{H}V(z,0)+[\omega_1+c\hat{H}+\eta_+(1-z)+\eta_-(1-z^{-1})]U(z,0)\ . \qquad (7.7)$$

The solution for the Lotka-Volterra process, found by Renshaw, is, of course, obtained from 7.5 by letting c equal zero.

If, initially, all the colonies are at equilibrium except for colony 0, which is perturbed by an influx of k predators, then

$$U(z,0) = 0\ , \qquad V(z,0) = k\ .$$

If we also let $\eta_-=\nu_-$ and $\eta_+=\nu_+$, then the solution simplifies to

$$h_1(t) = -k\frac{\alpha\mu}{\beta\theta}e^{-(c\hat{H}/2+\nu_++\nu_-)t}(\nu_+/\nu_-)^{1/2}$$

$$\times\ I_1(2t\ \sqrt{\nu_+\nu_-})[e^{\theta t/2}-e^{-\theta t/2}]$$

$$P_1(t) = \frac{k}{2\theta}e^{-(c\hat{H}/2+\nu_++\nu_-)t}\left[(c\hat{H}+\theta)e^{\theta t/2}-(c\hat{H}-\theta)e^{-\theta t/2}\right]$$

$$x \ (\nu_+/\nu_-)^{i/2} I_i (2t \ \sqrt{\nu_+\nu_-}) \qquad (7.8)$$

where $\theta = \sqrt{c^2\hat{H}^2 - 4\alpha\beta\hat{H}\hat{P}}$ and $I_i(z)$ is a modified Bessel function of the first kind, given by

$$I_i(z) = \left[\frac{z}{2}\right]^i \sum_{j=0}^{\infty} \frac{(z^2/4)^j}{j! \Gamma(i+j+1)}$$

(see Abramowitz and Stegun, 1965, result 9.6.10). Using the asymptotic expansion

$$I_i(z) \approx e^z/\sqrt{2\pi z} \ ,$$

for fixed i and large z, the expressions in 7.8 may be written more simply, for large t, as:

$$h_1(t) \approx -\frac{\alpha\mu k}{2\beta\theta} e^{-c\hat{H}t/2} [e^{\theta t/2} - e^{-\theta t/2}] \ [\nu_+/\nu_-]^{i/2} \left[\frac{e^{-t(\sqrt{\nu_+} - \sqrt{\nu_-})^2}}{\{\pi t \sqrt{\nu_+\nu_-}\}^{1/2}}\right]$$

$$P_1(t) \approx \frac{k}{4\theta} e^{-c\hat{H}t/2} \left[(c\hat{H}+\theta)e^{\theta t/2} - (c\hat{H}-\theta)e^{-\theta t/2}\right]$$

$$[\nu_+/\nu_-]^{i/2} \left[\frac{e^{-t(\sqrt{\nu_+} - \sqrt{\nu_-})^2}}{\{\pi t \sqrt{\nu_+\nu_-}\}^{1/2}}\right]. \qquad (7.9)$$

7.4.2. Discussion

By comparing the general solution 7.5 with the solution for $c=0$ (given by Renshaw, 1982), we see that the inclusion of the c factor does not greatly affect the format of the solution. The main difference is that the damping factor in $e^{\omega_1 t}$ is increased.

The effect of including the c factor is more apparent if we compare solution 7.9 with the relevant solution when c=0. In both cases, the solutions change geometrically with i at rate $[v_+/v_-]^{i/2}$. When c=0, h_i and p_i are both oscillatory. All colonies oscillate in phase, but the predator and prey are $\pi/2$ out of phase with each other. As t gets large, the solution decays to zero. When c is introduced into the model, the solution decreases to zero faster because of the extra damping factor, $e^{-c\hat{H}t/2}$. When c is small, the motion is still oscillatory. By writing 7.9 in terms of $\cos\psi$ and $\sin\psi$, where

$$\psi = \sqrt{4\alpha\beta\hat{H}\hat{P}-c^2\hat{H}^2} \; ,$$

we see that the predators and prey are no longer $\pi/2$ out of phase, but instead have a phase lag given by

$$B = \tan^{-1}[\psi/(c\hat{H})] \; .$$

When c is greater than $2\sqrt{\alpha\beta\hat{P}/\hat{H}}$, the motion is purely exponential.

7.5. Conservation of Motion for Finite Number of Colonies

In Section 5.3, we saw that, when the population was split into two colonies and the migration parameters were equal, motion was conserved. By 'conservation of motion', we mean that if h_1, h_2 are the linearised solutions for the prey perturbations in the two-colony model (p_1, p_2 for the predators), and h the one-colony solution for prey (p for predators), then

$$h_1(t)+h_2(t) = h(t)$$

$$p_1(t)+p_2(t) = p(t), \quad \text{for all } t, \qquad (7.10)$$

subject to identical initial conditions.

Renshaw (1982) examined the asymptotic solutions of the infinite colony Lotka-Volterra model – given by equations 7.1 with c equal to 0. When all the migration parameters are equal, that is, $\eta_+ = \eta_- = \nu_+ = \nu_-$, the solutions were found to decay to zero at the rate of $t^{-1/2}$, as can be seen from 7.9. Hence, motion is not conserved when the number of colonies is infinite. However, as we show here, the two-colony result does hold when the population is split into any finite number of colonies.

Suppose we have an N-colony system with each colony undergoing a Lotka-Volterra process. Migration of prey is allowed to the right or left at rate η, and similarly for predators at rate ν. The deterministic equations of the model are

$$\dot{H}_i = \lambda H_i - \alpha H_i P_i + \eta (H_{i-1} + H_{i+1} - 2H_i)$$

$$\dot{P}_i = \beta H_i P_i - \mu P_i + \nu (P_{i-1} + P_{i+1} - 2P_i), \qquad (7.11)$$

for $1 \leqslant i \leqslant N$, where for notational convenience, we define

$$H_0(t) \equiv H_1(t) \qquad H_{N+1}(t) \equiv H_N(t)$$

$$P_0(t) \equiv P_1(t) \qquad P_{N+1}(t) \equiv P_N(t), \quad \text{for all } t.$$

The equilibrium is identical in all colonies, and given by

$$H_i = \mu/\beta \equiv \hat{H}$$

$$P_i = \lambda/\alpha \equiv \hat{P} \quad . \qquad (7.12)$$

The equations linearised about this equilibrium are

$$\dot{h}_i = -\alpha \hat{H} p_i + \eta(h_{i-1} + h_{i+1} - 2h_i)$$

$$\dot{p}_i = \beta \hat{P} h_i + \nu(p_{i-1} + p_{i+1} - 2p_i) \; . \tag{7.13}$$

To solve by using the method of images, for $-\infty < i < \infty$, will require the following 4 boundary conditions:

$$h_0(t) \equiv h_1(t) \qquad h_{N+1}(t) \equiv h_N(t)$$

$$p_0(t) \equiv p_1(t) \qquad p_{N+1}(t) \equiv p_N(t), \quad \text{for all } t.$$

Summing the equations in 7.13 from 1 to N,

$$\sum_1^N \dot{h}_i = -\alpha \hat{H} \sum_1^N p_i \quad , \quad \sum_1^N \dot{p}_i = \beta \hat{P} \sum_1^N h_i \; . \tag{7.14}$$

These equations have the same form as in the one-colony case (see equation 2.8), and hence

$$\sum_1^N h_i(t) = h(t) \quad , \quad \sum_1^N p_i(t) = p(t), \quad \text{for all } t, \tag{7.15}$$

when the initial conditions are equal. Thus, motion is conserved when the number of colonies is finite.

This result may seem surprising. As N becomes large, we might expect our N-colony results to approach those of the ∞-colony situation. When the number of colonies is finite, edge effects will always influence the total fluctuation equations (7.14). It is possible that the non-zero fluctuations, after a time t, are due solely to the edge effects, so that when N becomes large, the colonies at a distance from the edges experience no fluctuations. When N becomes large, perturbations in the central colonies (that is, away from the

edges) decay to zero (for large t). In this way, the N-colony results would approach those of the ∞-colony case.

7.6. Migration in One Direction Only

7.6.1. Summary of two-colony result

In Chapter 5, we investigated the effect of one-way migration of prey and predators between two colonies undergoing the Lotka-Volterra process. Recall that, for large t, both colonies experienced oscillatory motion with identical periods of oscillation. There was, however, a phase difference between the colonies: when predators were migrating the second colony lagged the first (Section 5.5.2), and when prey were migrating the second colony led (Section 5.4.3). We now see if these results still hold in the multi-colony situation.

7.6.2. Migration of predators

Renshaw (1982) studied the system where the population is divided into colonies represented by the non-negative integers ($0 \leq i < \infty$). Each colony undergoes a Lotka-Volterra process, and predators are allowed to migrate to the right only, at rate ν (as illustrated in Figure 7.2). Renshaw linearised the equations of the model using

$$H_i(t) = \hat{H}_i + h_i(t)$$

$$P_i(t) = \hat{P}_i + p_i(t),$$

where $\hat{H}_i, \hat{P}_i$ are the equilibrium values. Subject to the initial conditions

$$h_i(0) = 0 \qquad i > 0$$
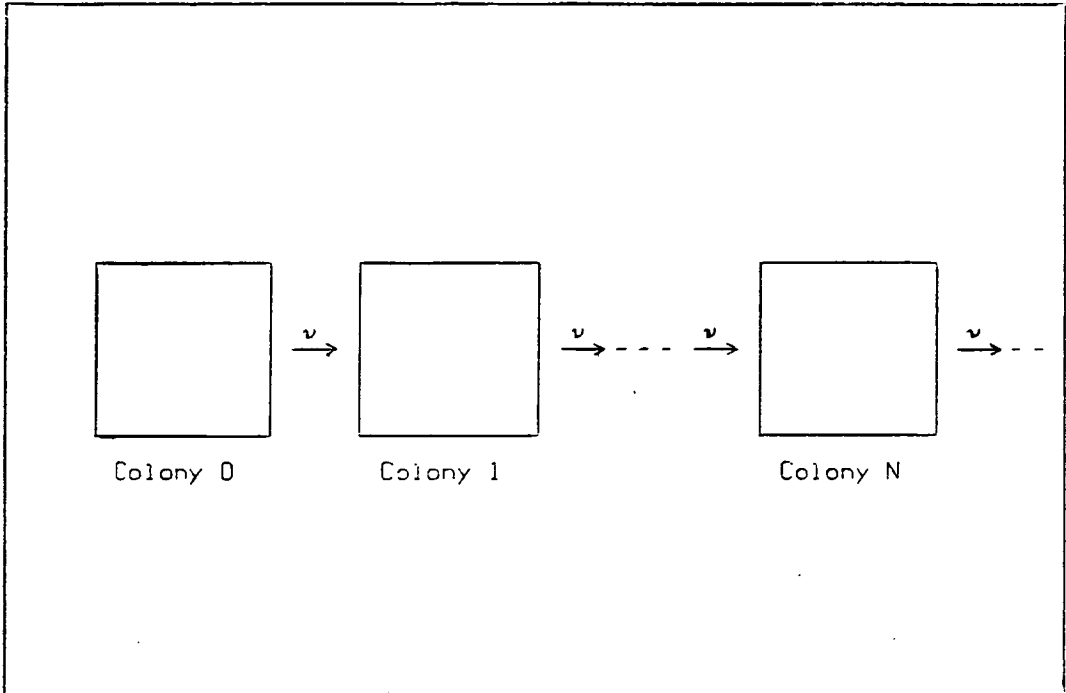
Figure 7.2. Diagram representing ∞-colony Lotka–Volterra model, with one-way migration of predators only, at rate ν.

$$p_i(0) = 0 \qquad i>0$$

$$p_0(0) = k \, , \tag{7.16}$$

the solutions to the linearised equations, for large t, were found to be

$$h_i(t) = -\alpha\mu/(\xi\beta) \, kr^i \sin(\xi t - i\delta)$$

$$p_i(t) = kr^i \cos(\xi t - i\delta) \, , \tag{7.17}$$

where

$$\xi = \sqrt{\lambda(\mu+\nu)}, \qquad r = \sqrt{\frac{\mu+\nu}{\lambda+\mu+\nu}}, \qquad \delta = \tan^{-1}\sqrt{\lambda/(\mu+\nu)} \, .$$

Thus, as we might expect from the two-colony results, each colony oscillates with the same period of oscillation, and colony i lags colony i-1 by δ. As ν increases, this phase lag δ, decreases to 0.

7.6.3. Migration of prey

Consider now the system described in 7.6.2 above, but, instead of predators migrating, we allow prey to migrate at rate η, as shown in Figure 7.3.
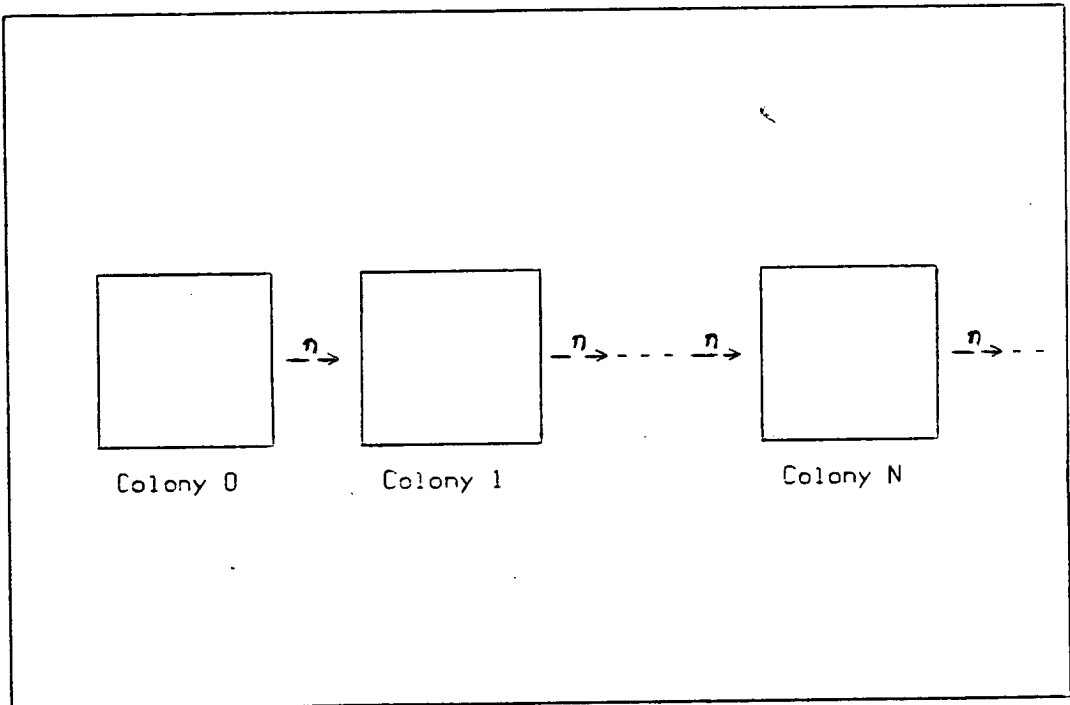
Figure 7.3. Diagram representing ∞-colony Lotka-Volterra model, with one-colony migration of prey only, at rate η.

That is, deterministically, the system is given by

$$\dot{H}_0 = \lambda H_0 - \alpha H_0 P_0 - \eta H_0$$

$$\dot{P}_0 = \beta H_0 P_0 - \mu P_0$$

$$\dot{H}_i = \lambda H_i - \alpha H_i P_i - \eta(H_i - H_{i-1}) \tag{7.18}$$

$$\dot{P}_i = \beta H_i P_i - \mu P_i, \qquad (i>0).$$

The equilibrium values occur at

$$\hat{H}_0 = \mu/\beta \qquad \hat{P}_0 = (\lambda-\eta)/\alpha$$

$$\hat{H}_i = \mu/\beta \qquad \hat{P}_i = \lambda/\alpha, \qquad (i>0). \tag{7.19}$$

Notice that η must be restricted to $\eta<\lambda$ in order to keep $\hat{P}_0$ positive. For $i=0$, the equations linearised about this equilibrium are

$$\dot{h}_0 = -(\alpha\mu/\beta)p_0$$

$$\dot{p}_0 = (\beta(\lambda-\eta)/\alpha)h_0. \tag{7.20}$$

The solution, subject to the initial conditions described in 7.16, for colony 0 is

$$h_0(t) = -\frac{\alpha}{\beta}k\sqrt{\frac{\mu}{\lambda-\eta}}\sin\theta t$$

$$p_0(t) = k\cos\theta t,$$

where $\theta = \sqrt{(\lambda-\eta)\mu}$. The linearised equations for $i>0$ are

$$\dot{h}_i = -\alpha\mu/\beta\, p_i - \eta(h_i - h_{i-1})$$

$$\dot{p}_i = (\lambda\beta/\alpha)h_i. \tag{7.21}$$

We solve these equations by the approach used by Renshaw (1982). Suppose that the cyclic behaviour in colony 0 forces an oscillatory behaviour in all other colonies with the same period of oscillation, $2\pi/\theta$ in all colonies. Then, for large t, a possible solution for $h_i(t)$ might be

$$h_i(t) = a_i \cos \theta t + b_i \sin \theta t \, , \qquad (7.22)$$

where a_i and b_i are constants. Then, from 7.21

$$p_i(t) = \lambda\beta/(\alpha\theta) \, [a_i \sin \theta t - b_i \cos \theta t] + C, \qquad (7.23)$$

where C is a constant of integration. Using 7.21, we find that C=0, and a_i and b_i satisfy the relationship

$$b_i \mu/\theta - a_i = -a_{i-1}$$

$$a_i \mu/\theta + b_i = b_{i-1} \, . \qquad (7.24)$$

This relationship allows us to calculate a_i and b_i, and hence, for large t, the approximate solutions are

$$h_i(t) = -k\alpha/\beta \, \sqrt{\mu/(\lambda-\eta)} \, s^i \sin(\theta t + i\psi)$$

$$p_i(t) = \lambda k/(\lambda-\eta) \, s^i \cos(\theta t + i\psi) \, , \qquad (7.25)$$

where

$$s = \sqrt{(\lambda-\eta)/(\lambda-\eta+\mu)} \, , \qquad \psi = \tan^{-1} \sqrt{\mu/(\lambda-\eta)} \, .$$

Thus, for large t, the system behaves as a series of linked elliptical cycles. Comparing these results with the solutions for

predator migration (7.17), the amplitude decreases geometrically with i, and the phase difference increases linearly. The main difference between the results is that here the phase difference, ψ, is positive: hence colony i leads colony i-1. As η approaches λ (its maximum value), ψ increases to $\pi/2$.

7.6.4. Conclusion

In the infinite-colony Lotka-Volterra process, with one-way migration of prey or predators, after a time t, the system forms a series of linked elliptical cycles. All colonies oscillate with the same period. When only predators migrate, colony i lags i-1, by δ (7.17). When prey migrate, colony i leads i-1, by ψ (7.25). Similar results were previously seen for two-colony models.

As the predator migration rate, ν, increases, δ decreases to zero, showing that the effects of spatial separation become negligible. As η, the prey migration rate increases, ψ also increases. However, in order that the equilibrium values are positive, a maximum bound is imposed on η, so that large values of η cannot be used.

7.7. Stochastic Model

In Section 4.6, we used the technique of probability linearisation to obtain the distribution of the approximating continuous process. The technique was used to find the moments of the two-colony model in Section 6.4. We now extend this result to the general N-colony stepping-stone model.

In this N-colony model, both prey and predators are allowed to migrate from colony i to i+1 at rates ν_i, η_i and from i to i-1 at rates γ_i, δ_i, respectively, as shown in Figure 7.4. Each colony undergoes a stable predator-prey process, though the parameters may vary with i. For example, the deterministic equations for colony i
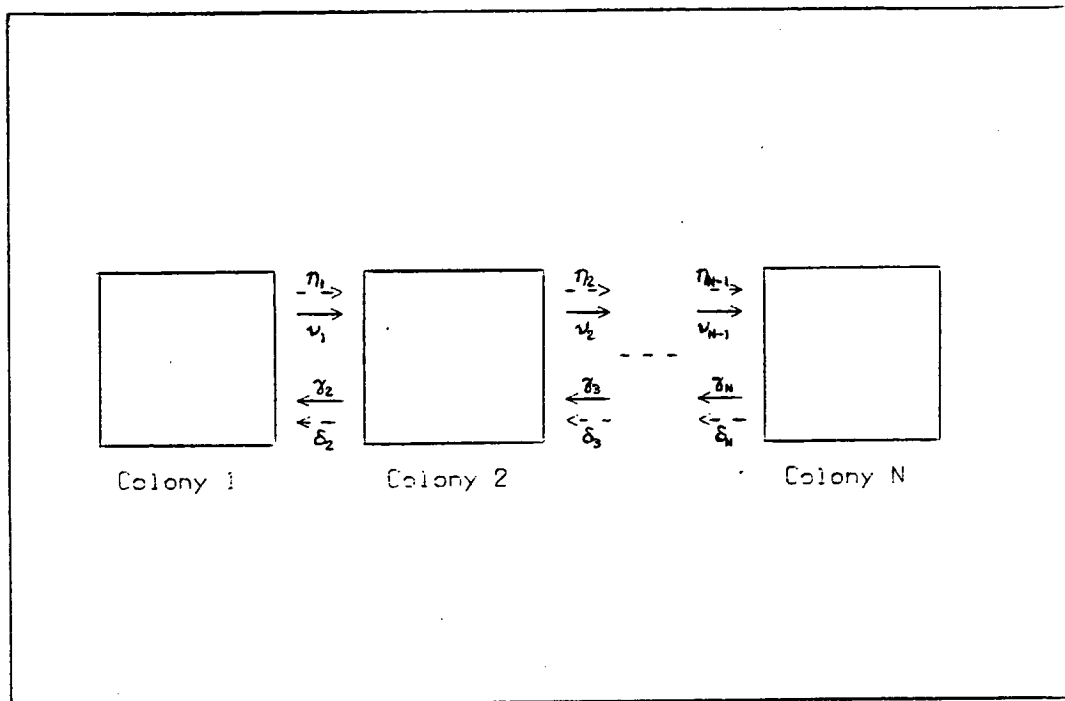
Figure 7.4. N-colony model with general migration rates, where - - - represents migration of the prey and ——— the predators.

would be

$$\dot{H}_i = \lambda_i H_i - c_i H_i^2 - \alpha_i H_i P_i - (\eta_i + \delta_i)H_i + \eta_{i-1}H_{i-1} + \delta_{i+1}H_{i+1}$$

$$\dot{P}_i = \beta_i H_i P_i - \mu_i P_i - (\nu_i + \gamma_i)P_i + \nu_{i-1}P_{i-1} + \gamma_{i+1}P_{i+1} \quad . \tag{7.26}$$

Following the method used in 6.4, we linearise the probabilities and find that the Kolmogorov forward equation of the approximating continuous process is

$$\frac{\partial p}{\partial t} = \frac{1}{2} \sum_{j=1}^{2N} \sum_{i=1}^{2N} \frac{\partial^2}{\partial x_i \partial x_j}(a_{ij}p) - \sum_{i=1}^{2N} \frac{\partial}{\partial x_i}(b_i p) \quad , \tag{7.27}$$

where $p \equiv p(x_1, x_2, x_3, \ldots\ldots, x_{2N}; t)$

= probability of having

x_1 prey, x_2 predators in colony 1,

x_3 prey, x_4 predators in colony 2,

etc.

at time t.

For notational convenience, let

$$i = \begin{cases} k/2 & \text{if } k \text{ is even,} \\ \\ (k+1)/2 & \text{if } k \text{ is odd.} \end{cases}$$

Then a_{kl} and b_k are given as follows:
if k odd, then

$$b_k = (\lambda_i - 2c_i\hat{H}_i - \alpha_i\hat{P}_i - \nu_i - \gamma_i)x_k$$

$$- \alpha_i\hat{H}_i x_{k+1} + c_i\hat{H}_i^2 + \alpha_i\hat{H}_i\hat{P}_i ,$$

$$+ \nu_{i-1}x_{k-2} + \gamma_{i+1}x_{k+2}$$

if k even, then

$$b_k = (\beta_i\hat{H}_i - \mu_i - \eta_i - \delta_i)x_k + \beta_i\hat{P}_i x_{k-1}$$

$$- \beta_i \hat{H}_i \hat{P}_i + \eta_{i-1} x_{k-2} + \delta_{i+1} x_{k+2} \cdot$$

if k odd, then

$$a_{kk} = (\lambda_i - 2c_i \hat{H}_i + \alpha_i \hat{P}_i + \nu_i + \gamma_i) x_k$$

$$+ \alpha_i \hat{H}_i x_{k+1} + c_i \hat{H}_i^2 - \alpha_i \hat{H}_i \hat{P}_i$$

$$+ \nu_{i-1} x_{k-2} + \gamma_{i+1} x_{k+2} \cdot$$

$$a_{k,k+2} = - \nu_i x_k - \gamma_{i+1} x_{k+2}$$

$$= a_{k-2,k} \cdot$$

if k even, then

$$a_{kk} = (\beta_i \hat{H}_i + \mu_i + \eta_i + \delta_i) x_k + \beta_i \hat{P}_i x_{k-1}$$

$$-\beta_i \hat{H}_i \hat{P}_i + \eta_{i-1} x_{k-2} + \delta_{i+1} x_{k+2} \cdot$$

$$a_{k,k+2} = -\eta_i x_k - \delta_{i+1} x_{k+2}$$

$$= a_{k-2,k} \cdot$$

All other elements of $A \equiv (a_{ij})$ are zero.

As in Section 6.4, we use a result from Arnold (1974) to show that $\underline{X}(t)$, where

$$\underline{X}(t) = (x_1(t), x_2(t), \ldots, x_{2N}(t)).$$

has a 2N-dimensional Normal distribution with mean and variance defined by

$$m_t(\underline{x}_0) = e^{C_1 t} [\underline{x}_0 + (\int_0^t e^{-C_1 u} du) C_2]$$

$$V_t(\underline{x}_0) = \int_0^t e^{C_1(t-u)} C_3 C_3^T e^{C_1^T(t-u)} du \quad , \tag{7.28}$$

where $\underline{x}_0$ is the initial value of $\underline{x}(t)$ (at $t=0$). The matrices C_1, C_2 and C_3 have dimension $2N \times 2N$, $2N \times 1$ and $2N \times 2N$ respectively, and are defined to be:

$$C_1 = \begin{bmatrix} r_1 & -\alpha_1 \hat{H}_1 & \gamma_2 & 0 & 0 & 0 & \cdots \\ \beta_1 \hat{P}_1 & s_1 & 0 & \delta_2 & 0 & 0 & \cdots \\ \nu_1 & 0 & r_2 & -\alpha_2 \hat{H}_2 & \gamma_3 & 0 & \cdots \\ 0 & \eta_1 & \beta_2 \hat{P}_2 & s_2 & 0 & \delta_3 & \cdots \\ & & & & \ddots & & \\ \cdots & & & & 0 & \eta_{N-1} & \beta_N \hat{P}_N & s_N \end{bmatrix}$$

where $r_i = \lambda_i - 2c_i \hat{H}_i - \alpha_i \hat{P}_i - \nu_i - \gamma_i$

$$s_i = \beta_i \hat{H}_i - \mu_i - n_i - \delta_i \quad ,$$

$$C_2 = (c_1\hat{H}_1^2 + \alpha_1\hat{H}_1\hat{P}_1, \quad -\beta_1\hat{H}_1\hat{P}_1, \quad c_2\hat{H}_2^2 + \alpha_2\hat{H}_2\hat{P}_2 \quad ,$$

$$-\beta_2\hat{H}_2\hat{P}_2, \quad \ldots\ldots, \beta_N\hat{H}_N\hat{P}_N)^T \quad ,$$

$$C_3 = \begin{bmatrix} a_1 & 0 & m_1 & 0 & 0 & \cdots \\ 0 & a_2 & 0 & m_2 & 0 & \cdots \\ m_1 & 0 & a_3 & 0 & m_3 & \cdots \\ 0 & m_2 & 0 & a_4 & 0 & \cdots \\ & & & & \ddots & \\ \cdots\cdots & & & m_{N-1} & 0 & a_N \end{bmatrix}$$

where

if k is odd:

$$a_k = \lambda_i\hat{H}_i - c_i\hat{H}_i^2 + \alpha_i\hat{H}_i\hat{P}_1 + (\nu_i + \gamma_i)\hat{H}_i$$

$$+ \nu_{i-1}\hat{H}_{i-1} + \gamma_{i+1}\hat{H}_{i+1}$$

$$m_k = -\nu_1\hat{H}_i - \gamma_{i+1}\hat{H}_{i+1} \quad ,$$

if k is even:

$$a_k = \beta_i \hat{H}_i \hat{P}_i + \mu_i \hat{P}_i + (\eta_i + \delta_i) \hat{P}_i$$

$$+ \eta_{i-1} \hat{P}_{i-1} + \delta_{i+1} \hat{P}_{i+1}$$

$$m_k = -\eta_i \hat{P}_i - \delta_{i+1} \hat{P}_{i+1} .$$

Thus, although the notation is tedious, when the deterministic equilibrium values $\hat{H}_i, \hat{P}_i$ are known, an approximate solution can be found for the probability structure of the continuous approximation of the general N-colony stepping-stone model. This method may also be used to find moments of the distributions for the higher dimensional models mentioned in Section 7.2. In higher dimensions, the matrices C_1 and C_3 are less sparse, making them more difficult to work with.

CHAPTER 8

SPATIAL DIFFUSION

8.1. Introduction

In this chapter, we discuss the effects of spatial diffusion, or dispersal, in population models. Instead of treating the location of the populations as a single point, or N discrete points (as in Chapter 7), we allow the individuals to diffuse continuously through a region, which may be single- or multi-dimensional.

An important analytical study of the dispersal of living organisms was carried out by Skellam (1951, 1973). Starting from the random-walk problem, he deduced the law of diffusion, and applied it to study the spatial distribution of a growing population. Much work has been done since then in applying diffusion to ecological models; comprehensive reviews on recent work may be found in McMurtrie (1978) and Okubo (1980).

We define the general reaction-diffusion model in Section 8.2. Studies of diffusional effects on ecological models fall into two main categories. Firstly, the ability of diffusion to damp out spatial pattern, and to stabilise the model, has been investigated - this will be discussed in Section 8.3. Secondly, in 8.4, we discuss how diffusion can be responsible for the emergence of spatial pattern in a spatially homogeneous environment. These two sections deal mostly with random diffusion - more general diffusion terms will be discussed in Section 8.5. Finally (in Section 8.6), a comparison is drawn between diffusion models, and the multi-colony discrete models

considered in Chapters 4 - 7.

8.2. The Reaction-Diffusion Equation

In three-dimensional space, the general N-species equation, incorporating diffusion of species, is

$$\frac{\partial S_i}{\partial t} = -\frac{\partial}{\partial x}(A_{x_i} S_i) - \frac{\partial}{\partial y}(A_{y_i} S_i) - \frac{\partial}{\partial z}(A_{z_i} S_i)$$

$$+ \frac{\partial}{\partial x}\left[D_{x_i}\frac{\partial S_i}{\partial x}\right] + \frac{\partial}{\partial y}\left[D_{y_i}\frac{\partial S_i}{\partial y}\right] + \frac{\partial}{\partial z}\left[D_{z_i}\frac{\partial S_i}{\partial z}\right]$$

$$+ F_i(S_j,x,y,z,t) \quad i,j=1,\ldots,N \quad , \tag{8.1}$$

where S_i is the density of the i'th species and F_i represents the population interaction terms. The D_{x_i}, D_{y_i} and D_{z_i} are the diffusion coefficients of the i'th species dispersing in the x, y and z directions, respectively. The A_{x_i}, A_{y_i} and A_{z_i} are known as advection coefficients for the x, y and z directions, respectively. We will outline the derivation of this equation, by using the explanations given by Okubo (1980). A more rigorous derivation is given by McMurtrie (1978), following the arguments of Skellam (1951, 1973).

For simplicity, suppose we have a single type of species, with density S, and diffusion is allowed in just one direction, x. The flux, J, is the number of particles flowing through a given area per unit time (where by 'area' in one-dimension, we mean length). According to Fick's law of diffusion (see Crank, 1956), the flux is proportional to the negative of the rate of change of the density. Thus

$$J = - D\frac{\partial S}{\partial x} , \qquad\qquad (8.2)$$

where D is known as the diffusion coefficient. Using this, we find

$$\frac{\partial S}{\partial t} = - \frac{\partial J}{\partial x} = \frac{\partial}{\partial x}\left[D\frac{\partial S}{\partial x}\right] . \qquad\qquad (8.3)$$

The diffusion terms in 3-dimensional space (the D terms in 8.1) are also obtained in this way.

Advection terms arise when the movement of species is no longer random, but may be subject to influences such as a current or variation in the environment. Let $A(x,t)$ be the instantaneous velocity of the species. Owing to changes in local conditions (that is, advection), A is variable. The flux of particles generated by this velocity is AS. Thus, when advection is included, the total flux is

$$J = AS - D\frac{\partial S}{\partial x} , \qquad\qquad (8.4)$$

which means that

$$\frac{\partial S}{\partial t} = -\frac{\partial}{\partial x}(AS) + \frac{\partial}{\partial x}\left[D\frac{\partial S}{\partial x}\right] . \qquad\qquad (8.5)$$

Equation 8.1 is found from this by generalising to N species, three spatial variables, and including the interaction terms.

The equation 8.1 deals only with self-diffusion: that is, diffusion of the i'th species merely affects the density of its own species. In Section 8.4.4, we will see that Jorné(1977) examined a model which included cross-diffusion terms.

In the next two sections, we will be considering models with random diffusion only. Advection effects will be included in Section 8.5.

8.3. The Damping Effect of Diffusion

8.3.1. Introduction

In the deterministic situation, when a region is undergoing a predator-prey process, random diffusion can have the effect of damping out all spatial variation. This will be seen in Section 8.3.2, when we consider a linear analysis of the Lotka-Volterra model with diffusion. This smoothing effect is not the result of linearising the model. More general non-linear studies (Section 8.3.3) also indicate the damping effect of diffusion.

8.3.2. Linear analysis

Consider the Lotka-Volterra model in which random diffusion is allowed in one spatial dimension, x. Then, equation 8.1 is reduced to

$$\frac{\partial S_1}{\partial t} = D_1 \frac{\partial^2 S_1}{\partial x^2} + \lambda S_1 - \alpha S_1 S_2$$

$$\frac{\partial S_2}{\partial t} = D_2 \frac{\partial^2 S_2}{\partial x^2} + \beta S_1 S_2 - \mu S_2 \ , \qquad\qquad (8.6)$$

where $S_1(x,t)$ and $S_2(x,t)$ are densities of the prey and predator species, respectively, and the D_i's are constant diffusion coefficients. The populations are allowed to diffuse uniformly (since the D_i's are constant) through a bounded region $(0,L)$, which is surrounded by an unfavourable environment.

Okubo (1980) performed a linear stability analysis on this model. Let $\hat{S}_1$ and $\hat{S}_2$ be the equilibrium points (for prey and predators, respectively) which the model would have, if we ignored spatial

separation and diffusion effects. Okubo linearised the equation 8.6 about these points. If s_1 and s_2 are the linear perturbations from the equilibrium, he suggested that appropriate boundary conditions are either

(i) $s_1 = s_2 = 0$ at x=0, x=L,

or (8.7)

(ii) $D_1 \dfrac{\partial s_1}{\partial x} = D_2 \dfrac{\partial s_2}{\partial x} = 0$ at x=0, x=L.

Under conditions 8.7(i), at the boundary, the linear perturbations are zero. This corresponds to an absorbing barrier (an ecological example of this would be a group of animals in a clearing in a forest – once outside the bounds of the clearing, the animals die or are lost). Conditions 8.7(ii) imply that there are no fluxes of population through the boundary. This corresponds to a reflecting barrier (an example is a group of animals inside a fenced field). Using these boundary conditions, a finite sine or cosine transformation simplifies the equations. When conditions 8.7(i) are used, consider the finite sine transform:

$$T_i(t,m) \equiv \int_0^L s_i(t,x) \sin (m_\pi x/L) \, dx \qquad (8.8)$$

$$i=1,2, \quad m=1,2,\ldots,$$

and take the sine transform of equations 8.6. Assume the solution is in the form

$$T_i = A_i e^{r_i t} \qquad i=1,2.$$

By substituting this into the transformed equations, we find a solution for the eigenvalues, r_1, r_2:

$$r_{1,2} = \left[-m^2\pi^2(D_1+D_2)/L^2 \pm \sqrt{m^4\pi^4(D_1-D_2)^2/L^4 - 4a_1a_2} \right]/2 . \qquad (8.9)$$

As both solutions for r_i have negative real parts, small perturbations decay as $t \to \infty$ and the population returns to the constant equilibrium value.

For boundary conditions 8.7(ii), use the cosine transform

$$\int_0^L s_i(t,x) \cos(m\pi x/L) \, dx \qquad (8.10)$$

$$i=1,2, \quad m=0,1\ 2,\ldots$$

The equation for the eigenvalues is again given by 8.9, except that now m may be zero. When m is zero, the solution corresponds to constant amplitude oscillations. Thus, using conditions 8.7(ii), spatially inhomogeneous terms decay for large t, leaving constant amplitude oscillations of period $2\pi/\sqrt{\lambda\mu}$.

Hence, Okubo has shown, using a linear analysis, that only spatially uniform solutions can exist for the Lotka-Volterra model with diffusion, in a bounded domain. This analysis shows, too, that, under certain boundary conditions (such as an absorbing barrier), diffusion can stabilise (that is, temporally stabilise) the Lotka-Volterra model.

8.3.3. Non-linear analysis

Although the above analysis was linear, non-linear studies have also shown that diffusion will damp out spatial inhomogeneities. Rosen (1975) studied the N-species model

$$\frac{\partial S_i}{\partial t} = D_i \nabla^2 S_i + (k_i + \beta_i^{-1} \sum_{j=1}^{N} \alpha_{ij} S_j) S_i \ , \qquad (8.11)$$

where

$$\nabla^2 S = \frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2} + \frac{\partial^2 S}{\partial z^2} \ , \qquad (8.12)$$

with x, y and z the spatial variables, D_i the diffusion coefficients, and $a_{ij} = -a_{ji}$. The a_{ij}'s represent the interactions between the i and j species, so that the rate of increase of S_i, through interaction with S_j, is α_{ij}/β_i, where $\beta_i > 0$, for all i. Thus, when N=2, equations 8.11 simplify to the Lotka-Volterra equations with random diffusion. The equations 8.11 are assumed to exist in a bounded region with the same boundary conditions as before (8.7). By assuming a temporally periodic solution and substituting it into the equations, Rosen showed that no spatial patterns are possible when the solution is periodic in time.

This model was studied in more detail by Murray (1975), who made the additional constraints that N is even and that $D_i = D$, for all i, D>0. Using the maximum principle (see Protter and Weinberger, 1967), he showed that in a bounded region, diffusion damps out all spatial variations, provided that all of the interaction terms (a_{ij}'s) are non-zero. He said (without proof) that, with minor modifications, the results should carry over to the infinite domain. By including a prey saturation term in the prey birth rate (that is, the c factor in the stable model), the effect is merely to enhance the damping of the inhomogeneities. Jorné and Carmi (1977) extended these results to allow for different diffusion coefficients for each species, but with the constraint that $\beta_i = 1$, for all i (that is, the changes, through interaction, in S_i and S_j are of equal size but opposite sign).

This decay of spatial pattern was extended to more general

situations by Conway et al. (1978). They looked at equations of N-species systems undergoing diffusion, advection and non-linear interaction

$$\frac{\partial S_i}{\partial t} = D_i \nabla^2 S_i + A_x \frac{\partial S}{\partial x} + A_y \frac{\partial S}{\partial y} + A_z \frac{\partial S}{\partial z}$$

$$+ F_i(S_1, S_2, \ldots, S_N) , \qquad (8.13)$$

in a bounded region. Provided the boundary is sufficiently smooth (for example, reflecting boundary conditions), and all the diffusion coefficients exceed a certain critical value, then when t gets large, the solutions decay to spatially homogeneous functions of time.

Thus, in a bounded region, when the diffusion coefficients are sufficiently large, only spatially uniform solutions exist asymptotically for coupled systems.

8.4. The Pattern-Developing Effect of Diffusion

8.4.1. Introduction

In the last section, we saw that diffusion usually tends to have a damping effect on the population, so that a spatially uniform density results. However, an important exception to this behaviour is known as 'diffusive instability'. This means that diffusion can destabilise an otherwise stable system and sometimes be responsible for the development of a new spatial pattern. We shall outline the results showing the ability of diffusion to destabilise a model through linear methods in Section 8.4.2, and non-linear methods in Section 8.4.3.

Although in most studies, it is only the effects of self-diffusion which are considered, it is interesting to see (Section

8.4.4) that cross-diffusion, too, may give rise to instability.

8.4.2. Linear analysis

The idea that diffusion may disturb the stability of a system was first noticed by Turing (1952). To model the growth of cell tissues, he proposed a system of equations involving both chemical reactions and diffusion. He showed that in a spatially homogeneous ring of tissue, a regular, stable, spatial pattern could emerge.

Diffusive instability was first considered in an ecological context by Segel and Jackson (1972). They considered the model of two interacting and diffusing species:

$$\frac{\partial S_1}{\partial t} = D_1 \frac{\partial^2 S_1}{\partial x^2} + F_1(S_1, S_2)$$

$$\frac{\partial S_2}{\partial t} = D_2 \frac{\partial^2 S_2}{\partial x^2} + F_2(S_1, S_2) \ . \tag{8.14}$$

The functions F_1 and F_2 are general functions of the densities. The D_1 and D_2 are diffusion coefficients, and diffusion is allowed in one spatial dimension (x). Let $\hat{S}_1$ and $\hat{S}_2$ be the equilibrium values which the system would have if spatial separation were ignored - the conditions necessary for the existence of an equilibrium value will be discussed. Then, Segel and Jackson wrote the equations 8.14 linearised about this point as

$$\frac{\partial s_1}{\partial t} = D_1 \frac{\partial^2 s_1}{\partial x^2} + a_{11}s_1 + a_{12}s_2$$

$$\frac{\partial s_2}{\partial t} = D_2 \frac{\partial^2 s_2}{\partial x^2} + a_{21}s_1 + a_{22}s_2 \ . \tag{8.15}$$

(The equations hold in a large domain so that boundary conditions can be ignored.) They performed a linear stability analysis on the model by assuming solutions of an exponential form, and examining eigenvalues. In this way, the conditions under which instability will occur can be found. In order to have an initial steady state equilibrium, we must have

$$a_{11} + a_{22} < 0$$

$$a_{11}a_{22} - a_{12}a_{21} > 0 . \tag{8.16}$$

Provided that $D_1D_2 \neq 0$, they showed that by introducing diffusion into the system, instability will occur if

$$a_{11}D_2 + a_{22}D_1 > 2 \sqrt{D_1D_2(a_{11}a_{22} - a_{12}a_{21})} . \tag{8.17}$$

To simplify these conditions, the authors pointed out that expressions in 8.16 imply

$$a_{11}a_{22} < 0$$

$$a_{12}a_{21} < 0 . \tag{8.18}$$

From 8.18, we see the a_{11} and a_{22} must have opposite sign. The species with positive a_{ii} is called the destabiliser (say S_1) and that with negative a_{ii} is the stabiliser. Condition 8.17 shows that $D_2 > D_1$ (when S_1 is the destabiliser), and also that the ratio of the two diffusion coefficients has a critical value beyond which diffusive instability will set in. Thus, Segel and Jackson summed up these necessary (but not sufficient) conditions for diffusive instability as

(i) self-reinforcement of one species must be positive (stabiliser),

(ii) self-reinforcement of other species must be negative (destabiliser),

(iii) coupling terms must be of opposite sign,

(iv) diffusion coefficient of stabiliser must be larger than diffusion coefficient of destabiliser.

This method was also used by Levin (1974) in studying a system of discrete intercommunicating 'patches' of species. This model is not strictly a diffusion model, because the habitat is not continuous, but composed of discrete areas. Instead of diffusing continuously throughout the region, the populations migrate between the patches at a rate proportional to the densities in the patches. However, we shall include it here because its spatially continuous analogue will be discussed in Section 8.4.3. In a set of M patches, with prey and predator densities in each patch i denoted by S_{1i} and S_{2i}, the equations for the model are

$$\frac{dS_{1i}}{dt} = S_{1i}(\lambda - c_1 S_{1i} - \alpha S_{2i}) + \sum_j d_{ij}(S_{1j} - S_{1i})$$

$$\frac{dS_{2i}}{dt} = S_{2i}(\beta S_{1i} - \mu - c_2 S_{2i}) + \sum_j d'_{ij}(S_{2j} - S_{2i}) . \qquad (8.19)$$

The parameters of the predator-prey process are the same on each patch. The terms c_1 and c_2 are self-limiting factors for the prey and predators, respectively. The d_{ij} terms represent the rate of migration of the prey from patch j to patch i, with the d'_{ij} terms representing the predator migration rates. Levin found that diffusive instability could set in provided that $c_1 c_2 < 0$. This is a special case of an Allee, or humplike, effect in the growth rate of a

species. That is, if f(S) is the growth rate of a species S, an Allee effect ⋯ ⋯ is present if there is some point S^* such that

$$f'(S) > 0 \text{ when } 0 \leqslant S < S^* ,$$

$$f'(S) = 0 \text{ when } S = S^* , \tag{8.20}$$

$$f'(S) < 0 \text{ when } S > S^* ,$$

which means that the growth rate reaches a maximum. Levin showed that provided an Allee effect is present in one species, diffusive instability is possible.

8.4.3. Non-linear analysis

The danger of performing these linear stability analyses was pointed out by Steele (1974). He looked at the Lotka-Volterra model with diffusion (given by equations 8.6) in a bounded region, with zero flux boundary conditions. By writing the solution in terms of Fourier series, he suggested that the non-linear terms create new modes of smaller and larger wavelengths, as time increases. From this he deduced that, by including non-linear terms, diffusion may never be able to damp out spatial variations. Steele's theory was incorrect for this model, since Murray (1975) showed that, in a bounded region, no temporally periodic, spatially non-uniform solutions can exist (see Section 8.3.3). Nevertheless, it emphasised the possible dangers of omitting non-linear terms.

Segel and Levin (1976) extended the work of Segel and Jackson (1972) and Levin (1974), which was mentioned in Section 8.4.2, by taking non-linear effects into account. Using a method of successive

approximations, they performed a non-linear stability analysis on both the discrete and continuous models. In the models considered by Segel and Levin (1976), the prey population had an autocatalytic effect. An autocatalytic effect occurs when the species reinforces itself, as opposed to self-damping. For example, if S_1 and S_2 are the prey and predator densities, respectively, and

$$\frac{dS_1}{dt} = S_1 F(S_1, S_2) \ ,$$

then an autocatalytic effect is present in the prey population if

$$\frac{\partial F}{\partial S_1} > 0 \ . \tag{8.21}$$

For ease of notation, let D_1 and D_2 be the diffusion coefficients of the prey and predators, respectively. Segel and Levin found that in a continuous homogeneous environment, random dispersal can destabilise a predator-prey model if there is an autocatalytic effect present in the prey population, and D_2 is sufficiently greater than D_1. As the perturbations increase, non-linear effects become evident and bring about a new steady, but now spatially heterogeneous, distribution.

In the discrete model, Segel and Levin noticed a similar effect. Random dispersal, combined with non-linear effects, can destabilise the model, and a spatially heterogeneous pattern can result. When the number of patches in the region is large, the conditions for this spatial pattern to occur approach those necessary in the case of the continuous model above. However, when the number of patches is fixed, unlike the continuous case, no destabilisation occurs if D_1 is strong enough, regardless of the ratio of D_1 to D_2.

One obvious application of this theory of spatial pattern emerg-

ing from a continuous homogeneous environment is in a marine ecosystem. Levin and Segel (1976) suggested that such behaviour might explain the spatial patchiness of oceanic plankton blooms. In another attempt to explain plankton distribution and movement in the sea, Mimura (1979) proposed the model

$$\frac{\partial S_1}{\partial t} = D_1 \frac{\partial^2 S_1}{\partial x^2} + [m(S_1) - \alpha S_2] S_1$$

$$\frac{\partial S_2}{\partial t} = D_2 \frac{\partial^2 S_2}{\partial x^2} - [n(S_2) - \beta S_1] S_2 \; . \tag{8.22}$$

The model represents two species of plankton, with one species (S_2) preying on the other (S_1). Mimura assumed that m and n are functions of only S_1 and S_2, respectively, and α and β are positive. This means that the birth rate of the prey is independent of the predator density, and the death rate of the predators independent of the number of prey. The diffusion coefficients D_1 and D_2 are both positive, meaning that the tendency is to diffuse away from high concentrations of one's own species. The equations are assumed to exist in a bounded region with smooth boundary. When m is monotonic non-increasing, and n is monotonic non-decreasing, and one of the diffusion coefficients is small, Mimura showed that the solution is asymptotically spatially homogeneous. Recall that in Section 8.3.3, Conway et al. (1978) showed that this is always true when D_1 and D_2 are large.

Mimura and Murray (1978) extended this study (still in a bounded domain) to cover the case where $m(S_1)$ exhibits an Allee effect (for example, self-saturation of the prey). In this case, patchiness will indeed result if D_1 is small, in particular small compared with D_2. This result is quite similar to that of Segel and Levin (1976),

except that Segel and Levin included an autocatalytic term in the growth rate, while here an Allee effect is included. The difference between Mimura and Murray's result and that of Segel and Jackson (Section 8.4.2) is that here the diffusion coefficient of the prey (D_1) is allowed to become very small, so that non-linear effects become important.

8.4.4. Cross-diffusion

Jorné (1977) investigated the effect of introducing cross-diffusion into the Lotka-Volterra model. The equations are

$$\frac{\partial S_1}{\partial t} = D_{11}\frac{\partial^2 S_1}{\partial x^2} + D_{12}\frac{\partial^2 S_2}{\partial x^2} + \lambda S_1 - \alpha S_1 S_2$$

$$\frac{\partial S_2}{\partial t} = D_{21}\frac{\partial^2 S_1}{\partial x^2} + D_{22}\frac{\partial^2 S_2}{\partial x^2} + \beta S_1 S_2 - \mu S_2 . \qquad (8.23)$$

The D_{ii} terms represent the effect of the diffusion of S_i on its own density (as before), whereas the D_{ij} terms represent the effect on S_i of the diffusion of S_j (for example, in a predator-prey situation, prey would diffuse away from predators). When the cross-diffusion terms (D_{12} and D_{21}) are zero, the model reduces to that of Jorné and Carmi (1977), discussed in Section 8.3.3, and the solution is spatially homogeneous. On the other hand, when self-diffusion is absent, and $D_{12} > 0$, $D_{21} < 0$, Jorné found that cross-diffusion may give rise to instability. Although cross-diffusion may be possible in electrolytic solutions, it is not usual in ecological systems. The conditions on the diffusion coefficients above, would require the prey to drift towards the predators, and the predators to drift away from the prey.

8.4.5. Conclusions

Random diffusion may destabilise a previously stable model, and a new, spatially heterogeneous, steady state may result.

In a linearised model, necessary conditions for diffusive instability are that D_1 (diffusion of prey) must be less than D_2 (diffusion of predators), and that D_1 and D_2 must both be larger than a certain critical value. In non-linear models, non-linear reaction terms (such as an Allee or autocatalytic effect) relax these conditions so that instability can occur when D_1 is small, provided D_2 is large enough. However, in a fixed patchy environment, if D_1 is large enough, no diffusive instability is possible for any value of D_2.

Finally, diffusive instability is also possible in models incorporating cross-diffusion, but the necessary conditions on the diffusion coefficients make this biologically unlikely.

8.5. More General Forms of Diffusion

In the last two sections, only the effects of random diffusion have been condidered. In many cases, this may be unrealistic as the movement of species through an environment may be influenced by such factors as a current or cross-wind, variability in the environment, or bias caused by large concentrations of population. We will now give a brief outline of the behaviour of a population which is diffusing under influences such as these.

Using three different forms of diffusion incorporating some of these factors, Gurney and Nisbet (1975) investigated the ability of a single population, in a spatially variable environment, to regulate its numbers through dispersal. The model they investigted is a single-species model only, but, nevertheless, it is interesting to look at their results to see what the effect of different types of

diffusion can be. If G(x) is the linear growth rate of the species at x, S(x,t) the density at x and time t, the three different models are:

(i) purely random dispersal

$$\frac{\partial S}{\partial t} = G(x)S + D\frac{\partial^2 S}{\partial x^2} \ ,$$

(ii) random plus density-dependent dispersal

$$\frac{\partial S}{\partial t} = G(x)S + D\frac{\partial^2 S}{\partial x^2} + k\frac{\partial}{\partial x}\left[S\frac{\partial S}{\partial x}\right] .$$

(movement is largely random but modified to a small extent by large concentrations of the species),

(iii) purely density-dependent dispersal

$$\frac{\partial S}{\partial t} = G(x)S + K\frac{\partial}{\partial x}\left[S\frac{\partial S}{\partial x}\right]$$

(movement of the species is entirely influenced by large concentrations).

Gurney and Nisbet showed that the species cannot be stabilised using type (i). The species will be stabilised using type (iii), and type (ii) also has a stabilising effect under certain conditions of the growth function. That is, wholly random motion, in a linear single-species system, is incapable of exerting any stabilising influence. Density-dependent dispersal stabilises the system by increasing the diffusion rate in densely populated areas.

Comins and Blatt (1974) looked at the effect of dispersal on models of predator-prey populations where both species have a preference to disperse towards the centre of the habitat. The model may

represent animal systems in which there is a favourable area of the habitat. The equations of the model are

$$\frac{\partial S_1}{\partial t} = D_1 \frac{\partial^2 S_1}{\partial x^2} + u_1 \frac{\partial S_1}{\partial x} \text{ sign } (x) + \lambda S_1 - \alpha S_1 S_2$$

$$\frac{\partial S_2}{\partial t} = D_2 \frac{\partial^2 S_2}{\partial x^2} + u_2 \frac{\partial S_2}{\partial x} \text{ sign } (x) + \beta S_1 S_2 - \mu S_2 \;, \qquad (8.24)$$

where

$$\text{sign } (x) = \begin{cases} +1 & \text{if } x > 0 \\ \\ -1 & \text{if } x < 0 \;. \end{cases}$$

The u_1 and u_2 terms are advection terms (described in Section 8.2), which arise because the movement is no longer random. Numerical analysis of the model showed that populations quickly settle down to stable spatial distributions, with the populations accumulating in the central region. Indeed, McMurtrie (1978) suggested that attraction to, or repulsion from, particular points in space tends, as a rule, to confer stability on predator-prey interactions.

The effects of a heterogeneous environment may be incorporated into the dispersive force, as shown by Shigesada et al. (1979), in a model of two competing species:

$$\frac{\partial S_1}{\partial t} = \frac{\partial^2}{\partial x^2} [(a_1 + b_{11} S_1 + b_{12} S_2) S_1] + k_1 \frac{\partial}{\partial x} \left[S_1 \frac{\partial \phi}{\partial x} \right]$$

$$+ (\alpha_1 - \beta_{11} S_1 - \beta_{12} S_2) S_1$$

$$\frac{\partial S_2}{\partial t} = \frac{\partial^2}{\partial x^2}[(a_2 + b_{21}S_1 + b_{22}S_2)S_2] + k_2\frac{\partial}{\partial x}\left[S_2\frac{\partial \phi}{\partial x}\right]$$

$$+(\alpha_2 - \beta_{21}S_1 - \beta_{22}S_2)S_2 \ . \qquad\qquad (8.25)$$

The interaction rates of the model are denoted by α_i, β_{ij}. The diffusion term is broken into two parts. The first part represents random diffusion (a_i), density-dependent self-diffusion (b_{ii}), and density-dependent cross-diffusion (b_{ij}). In the second part, ϕ is a measure of the favourability of the environment. This term represents diffusion influenced by the variability of the environment. Thus, the model given by equations 8.25 is one of two competing species which diffuse, partly, in a random fashion, but also subject to influences from variation in the environment, and large concentrations of both species. Shigesada et al. found that the combination of the environmental heterogeneity and the non-linear dispersive force gives rise to a spatial separation of the two species, and conjectured that this separation may stabilise the model. Their numerical work showed that this form of diffusion could stabilise the model, at least for certain values of the α_i's and β_{ij}'s.

From these examples, we see that diffusion which is not random — for example, non-linear, density-dependent, or diffusion with advection — may tend to have a stabilising influence on the system.

8.6. Implications for the Stepping-Stone Model

8.6.1. Continuous approximation

In this chapter, we have discussed the effects of spatial diffusion in a continuous environment. We will now develop a spatially continuous analogue of the discrete stepping-stone model, and, using this, consider what possible implications the results of this chapter

might have for the multi-colony model.

In the stepping-stone model, the equations are formed in terms of numbers of predators and prey in each colony. On the other hand, the diffusion model relates the densities of species present at a point, x. To find a continuous approximation for the discrete model, we must first associate an area with each colony, and hence a population density.

For simplicity, we develop this theory using the prey notation only. The results follow similarly for the predators. The prey equation in a stepping-stone model (from 7.1) is

$$\frac{\partial H_i}{\partial t} = F(H_i, P_i) + \eta_+(H_{i-1} - H_i) + \eta_-(H_{i+1} - H_i) \ , \tag{8.26}$$

where H_i and P_i are the numbers of prey, predators in colony i $(-\infty < i < \infty)$ and F represents the growth and interaction terms. If, with each colony i, we associate the region (i-1/2, i+1/2), then we may define $S_1(i), S_2(i)$ to be the densities of the prey, predator populations, respectively, in cell i. (This concept of population densities diffusing between discrete cell units has been discussed by Levin (1974, 1978), and is mentioned in Section 8.4.2.) Because the cell has unit area, $S_1(i) = H_i$.

In the approximating spatially continuous case, suppose that the individuals migrate in smaller steps. That is, instead of moving from i to i±1, the prey may move from x to x±δx. Equation 8.26 becomes

$$\frac{\partial S_1(x)}{\partial t} = F(S_1(x), S_2(x)) + \tilde{\eta}_+[S_1(x-\delta x) - S_1(x)]$$

$$+ \tilde{\eta}_-[S_1(x+\delta x) - S_1(x)] \ , \tag{8.27}$$

where $\tilde{n}_+$ and $\tilde{n}_-$ are suitably modified forms of n_+ and n_-. After expanding by Taylor's series, this becomes

$$\frac{\partial S_1}{\partial t} = F(S_1, S_2) + (\tilde{n}_+ + \tilde{n}_-)(\delta x)^2 \frac{\partial^2 S_1}{\partial x^2} + (\tilde{n}_- - \tilde{n}_+)(\delta x)\frac{\partial S_1}{\partial x} . \qquad (8.28)$$

In order that the continuous model does actually approximate the discrete one, we must impose constraints on the manner in which $\delta x \to 0$ (see Section 3.7.1). The constraints we impose are that the infinitesimal mean and variance of the change in position of prey remain constant. That is, $\delta x \to 0$ in such a way that

$$\delta x \quad (\tilde{n}_- - \tilde{n}_+) \to n_- - n_+$$

$$(\delta x)^2 (\tilde{n}_+ + \tilde{n}_-) \to n_+ + n_- . \qquad (8.29)$$

These constraints are possible, for example, if we let

$$\tilde{n}_- = \frac{n_+ + n_-}{2(\delta x)^2} + \frac{n_-}{\delta x}$$

$$\tilde{n}_+ = \frac{n_+ + n_-}{2(\delta x)^2} + \frac{n_+}{\delta x} . \qquad (8.30)$$

Thus, in the limit as $\delta x \to 0$, equation 8.28 becomes

$$\frac{\partial S_1}{\partial t} = F(S_1, S_2) + (n_+ + n_-)\frac{\partial^2 S_1}{\partial x^2} + (n_- - n_+)\frac{\partial S_1}{\partial x} . \qquad (8.31)$$

In the same way, the continuous approximation of the predator equation is

$$\frac{\partial S_2}{\partial t} = G(S_1, S_2) + (\nu_+ + \nu_-)\frac{\partial^2 S_2}{\partial x^2} + (\nu_- - \nu_+)\frac{\partial S_2}{\partial x} . \qquad (8.32)$$

Hence, we have seen that the discrete stepping-stone model may be approximated by a continuous diffusion model. If, in the discrete model, the population migrates with equal parameters in both directions $(\eta_+=\eta_-)$, then, in the continuous approximation, the population experiences random diffusion. If these parameters are unequal, then, in the continuous model, the population undergoes diffusion with advection. Using this continuous analogue, we will look at the implications of the results of this chapter for the discrete migrating models of the last chapter.

8.6.2. The damping effect

By applying the results of Section 8.3 to stepping-stone models, we consider when migration should have a damping effect. All the diffusion results mentioned here have been discussed in Section 8.3.

It has been shown (by Okubo, 1980, Murray, 1975, and Jorné and Carmi, 1977) that, in the bounded Lotka-Volterra model, random diffusion damps out all spatial variation. The corresponding discrete case is the N-colony stepping-stone model, with equal migration parameters $(\eta_+=\eta_-, \nu_+=\nu_-)$. From Okubo's result (using reflecting boundary conditions, 8.7(ii)), we would expect that, for large t, each colony would undergo constant amplitude oscillations with period $2\pi/\sqrt{\lambda\mu}$. This has been shown to be the case when N=2 (Section 5.3.3).

From Conway et al. (1978), this damping of spatial pattern may be applied to all N-colony models undergoing some predator-prey interaction, provided that all the migration parameters (which may be unequal) are large enough.

Murray (1975) claimed that even in an infinite domain, when the diffusion coefficients of predators and prey are equal, no spatial pattern is possible. This damping is further enhanced when the prey

growth rate has a self-inhibiting (c) factor. Previous results for the discrete case agree with this. When $\nu_+=\nu_-=\eta_+=\eta_-$, Renshaw (1982) showed that in the unbounded stepping-stone Lotka-Volterra model, perturbations in all colonies will decay to the equilibrium, at the rate $t^{-1/2}$ (Section 7.5). When the self-inhibiting c factor is included, we saw (result 7.9) that damping is increased by the factor $e^{-c\hat{H}t/2}$.

However, in the semi-infinite discrete case (colonies 0 to ∞), Renshaw (1982) showed that one-way migration does not stabilise the Lotka-Volterra model - each colony oscillates with decreasing amplitude. As one-way migration corresponds to advection with diffusion, this would appear to contradict McMurtrie's (1978) suggestion that advection tends to confer stability on the model. It can be argued that, in the discrete model, colony 0 forces a periodic solution in the other colonies. In the continuous model, the population from colony 0 is spread across an area from 0 to 1, say. This might imply that the force producing the spatially heterogeneous result is reduced - thus giving a stable result as McMurtrie suggested. However, in the continuous model, if we could regard the region (0,1) as a unit of population, this unit could have the same forcing effect as colony 0 in the discrete model. If this were so, we would expect the same solution in both cases, which contradicts McMurtrie's suggestion of stability.

8.6.3. Diffusive instability

In this section, we consider the results of 8.4, and see if it is possible for migration in a stepping-stone model to destabilise the system and cause a new spatially heterogeneous state to appear.

In the stable predator-prey process, the c factor in the prey birth rate may be regarded as an Allee effect. Consider an N-colony

model where each colony undergoes a stable process, with prey and predators migrating at rates η and ν, respectively, in both directions. Segel and Levin's (1976) results (Section 8.4.3) show that no instability will occur if η is large enough, regardless of the size of ν. But, by increasing the number of colonies, we can approximate the discrete model by a (bounded) continuous process. Then, by Mimura and Murray's (1978) result, diffusive instability will occur in the continuous process if η is small compared with ν, and a spatial pattern will result.

Diffusive instability may be a possible explanation of the results found when looking at the effect of migration on population variance in the two-colony model (Section 6.5). Recall that migration had three different effects depending on the quantity Q, where (6.70)

$$Q = c\hat{H} - \beta\hat{P} - \beta\hat{H} \ .$$

Looking at the effect of the change in Q on the predator variance, we saw that when Q was small, the variance decreased with migration. As Q increased, ν had to be sufficiently large in order to decrease the variance. When Q was very large, no decrease was possible. If we regard Q as some measure of the susceptibility of the model to diffusive instability, then, when Q is very large, instability will always occur and migration will only increase the variance.

When studying this two-colony model, only migration of predators was allowed. The result of Segel and Levin (1976) would imply that, if we also allowed prey to migrate, migration should always decrease the variance, provided η was large enough.

8.7. Conclusion

In a bounded region, diffusion will generally damp out all spatial variation, provided the diffusion coefficients are large enough. Murray (1975) suggested that damping should also occur in an infinite domain. Under certain conditions, diffusion may stabilise an otherwise unstable model, for example, the Lotka-Volterra model in Section 8.3.2.

On the other hand, it is possible for diffusion to destabilise a previously stable system. In a stable model with non-linear reaction terms, if the diffusion coefficient of the prey is small enough compared with that of the predator, instability may set in, and a new stable spatial pattern may emerge. Diffusion models have often been proposed to explain the appearance of spatial pattern in marine ecosystems (Section 8.4.3). This diffusive instability has been shown to occur in bounded regions with smooth boundary conditions, and in sufficiently large domains so that boundary conditions may be ignored.

By finding a continuous approximation of the discrete stepping-stone model, a comparison was made between continuous diffusion and discrete migration. In many cases, the stabilising effect of diffusion agreed with the stabilising effect of migration previously seen. One-way migration, however, which corresponds to diffusion with advection, did not confer stability, which seemed to be contrary to McMurtrie's (1978) proposals for continuous models. Though the concept of instability arising through migration was not noticed in discrete models, it might offer a possible explanation for the change in variance through migration, seen in Section 6.5.

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