Developments in Agricultural and Managed-Forest Ecology, 8

MANAGEMENT AND ANALYSIS OF BIOLOGICAL POPULATIONS

by

BEAN-SAN GOH

Developments in Agricultural and Managed-Forest Ecology, 8

MANAGEMENT AND ANALYSIS OF BIOLOGICAL POPULATIONS

by

BEAN-SAN GOH

Department of Mathematics, University of Western Australia, Nedlands,
W.A. 6009, Australia

ELSEVIER SCIENTIFIC PUBLISHING COMPANY
Amsterdam — Oxford — New York 1980

ELSEVIER SCIENTIFIC PUBLISHING COMPANY
335 Jan van Galenstraat
P.O. Box 211, 1000 AE Amsterdam, The Netherlands

Distributors for the United States and Canada:

ELSEVIER NORTH-HOLLAND INC.
52, Vanderbilt Avenue
New York, N.Y. 10017

Library of Congress Cataloging in Publication Data

Goh, Bean-San.
Management and analysis of biological populations.

(Developments in agricultural and managed-forest
ecology ; 8)
Bibliography: p.
Includes indexes.
1. Population biology--Mathematical models.
2. Wildlife management--Mathematical models. I. Title.
II. Series.
QH352.G63 574.5'24 79-17239
ISBN 0-444-41793-1

ISBN 0-444-41793-1 (Vol. 8)
ISBN 0-444-41515-7 (Series)

Printed in The Netherlands

PREFACE

In the real world, an ecosystem is subjected to large perturbations of its initial state and continual disturbances on its dynamics. Therefore it is important to establish that an ecosystem model is stable relative to finite perturbations of its initial state and its dynamics. One object of this book is to demonstrate that Liapunov and Liapunov-like functions can be successfully used to establish, in a nonlinear population model, stability relative to realistic perturbations.

It is shown that a complex ecosystem is stable relative to realistic perturbations if it is a collection of self-regulating species such that the sum total of the stabilizing intraspecific interactions dominates the interspecific interactions. A nontrivial criterion for a complex ecosystem model to have this property is given. For a complex ecosystem model to satisfy this criterion, it is desirable that it has many null interactions between pairs of species.

Another object of this book is to demonstrate the usefulness of optimal control theory in the management of biological populations. Management policies should always be implemented in a *feedback* manner. This would reduce some of the adverse effects of uncertainties in an ecosystem in the real world. After all, Nature itself uses feedback to cope with uncertainties in many processes.

Chapter 2 contains a brief survey of static optimization techniques and optimal control theory for systems which are modelled by differential and difference equations. Chapter 3 contains methods which use Liapunov and Liapunov-like functions to establish that a given population model is stable relative to finite perturbations of its initial state and that it is nonvulnerable relative to large continual disturbances. These methods are applied to single species and two-species populations which are modelled by differential and difference equations. Fisheries provide some of the best examples of the usefulness of mathematics in the management of biological populations. A few management problems in fisheries are examined in Chapter 4. They utilize stability and optimal control theories. Chapter 5 considers stability in an ecosystem model with complexities due to species richness, nonlinearities, time delays and spatial heterogeneity. The very interesting and important problem of pest management is considered in Chapter 6.

I have greatly benefited from discussions with T.T. Agnew, C.W. Clark, M.E. Fisher, G.W. Harrison, A. Hastings, C.S. Hsu, L.S. Jennings, G. Leitmann, D. Ludwig, T.L. Vincent and C.J. Walters. Many of the results in this book were obtained in collaboration with Tom Vincent. This book was completed during my sabbatical leave which was supported by NRC grant No. 3990. I thank Colin Clark and members of the Mathematics Department of the University of British Columbia for their hospitality.

CONTENTS

Chapter 1

INTRODUCTION

1.1. MODELS IN ECOLOGY

As in other areas of science and engineering, there exists a wide spectrum of models in ecology. At one end of the spectrum are relatively simple but general models which are used to analyse theoretical questions in ecology. These models are called strategic models by theoretical ecologists. At the other end of the spectrum are detailed computer simulation models; theoretical ecologists call these tactical models. However, some system analysts prefer to refer to simulation models as realistic models. Disclosed in this difference in terminology is the difference in the emphasis that each group places on the models.

It is desirable to have a wide range of models in order to achieve different purposes. For example, consider the flight of a plane between two cities. For the average passenger on the plane, it would be adequate to model the flight of the plane by a particle moving at a constant speed in a straight line over a flat earth from one city to another. The pilot, however, needs a cluster of models which includes strategic models of the dynamics of the plane, and relatively detailed models of the control systems which operate the wings and tail of the plane, the engines, the wheels, the brakes and other subsystems. The pilot's understanding of these models, which are not necessarily specified in explicit mathematical terms, is obtained from introductory courses on aerodynamics and experiences on simulators and planes. Finally, the team of engineers who design the plane requires a deep understanding of the detailed (tactical) models of the aerodynamics of the plane, the engines, the control systems and other subsystems. This understanding of the behavior of the detailed conceptual and mathematical models is obtained from mathematical analyses, simulations on computers, simulations of physical models of the plane in wind tunnels and test flights of the prototype plane.

In the field of ecology, a broad range of models serves different objectives. Strategic models are needed for isolating theoretical questions and studying them one at a time. They also serve as a means of communicating with colleagues, students of ecology and scientists in other fields, in a precise and objective manner the latest advances achieved in the understanding of the dynamical behavior of ecosystems.

On the other hand, tactical models are required for formulating the appropriate control policies in the management of a particular renewable resource or a specific pest population. In this case, only the user of the model needs to have a good understanding of the behavior of the model. The solution of these applied problems is very important in order to maintain strong support for ecological studies. Moreover, simulation models pose many interesting and pertinent questions for the theoretical ecologist to study.

The analyses of strategic models of an ecosystem may provide useful guidelines in the construction of a detailed simulation model. They can also provide suggestions on how to exercise a computer model of a community. For instance, the analysis of a simplified pest—predator system suggests that in the control of pest population, it is sometimes desirable to release pests. Without this result from the simplified model, it would sound absurd to consider the release of pests in a simulation model for managing a pest population. Ideally we should use a combination of strategic and tactical models in studying ecological problems.

1.2. STABILITY CONCEPTS IN ECOLOGY

The word "stability" is used for various purposes in ecology. It is used to describe a lack of change in population levels or population parameters; and to describe the persistence of an ecosystem. In mathematics there are many distinctly different concepts of stability (Kalman and Bertram, 1960 a; Willems, 1970). Recently, several authors (Lewontin, 1969; Holling, 1973; May, 1974; Maynard Smith, 1974; Goh, 1975) have attempted to reconcile the various concepts of stability which are used in ecology and mathematics.

Each concept of stability in ecology could be made more precise by applying it to a mathematical model of an ecosystem. For a precise definition of a concept of stability it is necessary to specify explicitly: (i) the class of admissible perturbations; (ii) the set of admissible initial states; (iii) a set of system responses which characterize desirable or undesirable behavior; and (iv) a time interval. Usually the infinite time horizon $(0, \infty)$ is used. Each set of specifications of these components of stability leads to a particular concept of stability.

Four types of perturbations on an ecosystem model are: (i) impulsive and infrequent perturbations of the initial states; (ii) continual disturbances on the system dynamics; (iii) impulsive and infrequent changes in the system parameters; and (iv) slow and continual changes in the system parameters. The effects of types (i) and (iii) perturbations can be examined together; and those of types (ii) and (iv) can be studied together.

The most common method of studying stability in an ecosystem model is by an examination of the eigenvalues of a matrix at an equilibrium. This method establishes stability only relative to small perturbations of the initial state. Hence it is called *local* stability. It implies that if the initial state is displaced a small distance from an equilibrium and the system is thereafter left alone, then the natural dynamics will drive the state into a decreasing neighbourhood of the equilibrium. Clearly an eigenvalue analysis is only a small initial step in understanding the dynamical behavior of an ecosystem model.

In the real world ecosystems are subjected to large perturbations of the initial state and system dynamics. The most powerful analytical method for studying stability relative to finite perturbations of the initial state of an ecosystem model is the direct method of Liapunov. This method was discovered in 1892 by the Russian mathematician A.M. Liapunov (see Liapunov, 1966). But the method was ignored by mathematicians for a long time. In the West, it was not till the nineteen-fifties that it became a popular tool for the analysis of nonlinear systems.

The direct method of Liapunov requires the construction of certain functions called Liapunov functions. For physical systems the direct method of Liapunov generalizes the principle that a system, which continuously dissipates energy until it attains an equilibrium, is stable.

The population of each species in a spatially homogenous and well mixed ecosystem must be nonnegative. This requires that the concept of global stability for engineering systems must be modified in ecological models. By definition an ecosystem model is globally stable if every trajectory of the model which begins at a positive state remains in the positive orthant for all finite values of the time variable t, and converges to a positive equilibrium as $t \to \infty$. The fact that the density of a viable population in a spatially homogeneous ecosystem must be positive requires that a two-sided energy principle should be used for constructing Liapunov functions for this class of models (Goh, 1977 a). A viable spatially homogeneous single-species population must have net energy absorption when its population level is low; and it must have net energy dissipation when its population level is high. In a spatially homogenous ecosystem the population of each species at extreme densities should have the behavior of a viable single species population.

In an ecosystem model, let $S(0)$ be a set of desirable initial states, $Z(T)$ be a set of undesirable initial states, U be a set of admissible disturbances, and $[0, T]$ be a given time interval. By definition, the ecosystem model is *nonvulnerable* relative to the sets $S(0)$, $Z(T)$ and U during the time interval $[0, T]$, if there is no admissible disturbance which drives the system from a state in $S(0)$ to the set $Z(T)$ during the time interval $[0, T]$. Liapunov-like functions can be used in an effective manner to study nonvulnerability in the class of generalized Lotka—Volterra models, and in a class of nonlinear models.

1.3. ECOLOGICAL ENGINEERING

Ecological engineering problems may be divided into two classes, namely, *design* problems and *control* problems. The question as to whether or not it is desirable to import and introduce a species into an ecosystem is a design problem. On the other hand the formulation of spraying programs for applying an insecticide in the management of a pest is a control problem.

To obtain good and reliable solutions to a design problem, it is necessary to have a relatively accurate model (mathematical or conceptual) of the ecosystem which is being manipulated or created. A reason for this stringent requirement is that it may not be possible to reverse the effects of a decision in a design problem.

In a control problem, there are usually some variables or parameters that can be easily manipulated between certain bounds. These variables may be used in a control program in two ways: (i) in an *open-loop* manner, e.g. the harvesting of a population under a constant quota (yield) policy; and (ii) in a *feedback* (closed-loop) manner, e.g. the harvesting of a population using a fixed effort policy. In the second example, the rate of harvesting is proportional to the product of the applied effort and the population. It is interesting to note that in this example, the state of the system need not be monitored at all, the reason being that the feedback nature of the impact of the control variable on the population dynamics is built-in.

Let x denote the state vector $(x_1, x_2, \ldots, x_n)$ of a system, and u denote the control vector $(u_1, u_2, \ldots, u_m)$. By definition, each function $u(x)$ determines a control policy. A feedback control policy $u(x)$ is usually determined from an analysis of a deterministic model of the system. In feedback control we must specify a target to which the state of the system must be driven. The target could be a point or a region in the state space. A control policy must be able to drive the system from every admissible (operating) initial state to the target. If otherwise, the system is not fully controllable.

The way in which a feedback control policy is *implemented* is very important. In feedback control the state of the system is continuously monitored, and the control variables are adjusted according to a prescribed control policy $u(x)$. It is the updating of the control variables which enables a feedback control system to neutralize some of the adverse effects of uncertainties.

In practice the state of the system is sampled only at discrete times $t, t + \Delta t, t + 2\Delta t, \ldots$ and the control variables are adjusted accordingly. The effectiveness of feedback control to neutralize the adverse effects of a given class of uncertainties decreases as Δt increases. It is usually very difficult to make good estimates of the population levels in an ecosystem. In many cases the interactions between species are not well understood. In spite of these difficulties, management control policies should always be implemented in a feedback manner using the best estimates of the state of the system. A management policy which is not in a feedback form is an improperly designed policy.

Walters and Hilborn (1978) have suggested that generally stochastic optimal control policies which take into account random disturbances on the system dynamics and random observation errors are similar to feedback control policies which are formulated using deterministic models. This problem on the relative merits of using a stochastic optimal control policy and a feedback optimal control based on a deterministic model of a system is very important in the management of ecosystems. For the general linear regulator problem, Fleming and Rishel (1975, p.166) have rigorously proved that the optimal feedback control law is the *same* for the stochastic model as for the deterministic model. For nonlinear problems this question requires further studies (Reed, 1974; Walters, 1975; Walters and Hilborn, 1976).

It is possible to design an efficient feedback control policy using only a crude model of a system if we have available an independent control variable for each state equation. In this case the control variables can be used to enhance the desirable trends in the dynamics of a system and drive it to a prescribed target. This will be demonstrated in Section 6.3.

1.4. LIAPUNOV FUNCTIONS

We shall discuss briefly the properties of a Liapunov function and a general method for constructing Liapunov functions. The applications of Liapunov functions are considered in subsequent chapters.

Let us consider the properties of a Liapunov function for a model in which there are no sign restrictions on the state variables. Suppose the system

$$\dot{x}_i = f_i(x_1, x_2, \ldots, x_m), \quad i = 1, 2, \ldots, m \tag{1.4.1}$$

has an equilibrium at $x = (0, 0, \ldots, 0)$. We have

$$f_i(0) = 0, \quad i = 1, 2, \ldots, m. \tag{1.4.2}$$

Let $\|x\|$ be a norm of x. For example,

$$\|x\| = \min\{|x_1|, |x_2|, \ldots, |x_m|\}, \tag{1.4.3}$$

where $|x_1|$ denotes the absolute value of x_1. Let $r = \|x\|$. Let $G(r)$ be a strictly increasing function of r such that $G(0) = 0$, and $G(r) \to \infty$ as $r \to \infty$. By definition, a continuous scalar function $V(x)$ is radially unbounded if there exists a G function with the above properties such that

$$V(x) \geqslant G(\|x\|) \tag{1.4.4}$$

for all x in the state space $\mathrm{R}^m = \{x \mid (x_1, x_2, \ldots, x_m)\}$,

Let R be an open region of the state space. Let $V(x)$ be a continuously differentiable scalar function in R. By definition $V(x)$ is a Liapunov function of model (1.4.1) if it has the following properties:

(i) $V(0) = 0$; (1.4.5)

(ii) $V(x)$ is radially unbounded; (1.4.6)

and

(iii) $$\dot{V}(x) = \sum_{i=1}^{m} \frac{\partial V}{\partial x_i} f_i(x) \leqslant 0 \quad \text{for all } x \in \mathrm{R}. \tag{1.4.7}$$

Condition (i) is trivial. It can be replaced by the condition, $V(0) = a$, where a is a positive or a negative constant. Condition (ii) can be weakened considerably. For example, LaSalle (1976, p.30) uses a definition of a Liapunov function which only requires that $V(x)$ is a continuous function and that it satisfies condition (iii). However, if condition (ii) is weakened it is necessary to give additional conditions which ensure that every solution of (1.4.1) which begins in a given closed bounded subset of R remains in it for all positive values of t. This requirement will be demonstrated in Example 1.4.1. Condition (ii) ensures that the equations, $V(x) = K_p$, $K_1 < K_2 < K_3 < \cdots$, represent a set of nested closed hypersurfaces (Hahn, 1976, p.99). Condition (iii) can be weakened to handle the case when $V(x)$ is not continuously differentiable, and when $f(x)$ is not a continuous vector function (LaSalle, 1976, p.29).

For population models, the $V(x)$ function is often a separable function. This means that

$$V(x) = c_1 V_1(x_1) + c_2 V_2(x_2) + \cdots + c_m V_m(x_m) \tag{1.4.8}$$

where $c_1, c_2, \ldots, c_m$ are positive constants. In this case $V(x)$ is radially unbounded if, for $i = 1, 2, \ldots, m$, $\mathrm{d}V_i/\mathrm{d}x_i < 0$ for all $x_i \in (-\infty, 0)$, $\mathrm{d}V_i/\mathrm{d}x_i > 0$ for all $x_i \in (0, \infty)$, and $V(x_i) \to \infty$ as $|x_i| \to \infty$. This property of a separable function can be established by using the norm given in (1.4.3).

Example 1.4.1. The following counter-example was constructed by Barbashin and Krasovskii (1952) (see also Hahn, 1967, p.109) to demonstrate that a Liapunov function for global asymptotic stability must be radially unbounded.

Let $u = 1 + x^2$ and

$$\begin{aligned} \dot{x} &= -6x/u^2 + 2y, \\ \dot{y} &= -2(x + y)/u^2. \end{aligned} \tag{1.4.9}$$

Consider the function

$$V(x, y) = (x^2/u) + y^2. \tag{1.4.10}$$

We have $V(x, 0) \to 1$ as $x \to \infty$. Hence for $K > 1$, the equation $V(x, y) = K$ does not define a closed surface. It follows that $V(x, y)$ is not radially unbounded.

Computing $\dot{V}$ along solutions (1.4.9) we get

$$\dot{V} = -4(3x^2 + y^2 u^2)/u^4. \tag{1.4.11}$$

Clearly $\dot{V}(x, y) < 0$ for all $(x, y) \neq (0, 0)$. But we shall show that $(0, 0)$ is not globally asymptotically stable.

The hyperbola

$$y = 2/(x - \sqrt{2}), \quad x > \sqrt{2}, \tag{1.4.12}$$

is a barrier to the trajectories of (1.4.9) which begin in the set $\{(x, y) \mid x > \sqrt{2}, y > 2/(x - \sqrt{2})\}$. This is established by comparing the slope of the hyperbola of (1.4.12) and the slopes of the trajectories of (1.4.8). The slope of the hyperbola is

$$p = \mathrm{d}y/\mathrm{d}x = -2/(\sqrt{2} - x)^2 \tag{1.4.13}$$

The slope of the trajectory of (1.4.9) which passes through the same point on the hyperbola is

$$q = \dot{y}/\dot{x} = -1/(1 + 2\sqrt{2}x + 2x^2). \tag{1.4.14}$$

Eqs. (1.4.13) and (1.4.14) imply that $q > p$ for all points on the hyperbola given in (1.4.12). Hence the solutions of (1.4.9) which begin in the set $\{(x, y) \mid x > \sqrt{2}, y > 2/(x - \sqrt{2})\}$ do not intersect the hyperbola in (1.4.12), i.e. they do not converge to (0, 0) as $t \to \infty$. Therefore (0, 0) is not globally asymptotically stable.

The next theorem gives a simple set of conditions for global stability.

Theorem 1.4.1. *The equilibrium* $x = 0$ *of (1.4.1) is globally asymptotically stable if there exists a Liapunov function in* R^m *such that*

$$\dot{V}(x) < 0 \tag{1.4.15}$$

for all $x \in \mathrm{R}^m$ *and* $x \neq 0$.

Proof. Let the solution of (1.4.1) which begins at the point $x(0) = a$ converge to the point $x(\infty) = b \neq 0$. It follows that $V(b) = L$ where L is a positive constant.

The region $A = \{x \mid L \leqslant V(x) \leqslant V(a)\}$ is a closed bounded region. The function $V(x)$ is a continuous function. It follows that the minimum of $\dot{V}(x)$ for all $x \in A$ exists. Let this be $-M$. The equations, $V(x) = K_p, K_1, < K_2 < K_3 < \cdots$, represent a set of nested closed hypersurfaces. The conditions, $\dot{V} < 0$ and $\lim V[x(t)] = V(b)$ as $t \to \infty$, imply that $x(t)$ remains in A for all $t > 0$. Along the solution which begins at $x(0) = a$, we have

$$V[x(t)] - V[x(0)] = \int_0^t \dot{V}\,\mathrm{d}t < \int_0^t -M\,\mathrm{d}t = -Mt. \tag{1.4.16}$$

It follows that $V[x(t)] \to -\infty$. As this is impossible, we conclude that the equilibrium $x = 0$ is globally asymptotically stable.

We shall now consider the modifications which are necessary before a Liapunov function, as defined above, can be applied to a population model.

Suppose a model of a spatially homogenous community is

$$\dot{N}_i = N_i F_i(N_1, N_2, \ldots, N_m), \quad i = 1, 2, \ldots, m \tag{1.4.17}$$

where N_i is the population of the ith species. In this model the state variables must be nonnegative. For all the species to persist it is necessary for model (1.4.17) to have a positive equilibrium or a limit cycle. It is also necessary for all the species to be present initially. Thus a natural concept of global stability for a positive equilibrium of (1.4.17) at N^* is that every solution of the model which begins in the positive orthant $\mathbf{R}_+^m = \{N \mid N_i > 0, i = 1, 2, \ldots, m\}$ must remain in $\mathbf{R}_+^m$ for all finite values of t and converge to N^* as $t \to \infty$.

We can establish that N^* is globally stable by transforming the positive orthant $\mathbf{R}_+^m$ into $\mathbf{R}^m = \{x \mid (x_1, x_2, \ldots, x_m)\}$, and then using Theorem 1.4.1. For example, we could employ the transformation

$$x_i = \ln(N_i/N_i^*), \quad i = 1, 2, \ldots, m. \tag{1.4.18}$$

However, this preliminary transformation is unnecessary. It may also be undesirable because the transformed model could be more complex.

The alternative and better approach is to translate the stability conditions so that they can be used directly for establishing global stability in the positive orthant. This is achieved by translating condition (ii) of (1.4.6) into an appropriate condition.

Using (1.4.18) we deduce that a scalar function $V(N)$ is "radially unbounded" in $\mathbf{R}_+^m$, if the function

$$W(x) = V(N_1^* \exp x_1, N_2^* \exp x_2, \ldots, N_m^* \exp x_m) \tag{1.4.19}$$

is radially unbounded in $\mathbf{R}^m$. This implies that the equations, $V(N) = K_p$, $K_1 < K_2 < K_3 < \cdots$, represent a set of nested closed hypersurfaces, and that $V(N) \to \infty$ as $N_i \to \infty$ and as $N_i \to 0+$ for $i = 1, 2, \ldots, m$.

In brief, a continuously differentiable function $V(N)$ is a Liapunov function of (1.4.17) in $\mathbf{R}_+^m$ if it has the following properties:

(i) $V(N^*) = 0$; (1.4.20)

(ii) The equations, $V(N) = K_p$, $K_1 < K_2 < K_3 < \cdots$, represent a set of nested closed hypersurfaces, and $V(N) \to \infty$ as $N_i \to \infty$ and as $N_i \to 0+$ for $i = 1, 2, \ldots, m$; and

(iii) $$\dot{V}(N) = \sum_{i=1}^{m} \frac{\partial V}{\partial N_i} N_i F_i(N) \leqslant 0 \quad \text{for all } N \in \mathbf{R}_+^m. \tag{1.4.21}$$

Theorem 1.4.2. *The positive equilibrium of model (1.4.17) at N^* is globally stable in the positive orthant, if there exists a Liapunov function $V(N)$ in $\mathbf{R}_+^m$, and*

$$\dot{V}(N = \sum^{m} \frac{\partial V}{\partial N_i} N_i F_i(N) < 0 \quad \textit{for all } N \in \mathbf{R}_+^m \textit{ and } N \neq N^*. \tag{1.4.22}$$

The proof of this theorem follows directly from that for Theorem 1.4.1, and the use of the properties of the Liapunov function $V(N)$ in the positive orthant $\mathbf{R}_+^m$.

Example 1.4.2. The function

$$V(N) = (\ln N)^2 \tag{1.4.23}$$

is a Liapunov function for the logistic model

$$\dot{N} = N(1 - N). \tag{1.4.24}$$

It can be used to establish that $N = 1$ is globally stable.

The function $(\ln N)^2$ is none other than x^2 under the transformation in (1.4.18). Clearly the change of variables given in (1.4.18) may be used to convert a Liapunov function of model (1.4.1) into a Liapunov function for model (1.4.17).

But for establishing global stability in the positive orthant, the quadratic function

$$V(N) = (N - N^*)^{\mathrm{T}} P(N - N^*) \tag{1.4.25}$$

where P is a positive definite matrix, is not a Liapunov function according to the above definition. This is because $V(N)$ does not tend to infinity as $N_i \to 0+$ for $i = 1, 2, \ldots, m$. Hence it cannot be used with Theorem 1.4.2 to establish global stability in the positive orthant without using additional conditions. This is a common shortcoming in proofs of global stability of a competitive equilibrium in economics (Arrow et al., 1959; Quirk and Saposnik, 1968; Arrow and Hahn, 1971; Takayama, 1974).

There is a large amount of literature on the construction of Liapunov functions (Schultz, 1965; Hahn, 1967; Gurel and Lapidus, 1968, 1969; Willems, 1970; Gilpin, 1974; Gatto and Rinaldi, 1977; Goh, 1977 a; Hsu, 1978 a; Harrison, 1979 b). However, most of the Liapunov functions that have been used successfully in the analyses of biological populations can be generated by the variable gradient method.

In the variable gradient method, we guess the gradient of $V(N)$ instead of the function $V(N)$. We choose a set of continuous functions, $G_1(N)$, $G_2(N)$, $\ldots$, $G_m(N)$, such that

$$\frac{\partial G_i}{\partial N_j} = \frac{\partial G_j}{\partial N_i}, \quad i, j = 1, 2, ; \ldots, m \tag{1.4.26}$$

for all $N \in \mathbf{R}_+^m$, and such that the function

$$V(N) = \sum_{i=1}^{m} \int_{N_i^*}^{N_i} G_i(N_1, N_2, \ldots S_i, \ldots, N_m)\, \mathrm{d}S_i, \tag{1.4.27}$$

is a Liapunov function for (1.4.17). In other words, the set of functions

$\{G_i(N)\}$ are chosen so that they satisfy the conditions: (i) the integrability conditions in (1.4.26); (ii) the function $V(N)$ in (1.4.27) is "radially unbounded" in $\mathbf{R}_+^m$; and (iii)

$$\dot{V}(N) = \sum_{i=1}^{m} G_i(N)\, N_i F_i\,(N) \leqslant 0 \quad \text{for all } N \in \mathbf{R}_+^m. \tag{1.4.28}$$

Example 1.4.3. Let $c_1, c_2, \ldots, c_m$ be a set of positive constants, and $G_i = c_i\,(S_i - N_i^*)/S_i$ for $i = 1, 2, \ldots, m$. Clearly condition (1.4.26) is satisfied. Using (1.4.27) we get

$$V(N) = \sum_{i=1}^{m} c_i\,[N_i - N_i^* - N_i^* \ln(N_i/N_i^*)]. \tag{1.4.29}$$

This is a separable function, and $V(N) \to \infty$ as $N_i \to 0+$ and as $N_i \to \infty$ for $i = 1, 2, \ldots, m$. It is "radially unbounded" in $\mathbf{R}_+^m$.

If the constants $c_1, c_2, \ldots, c_m$ are chosen so that

$$\dot{V}(N) = \sum_{i=1}^{m} c_i(N_i - N_i^*)F_i(N) \leqslant 0 \tag{1.4.30}$$

for all $N \in \mathbf{R}_+^m$, then $V(N)$ is a Liapunov function for (1.4.17).

Example 1.4.4. The following general prey—predator model was considered by Harrison (1979 b):

$$\dot{X} = b(X) - f(X)a(Y),$$
$$\dot{Y} = g(X)h(Y) + d(Y). \tag{1.4.31}$$

We assume that it has a positive equilibrium at (X^*, Y^*).

Consider the function

$$V(X, Y) = \int_{X^*}^{X} \frac{g(X) - g(X^*)}{f(X)}\, \mathrm{d}X + \int_{Y^*}^{Y} \frac{a(Y) - a(Y^*)}{h(Y)}\, \mathrm{d}Y. \tag{1.4.32}$$

Let the equilibrium (X^*, Y^*) belong to an open region R. Suppose $V(X, Y) > 0$ for all $(X, Y) \in \mathrm{R}$ and $(X, Y) \neq (X^*, Y^*)$. We can show that the equations $V(X, Y) = K_p$, $K_1 < K_2 < K_3 < \cdots$, represent a set of nested closed hypersurfaces in a subregion of R.

Computing $V(X, Y)$ along the solutions of (1.4.31), we get

$$\dot{V} = [g(X) - g(X^*)]\,[b(X)/f(X) - b(X^*)/f(X^*)]$$
$$+ [a(Y) - a(Y^*)]\,[d(Y)/h(Y) - d(Y^*)/h(Y^*)]. \tag{1.4.33}$$

Hence $V(X, Y)$ is a Liapunov function in a neighbourhood of (X^*, Y^*) if: (i) $V(X, Y) > 0$ for all $(X, Y) \in R$ and $(X, Y) \neq (X^*, Y^*)$; and (ii) $\dot{V}(X, Y) \leqslant 0$ for all $(X, Y) \in R$. For a function to be a Liapunov function in a finite neighbourhood of an equilibrium, it need not be radially unbounded.

Hsu (1978 a) and Harrison (1979 b) have shown that the Liapunov function (1.4.32) can be used to establish stability in a wide range of prey—predator models.

1.5. DIFFERENTIAL EQUATIONS AND DIFFERENCE EQUATIONS IN ECOSYSTEM MODELLING

The application of nonlinear difference equations in ecosystem modelling is becoming popular. One reason for this is that nonlinear difference equations can be solved directly on a digital computer. However, in theoretical ecology a difference equation model is often constructed initially, and a limiting process is used to convert it into a differential equation model. Since it is usually impossible to solve analytically a system of nonlinear differential equations, it is solved on a digital computer. In doing so, it is reconverted into a system of difference equations. Depending on the numerical algorithm for solving differential equations, the resulting system of difference equations may not be the same as in the initial model.

This process is unnecessary. Moreover, sometimes incorrect conclusions are obtained when a difference equation is converted into a differential equation. An example of this occurs in the modelling of the adult population of a single-species population with nonoverlapping generations whose dynamics has a two-point limit cycle. The analogous differential equation would not have an oscillatory behavior. Thus it may be more natural to use difference equations to model ecosystems (Van der Vaart, 1973; Innis, 1974 a).

The present extensive use of differential equations in theoretical ecology may be attributed to the fact that analytical methods for studying them are better developed and are more widely taught than those for difference equations. For instance, optimal control theory for systems of differential equations is better developed than that for difference equations. Moreover differential equation models of two species interactions can be analysed graphically.

For the management of a population with a discrete time delay, there is good reason to use a difference equation model rather than a delay-differential equation model. This is because the optimal control of a delay difference equation produces no more difficulties than that of a model without a delay. In contrast, the optimal control of a delay-differential equation generally leads to considerable mathematical difficulties.

There are two other interesting differences between a differential equation model. It may be difficult to establish the existence of a solution to a nonlinear differential equation during a long period of time. On the other hand,