PREDATOR-PREY DYNAMICS:
A REVIEW

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ABSTRACT

With the recent publication explosion in population ecology, there is an increasing need for a review of the diverse approaches towards modelling. This thesis is concerned with modelling of two-species predator-prey ecosystems using two-dimensional dynamic systems of first-order differential equations.

Chapters one and two are introductory in nature, discussing the place of theoretical models in ecology, and the development of the classical Lotka-Volterra model and its subsequent fall from favour.

Chapter three looks at general aspects of predator-prey modelling. Graphical and analytical approaches are outlined in detail, as is the more recent curvature approach. Further results are obtained when growth and predation factors are considered separately, viewed as components to the model equations. Recent work on the consequences of enrichment, harvesting, stocking and natural selection are also dealt with.

In chapter four, more specific predator-prey models are presented. Other, more variable qualities of predator-prey ecosystems are also considered, such as age structure and predation responses in chapter four; and time delays, spatial heterogeneity and migration in chapter five.

Chapter six is a mathematical digression from the main body of the review. An analytical result for dynamic systems with a centre is proven, in an attempt to support an alternative outlook on the relationship between predator-prey ecosystems and their representative models.

Finally, chapter seven briefly discusses potential applications in the future, the most promising being aspects of harvesting and control theory in resource management systems.

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1 PRELIMINARIES

§1.1 Introduction

A mathematician's attitude towards mathematics will vary; to most it is a tool, to many it is a discipline, and to a select few it is an art. As a tool, a tremendous amount of theory has been generated to support and enhance its usefulness. This is clearly evident in the physical sciences; and with the advent of optimization and control theory, the scope for application appears endless.

Ecology is a relatively young science. The diversity of ecosystems and complexity of inter-relationships within each system had made the development of principles analogous to natural laws in the physical sciences well nigh impossible. In spite of this, mathematical modellers have made an all-out assault to plunder the well-hidden secrets of ecological dynamics. Suddenly a whole new frontier has opened up.

The problem is that frequently modellers are not ecologists. Physicists, chemists, engineers, economists and applied mathematicians have all attempted to squeeze the complexities of ecology into a traditional mould originally designed for use within their own disciplines. This has lead to two unfortunate consequences.

Firstly, it has raised the ire of many biologists [see Slobodkin's (1975) "Comments from a biologist to a mathematician"]. It is interesting to note that some of the best approaches to ecological modelling have come from joint efforts, combining the skills of the mathematician with the knowledge of the biologist.

Secondly, the great volume of literature that has appeared on population ecology is so diverse, that a cohesive, unified approach seems more distant than ever. The following is an attempt to review only a small part of this vast topic; to establish an overall perspective. There is a need for such a review, if for no other reason than that so much has already been written on the subject.[*]

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[*] Dubois (1979) presented a 'State-of-the-Art' of predator-prey systems modelling. This so called review is surely only of limited value; of the 60 references cited in the bibiliography, over a third of them are either written or cowritten by Dubois himself! As a result more than 50% of the paper is devoted to his own specialist interest - that of spatial heterogeniety.

For these reasons, providing a structure for this work has proved to be a daunting task. In order to discuss certain aspects of population biology, it becomes essential to devise some form of categorization on the diverse material available. This is not the mathematician in me extracting equivalence classes out of every situation (Nature does not provide us with any cut-and-dried equivalence relations); it is simply a matter of convenience. So that it if any partitions into various families of types, methods and approaches appear trite, artificial or even arbitrary .... well, they probably are.

Where possible, the various papers, articles and extracts discussed in chapters 2-7 have been presented in some semblance of chronological order - to preserve the sense of development of each topic.

§1.2 A Brief Account Of Ecosystem Modelling

Population Biology can be divided into three major components:

(i) population genetics - treating each species individually, varying time to observe long-term evolutionary changes.

(ii) population ecology - recognising multi-species systems and their inter-relationships under a changing environment.

(iii) mathematical biogeography - obtaining an overall picture of changing population, with evolutionary and demographic time on an equal footing.

Population ecology is our main concern. There are several alternatives available amongst modelling approaches, and the prospective modeller's choice will depend on what is hoped to be achieved. Unfortunately, the literature contains many instances of failing to match the ends with the appropriate means. Such dangerous practices include attempting to fit data accurately with a highly theoretical model, or trying to infer too much about the behaviour of a system from data analysis or simulation techniques.

Levins (1966) explains that a naive approach would be to set up a mathematical model which represents a faithful, one-to-one reflection of the particular system under scrutiny. The absurdity of such a model becomes apparent when one realizes what is involved. There would be countless parameters to measure, many of which are still only vaguely defined and often difficult to measure. These would be incorporated into hundreds of partial differential equations which would more than likely require numerical solution (even if analytical solutions in terms of the system parameters existed, they would be likely to have little meaning in terms of intuitive interpretations).

Clearly assumptions must be made. But what assumptions are reasonable, given that what might look justified for one environment may be wholly unsuitable for another? Levins suggests that there are three qualities that should be present in an ideal model: generality (applicable to a number of situations), realism (ensuring the model does reflect what is going on in the system), and precision (the numerical details are accurate). With such an ideal model, one would have high hopes of understanding most systems, and not only making predictions, but perhaps even understanding the consequences of modifying such a system. In practice, at least one of these desirable qualities must be sacrificed. Through this concept, Levins provides three broad approaches to modelling:

(i) Preserve realism and precision. Reduce the parameters to only short term behaviour of the species, make reasonably accurate measurements, and solve the equations numerically on the computer. The result is a simulation model which can often give accurate predictions, though it is only applicable to the specific systems under observation.

(ii) Preserve generality and precision. Accurate numerical results are taken from very general equations, ignoring many realistic effects observed, in the hopes that small deviations from reality will result in only small deviations in the results. Although quite successful in physical systems, the usefulness of this approach in ecology is questionable.

(iii) Preserve generality and realism. This is a somewhat strategic approach, obtaining qualitative rather than quantitative results. The models will be flexible, and specific requirements can be expressed in a universal fashion (inequalities, shapes of curves in a graph, etc.), without specifying the precise mathematical form.

Before discussing the approach types in detail, we note several other difficulties facing the modeller. Once assumptions are made, will the results obtained depend on the essentials of the model, or on the details of the simplifying assumptions? The confidence in such a result should increase if it proves to be a common factor of several alternative models, each based on different assumptions. In this case, Levins defines the result as robust.

The other point to note is the great number of parameters requiring repesentation at a more simplified level. A smaller number of sufficient parameters at a higher level would help, but such high level parameters often lack intuitive meaning, and are not necessarily independent of each other any longer.

Undoubtedly approach type (i) is the most widely employed currently at management levels. The view that a complex system can be treated as a large number of very simple processes certainly suggests that systems analysis is a most practical approach. Watt (1966) sets out the strategy of systems analysis, as applied to ecology:

(a) As much raw data as possible is obtained, and a comprehensive list of potentially important variables and pathways is drawn up. It is unfortunate that this, the first step, often proves to be the hardest. Obtaining suitable information, devising measurement techniques to ensure some variables remain constant, obtaining sufficient data to allow for reasonable predictions, and even being sure that the data is correct are all difficulties that inevitably arise.

(b) Multiple regression techniques are used to distinguish between the dependent and independent variables.

(c) The above information is then structured into a systems model. Note that further experimentation and observation may be necessary to determine how the various components fit into the model.

(d) The model is subjected to simulation on a computer, and optimal strategies are determined for management decisions.

The lack of generality in this approach does not appear to be of great concern, but there is a greater danger present. Such an approach takes no account of the underlying dynamics of the system, and there is no guarantee that the behaviour of such a system will remain the same even under small perturbations. For example, approach type (i) is extensively used in the management of fisheries, despite the fact that it is totally dependent on data - data which has not always been proven to be reliable. Yet overexploitation of many conventional fish stocks still occurs, and a recent paper by May et al (1979) expesses concern over the recent collapse of several major fisheries in Great Britain. It was felt that there is an increasing need for managers to take into account the interactions among species.

This is where it is hoped that approach type (iii) [and to a lesser degree (ii)] can be put to good purpose. It is a pity that the current status of such theoretical models is not high amongst ecologists. After all, such models do not provide immediate answers to pressing problems, and they often include unreasonable assumptions (particularly when the modeller has obviously not consulted the ecological literature in any depth). Pielou (1977) states that the mathematical models developed so far are no more than "interesting and thought-provoking" and "relate only to simple mathematical systems". Whether this criticism is justified or not is debatable, but it must be stressed that the potential for theoretical ecological models far exceeds that of just fitting data. Perhaps May (1974a) best summarizes this feeling:

> "In ecology, I think it is true that tactical models of of the systems analysis kind, applied to specific individual problems of resource and environmental management, have been more fruitful than has general theory, and they are likely to remain so in the near future. But in the long run, once the 'perfect crystals' of ecology are established, it is likely that a future ecological engineering will draw upon the entire spectrum of theoretical models, from the very abstract to the very particular, just as the more conventional branches of science and engineering do today."

No matter what approach is chosen, ultimately the question of stability will emerge like a spectre from the fog of environmental debate. Indeed the word stability is almost mythological in nature when applied to ecology - everyone believes in it, some claim to have seen it, yet few can agree as to what it is exactly, how it can be measured, what causes it to exist (or disappear) and to what degree, if at all, it can be manipulated!

Recent attempts have been made by Holling (1973), Innis (1975) and Harrison (1979) to rectify the situation by defining such concepts as ecosystem resistance, persistence, resilience, sensitivity and reliability. I shall beg the question by defining various types of stability as it suits. The current controversy on ecological stability centres on whether a large, complex multi-species system is necessary to assure stability or not. As the bulk of this work on multi-species systems is still in its infancy, we shall tacitly assume that complexity is not essential for a stable system (there are examples given in §2.1 which demonstrate that an ecosystem with very few trophic levels can survive).

Let us restrict our attention to a two-species system. Reducing further to a one-species system, while simpler, loses the potential impact of interactions between species. Experience has shown that a two-species system is analytically tractible,as two-dimensional spaces can be discussed on paper far more conveniently than spaces of three or more dimensions.

Two species can interact (if at all) in three different ways: commensalism, where each species has an accelerating effect on the growth of the other; competition, where each species has an inhibiting effect on the growth of the other; and predation, where one species (the predator) inhibits the growth of the other (the prey), whereas the prey accelerates the growth of the predator.

I have chosen predation for the topic of this review, as it seems to fit best the concept of ecology in action. Certainly the approaches devised to deal with the predator-prey interaction can be modified in most cases to model competitive situations as well.

From here on we are primarily concerned with the qualitative behaviour of predator-prey systems. There have been several attempts to model fairly general predator-prey situations using systems analysis and simulation techniques [see Jones (1979), Dixon and Cornwell (1970) and Engstrom-Heg(1970) for example], but these will not be considered.

§1.3 Mathematical Aspects

Having decided on a qualitative approach, it now remains for us to establish the necessary mathematical tools. Strictly speaking, virtually all the biological processes that constitute an ecosystem are stochastic in nature. But there are certain advantages in using deterministic models, particularly as more is known about them than their stochastic counterparts. It is questionable whether, at such an earlier stage of ecosystem modelling, the extra complexity of analysis is justified by the inclusion of a probability structure. Since we are often concerned with equilibrium solutions, it would seem sensible to adopt Maynard-Smith's (1974) attitude:

> "... if the deterministic model shows a stable equlibrium, the corresponding stochastic model would predict long-term survival, whereas if the deterministic model shows no equlibrium, or an unstable one, the stochastic model would predict extinction with a high probability."

This is not to say that stochastic fluctuations, no matter how small, are not important. In §3.1 the potential dangers of such fluctuations in the population densities are stressed, and ways for incorporating these factors into the deterministic models are discussed. Furthermore, fluctuations in the environmental parameters are also important, as demonstrated in chapter 6. Finally, we note that some attempts at stochastic modelling of predator-prey systems have been made, and these are briefly covered in §4.5.

Within the deterministic realm, there are two schools of thought on modelling predator-prey ecosystems. The time scale can be measured either as a continuous independent variable (hence the use of differential equations), or in terms of discrete time intervals (so that difference equations are more suitable). Traditionally the latter approach has only been used where the species involved have fairly fixed generation times. Such models seem particularly appropriate for host-parasite systems [see Hassell (1978) for a thorough survey of the use of difference equations in these and other predator-prey systems]. More recently, Innis (1974) and Van Der Vaart (1973) have presented strong arguments in favour of the use of difference equations for ecological modelling in general. Again, the problem is that less is known of difference equation systems, and they lack an illustrative medium for presenting qualitative results corresponding to the phase plane portraits of two-dimensional differential equation dynamic systems. Even less is known of the state of 'chaos', where the behaviour of the systems can become (as far as present analysis is concerned) wholly unpredictable. Chaos cannot occur in two-dimensional differential equation systems [Rössler (1976) discusses chaos in three-dimensional systems], yet it had appeared in some of the simplest one-dimensional difference equation models [see May (1975) and May and Oster (1976)].

Most of the models discussed in this review will be represented by a pair of autonomous, first-order differential equations of the form:

$$\begin{aligned}\frac{dx}{dt} &= P(x,y)\\ \frac{dy}{dt} &= Q(x,y)\end{aligned} \qquad \ldots \quad (1.3.1)$$

where the details of the functions P and Q, and the variables x and y will be developed over the next two chapters. Models contained in a wider class of systems than that of (1.3.1) are presented in chapter 5.

Frequent use of standard linearization techniques will be made throughout, so a brief outline is provided below. If an equlibrium point $P^* = (x^*, y^*)$ exists for system (1.3.1), then we have:

$$P(x^*,y^*) = 0 = Q(x^*,y^*)$$

and the Jacobian of the system is given by

$$\Delta(x^*,y^*) = \begin{bmatrix} \frac{\partial P}{\partial x}(x^*,y^*) & \frac{\partial P}{\partial y}(x^*,y^*) \\ \frac{\partial Q}{\partial x}(x^*,y^*) & \frac{\partial Q}{\partial y}(x^*,y^*) \end{bmatrix}$$

so that the eigenvalues associated with P^* can be calculated from the equation

$$| \Delta(P^*) - \lambda I | = 0 \qquad \ldots \quad (1.3.2)$$

Having obtained the eigenvalue pair $\{\lambda_1, \lambda_2\}$, the following can be deduced about the local behaviour of trajectories near P^*.

(1) If λ_1, λ_2 are both real, and of the same sign, then P^* will be a node, either stable (if both λ are negative) or unstable (if both λ are positive).

(2) If λ_1, λ_2 are both real, and of opposite sign, then P^* will be a saddle point.

(3) If λ_1, λ_2 are both complex, and their real parts are non-zero, then P^* will be a focus, either stable (if both λ have negative real parts) or unstable (if both λ have positive real parts).

(4) If λ_1, λ_2 are complex, and their real parts are zero, then P^* is either a focus or a centre, depending on the nonlinear effects of P and Q. In this case P^* will be structurally unstable.

If either eigenvalue is zero, then further investigations will be necessary. All other mathematical aspects are either assumed or developed as they are required.

2 THE LOTKA-VOLTERRA MODEL

§2.1 Observations

It is often said that the best way of investigating the mechanisms involved in a stable system is to study what makes this system become unstable. Yet most of the predator-prey systems available for observations are in some sense stable by their very existence - as we tend to link the concept of instability in population numbers with fluctuations in numbers of one or both species, inevitably leading to extinction.

Alternatively, there are several well-documented examples of unstable systems created by the intervention of Man, through either the eradication of an existing species, or the introduction of a new species. Murdoch and Oaten (1975) provide several instances, such as the introduction of the alewife fish into Crystal Lake. Within twenty years, some species of zooplankton in the lake were heavily reduced in numbers, while others disappeared altogether. The effects of introducing the lamprey into the Great Lakes were apparently devastating, as many of the fish populations were driven to near extinction through predation.

There are a few naturally occurring unstable systems, where prey numbers may increase so rapidly that the predators are unable to keep up. The spruce budworm is a case in point; periodically a pest in Canada, its numbers can accelerate on a grand scale when environmental conditions are suitable.

Clearly few predators restrict their feeding to only one kind of prey; similarly the prey species are seldom exploited by a single predator. The best we can hope for, then, is an environment where the predator-prey pair can be treated as an isolated subsystem of the ecosystem as a whole; where the effects of other species in the same environment will be either constant or negligible. Thus, to preserve our two-variable system, extraneous effects will be banished to the set of environmental parameters. This ideal sort of arrangement produces what we call a 'classical' predator-prey system.

Now the prospective modeller must have data to play with, and the shortage of field studies in this area presents another major hurdle. Time is often a problem; observing appropriate changes in populations due to long-term factors and recording the relevant data may require years - particularly if the generation times of the species involved are relatively large.

The chief difficulty is the great dearth of classical predator-prey systems available for scrutiny, as they are usually found in the more extreme environments where the ecosystems are not so complex. The awkwardness and unreliability of the population estimation techniques in such areas does not improve matters. As a result, only a handful of such system studies exist that include sufficient data to work with [see Tanner (1975) for details]. The most popular of these include the snow-shoe hare and lynx in northwest Canada, and the moose and wolf on Isle Royale in Lake Superior.

Laboratory experiments circumvent most of the above difficulties. But curiously, such experimental systems tend to be highly unstable, unlike their natural counterparts, and require continual manipulation just to ensure the survival of both species is long enough to obtain sufficient data. Bazin et al. (1974) provide several useful recommendations, and suggest that experiments involving microbial systems would be the most suitable for predator-prey studies. The advantages include short generation times, greater experimental control, and observations are easily made, providing dependable and regular data. Of course, there are other invertebrate systems which could be just as useful [see the experiments of Huffaker (1958), for example].

One thing is certain; both experimental evidence and field studies indicate that cyclic behaviour in both the predator and prey populations is an inherent feature of a classical predator-prey system; the cycles being typically out of phase. Slobodkin (1962) noted that cyclic phenomena are observed in the more extreme environments such as deserts, islands and the arctic regions. He suggests that these oscillations may be solely dependent on outside energy sources, that the environment dictates the type of oscillating behaviour displayed by the predator-prey system. This indicates some sort of conservation of ecological energy at work - certainly an intuitively pleasing concept, if a bit difficult to justify with empirical evidence.

Of course, there are suggestions that oscillations may only be indirectly related to the predator-prey relationship. Even the regular cycles of the snow-shoe and lynx have come under close scrutiny. Analysing the data available, Leigh (1968) concluded that the predator-prey interaction was notthe cause, though he also confessed that the mechanism eluded him, finding "...the whole oscillation most mysterious". Gilpin (1973) tested the data in one of his models [see §4.1], only to obtain the puzzling result that the hares seemed to be preying on the lynx! He attributed this apparent paradox to the interference of the Canadian trappers (from whence the data was obtained), or perhaps the spread of disease from the hares to the lynx.

It is our purpose to investigate the nature of these oscillations, the mechanisms behind them, and their possible consequences. It is interesting to note that before these cyclic phenomena were properly observed, they had already been predicted for the classical predator-prey system in a theoretical model devised independently by Alfred Lotka and Vito Volterra!

§2.2 The Lotka-Volterra Model

In 1925, Alfred Lotka published a book entitled *Elements of Physical Biology*, which included the following model:

$$\begin{aligned} \frac{dN_1}{dt} &= N_1(\varepsilon_1+\gamma_1 N_2) \\ \frac{dN_2}{dt} &= N_2(\varepsilon_2+\gamma_2 N_1) \end{aligned} \qquad \ldots \ (2.2.1)$$

where: N_1, N_2 represent the two species populations.

ε_1, ε_2 are the coefficients of self-increase.

γ_1, γ_2 are the interaction coefficients.

As a predation model, the phase plane of system (2.2.1) demonstrated a family of closed curves in the first quadrant [see Figure 2.2.1]. Each of these closed, periodic paths depended solely on the initial population size. Lotka recognised that small oscillations in the neighbourhood of the unique fixed point can be approximated by ellipses, and that if cubic terms were added to (2.2.1), the internal equilibrium became a global attractor.

Meanwhile, Vito Volterra had also developed this model, and included a very thorough investigation in a 1927 monograph. Amazingly, it was not until Scudo (1971) and Scudo and Ziegler (1978) had revived and translated a great deal of his work, that the extent of Volterra's studies in this area were known. In the following, we elaborate on his conception of the model and some of the results [from Scudo and Ziegler (1978)].

Let $x(t)$ and $y(t)$ be the prey and predator densities respectively at time t. If predators are not present, we assume the prey grow exponentially with constant birth rate $\alpha > 0$. If prey are not present, we assume the predators die exponentially with constant death rate $\gamma > 0$. Thus we have:

$$\frac{dx}{dt} = \alpha x \quad \text{and} \quad \frac{dy}{dt} = -\gamma y$$

Now suppose the two species occupy the same environment. The greater the number of times predators meet prey, the more we would expect α to decrease (say in proportion to y), and $-\gamma$ to increase (say in proportion to x). The result is a predator-prey system modelled by coupled differential equations:

$$\begin{aligned} \frac{dx}{dt} &= (\alpha-\beta y)x \\ \frac{dy}{dt} &= (-\gamma+\delta x)y \end{aligned} \qquad \ldots (2.2.2)$$

with $\alpha,\ \beta,\ \gamma,\ \delta\ >\ 0$.

Zero-isoclines of (2.2.2) are given by $x = 0$, $y = 0$ and $x = \gamma/\delta$, $y = \alpha/\beta$. We are only interested in the first quadrant of the phase plane, so we restrict our studies to:

$$\begin{aligned} E &= \{(x,y) \in R^2\colon\ x \geq 0,\ y \geq 0\} \\ \text{and } E^0 &= \{(x,y) \in R^2\colon\ x > 0,\ y > 0\} \end{aligned} \qquad \ldots (2.2.3)$$

System (2.2.2) has two equilibria, one at $(\gamma/\delta,\alpha/\beta)$ and a trivial one at $(0,0)$. Though no explicit form has been found for solutions to this system, Volterra presented implicit solutions:

Let $n_1 = \frac{\delta x}{\gamma}$; $n_2 = \frac{\beta y}{\alpha}$

then the system becomes: $$\left\{\begin{aligned} \frac{dn_1}{dt} &= \alpha n_1(1-n_2) \\ \frac{dn_2}{dt} &= -\gamma n_2(1-n_1) \end{aligned}\right. \qquad \ldots (2.2.4)$$

$$\Rightarrow \quad \left\{\begin{aligned} \gamma\,\frac{dn_1}{dt} &= \alpha\gamma n_1(1-n_2) \\ \alpha\,\frac{dn_2}{dt} &= -\alpha\gamma n_2(1-n_1) \end{aligned}\right.$$

Adding, we get: $$\frac{d}{dt}(\gamma n_1+\alpha n_2) = \alpha\gamma(n_1-n_2) \qquad \ldots (2.2.5)$$

Similarly, multiplying (2.2.4) by $\frac{\gamma}{n_1}$ and $\frac{\alpha}{n_2}$ respectively, and again adding, we get:

$$\frac{\gamma}{n_1}\frac{dn_1}{dt}+\frac{\alpha}{n_2}\frac{dn_2}{dt} = \alpha\gamma(n_1-n_2)$$

$$\Rightarrow \frac{d}{dt}\left[\log(n_1{}^{\gamma})+\log(n_2{}^{\alpha})\right] = \alpha\gamma(n_1-n_2) \qquad \ldots (2.2.6)$$

Equating (2.2.5) with (2.2.6) and integrating:

$n_1^{\gamma}n_2^{\alpha} = C\, e^{\gamma n_1+\alpha n_2}$ where $C > 0$ is a constant.

$$\Rightarrow \left(\frac{n_1}{e^{n_1}}\right)^{\gamma} = C\left(\frac{n_2}{e^{n_2}}\right)^{-\alpha} \qquad \ldots (2.2.7)$$

A lengthy argument then follows establishing that the trajectories in E^0 are closed paths, nested in one another [see Figure 2.2.1], so that the equilibrium point $(\gamma/\delta, \alpha/\beta)$ is a centre.

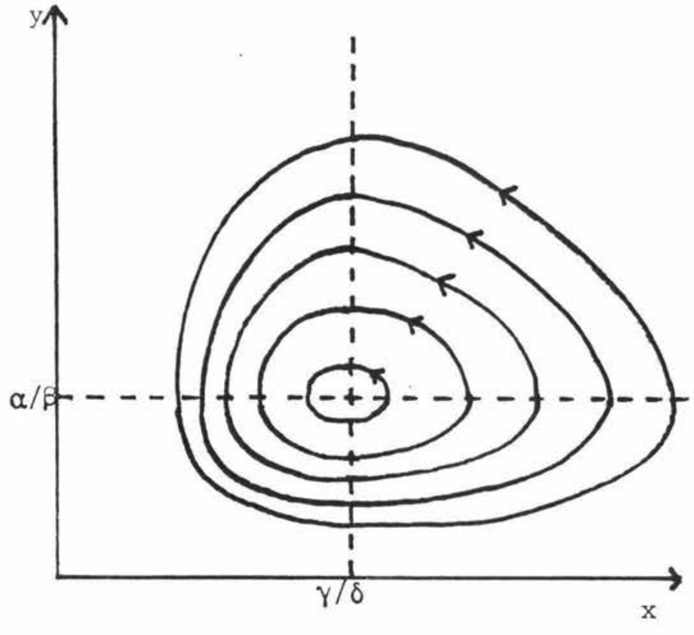


Figure 2.2.1

From equation (2.2.7), the period T of any particular closed path will only depend on the parameters α, γ and the constant C. By ignoring higher order terms, Volterra demonstrated how the trajectories became elliptical near the centre, and that the period can be approximated by:

$$T \approx \frac{2\pi}{\sqrt{\alpha\gamma}} \qquad \dots (2.2.8)$$

By integrating over one complete cycle of a particular closed path, the average number of individuals of each species for this path was obtained. As a result, Volterra discovered the interesting property that these averages remained constant, regardless of which closed path was considered. As one might expect these averages were given by the equilibrium values:

$$\bar{x} = \frac{\gamma}{\delta} \qquad \bar{y} = \frac{\alpha}{\beta} \qquad \dots (2.2.9)$$

As Volterra had applications to fishing in mind when he originally broached this problem, he also investigated what the effects of removing a proportionate number of the species from the system would be. Using (2.2.2), it was found that $\bar{x}$ increased, while $\bar{y}$ decreased. Whereas, if the prey were protected to a greater degree, both $\bar{x}$ and $\bar{y}$ increased.

This 'law of conservation of averages' ties in well with the concept of 'conservation of ecological energy' as noted in §2.1. This can be seen more directly from the following:

Rewrite (2.2.2) to give: $\frac{1}{\beta}\frac{dx}{dt} = (\frac{\alpha}{\beta} - y)x$

$$\frac{1}{\delta}\frac{dy}{dt} = (\frac{-\gamma}{\delta} + x)y$$

Adding these two equations, gives: $\frac{1}{\beta}\frac{dx}{dt} + \frac{1}{\delta}\frac{dy}{dt} - \frac{\alpha}{\beta}x + \frac{\gamma}{\delta}y = 0$

and integrating: $\frac{1}{\beta}x + \frac{1}{\delta}y - \frac{\alpha}{\beta}\int_0^t x\,dt + \frac{\gamma}{\delta}\int_0^t y\,dt = C$ (constant).

Let $U = \frac{1}{\beta}x + \frac{1}{\delta}y$

$$V = -\frac{\alpha}{\beta}\int_0^t x\,dt + \frac{\gamma}{\delta}\int_0^t y\,dt$$

Volterra refers to U as the "actual demographic energy" of the system, and V as the "potential demographic energy" of the system. Thus the "total demographic energy", H = U + V, remains unchanged in a fixed environment, regardless of how the species numbers change. He noted how analogous this result appeared to many conservation laws of physics.

Volterra was well aware of the biological limitations of this model, as it only applied to species without any age structure or memory, and assumed that all prey encountered by predators were instantaneously devoured and converted into more predators. To be any more realistic in this respect, the introduction of time-delays in the equations would be necessary. So Volterra handled these modifications by using integro-differential equations (see chapter 6 for details), and produced a number of interesting properties. For example, he was one of the first to describe stable oscillatory behaviour in ecological models, the importance of which was not fully realised until many years later (see the discussion on limit cycles in §3.2).

Volterra's thoroughness and technical manipulations of the model were truely amazing, and it is lamentable that many of his contributions to ecology are insufficiently known or improperly understood. Over the last twenty years, criticisms of the Lotka-Volterra model have been many and varied, often pointing out faults that Volterra had already been aware of. Many of these criticisms are accepted at their face value,and it has become standard practice to quote them along side the model itself in any preliminary discussion on ecological models. It is hoped that this currently negative attitude can be stemmed by breathing new life into the model in chapter 6, where an alternative viewpoint is discussed - perhaps more in the spirit of Volterra's intentions.

§2.3 Criticisms

After the appearance of the Lotka-Volterra model, many sought to verify its validity through quantitative tests, either by the use of field data or by conducting experiments [particularly those of Gause (1934, 1935) and Gause, Smaragdova and Witt (1936)]. Citing this model as a typical example, Smith (1952) expressed great concern over the amount of data fitting going on in theoretical models. He stated that fitting deterministic curves to empirical data as a means of 'testing' theories is indefensible on at least three counts:

(i) Deviations from the best-fit curves inevitably occur, yet the evaluation of the fit is often subjective,

(ii) As the likelihood of the fit being good is high, the method is uncritical since it fails to discriminate among a host of apparently similar situations which may have markedly different underlying dynamics.

(iii) A fit is often judged as a whole, rather than on its parts. Thus we may say the overall fit is 'nice', even if parts of it may have significant deviations.

Even Volterra evaluated the model using fishing data, but his interest seemed to lie more with the nature of the oscillations rather than any precise numerical agreement. It is perhaps more reasonable to investigate whether the Lotka-Volterra model reflects in any way, the cyclic properties we have observed in predator-prey interactions.

Recall from §2.1 that while such an interaction may imply some kind of cyclic behaviour in the system, the converse may not be true. Wangersky (1978) noted with some dismay that "... almost every population that showed periodic fluctuations was once considered to be part of such a predator-prey interaction." This misplaced faith in the power of such models may be partly responsible for their unpopularity today.

Fredrickson et al. (1973) presented a detailed critique of the Lotka-Volterra model, yet emphasis was placed on what was missing from the model (time delays, age and sex differences, stochastic and spatial effects, and species diversity to name but a few), rather than on what was included.

However there were two criticisms, which the authors stressed as important, challenging the model on a more fundamental basis. Firstly, the nonlinear terms in (2.2.2) express the exchange of food energy, converting prey devoured into new predators. Fredrickson et al. observe that most of this captured energy is expended into the maintenance and growth of the predators, rather than their reproduction. Again, the authors seem to have missed the point. The model is an attempt at understanding the raw mechanism of the predator-prey interaction. Dispensing with age structure and time delays, we expect this transfer of energy to appear ultimately in the creation of more predators, treating growth and maintenance as intermediate steps towards this end. Furthermore, we are investigating this interaction in terms of population changes, so that energy lost in maintaining and improving the predators already present can simply be incorporated into the conversion rate.

Secondly, the Lotka-Volterra model assumes the predator birth rate is directly proportional to prey density, yet the predator death rate is totally independent of prey density. The authors felt that if anything, the reverse is more likely to be true. In other words, the availability of prey affects the overall predator growth rate by increasing the death rate through starvation (the Malthusian approach), rather than by increasing the birth rate when prey are abundant. Undoubtedly ecologists could argue this point one way or the other, but what changes in the qualitative picture occur using this alternate view point? It is worth following this up, as Fredrickson et al. have not done so.

Using standard linearization techniques on the Lotka-Volterra model given by (2.2.2), we have the Jacobian:

$$\Delta(x^*,y^*) = \begin{bmatrix} \alpha-\beta y^* & -\beta x^* \\ \delta y^* & -\gamma+\delta x^* \end{bmatrix}$$

so that the eigenvalues of the system for (0,0) are given by:

$$|\Delta(0,0)-\lambda I| = \begin{vmatrix} \alpha-\lambda & 0 \\ 0 & -\gamma-\lambda \end{vmatrix}$$

$$\Rightarrow \quad \lambda = \alpha, \ -\gamma$$

Hence (0,0) represents a saddle point.

The eigenvalues for $(\frac{\gamma}{\delta}, \frac{\alpha}{\beta})$ are given by $\lambda = \pm i\sqrt{\alpha\gamma}$, so that this equilibrium is either a centre or a focus (higher order terms must be considered to prove it is a centre).

Now suppose we take up the suggestion of Fredrickson et al. and modify the model to give:

$$\frac{dx}{dt} = (\alpha-\beta y)x$$
$$\frac{dy}{dt} = (-\gamma f(x)+\delta)y \qquad \ldots (2.3.1)$$

where f(x) is continuously differentiable, and satisfies

$$f(0) > \delta/\gamma; \ f'(x) \le 0 \text{ for } x \ge 0; \ \exists x > 0: f(x) < \delta/\gamma \qquad \ldots (2.3.2)$$

Thus f(x) is a decreasing function of x, ensuring that $\frac{dy}{dt} < 0$ for low values of x, and $\frac{dy}{dt} > 0$ for large values of x. We also have:

$$\exists \tilde{x} > 0: f(\tilde{x}) = \delta/\gamma$$

Hence there is a unique equilibrium point $(\tilde{x}, \frac{\alpha}{\beta})$ in E^0.

Now $$\Delta(x^*,y^*) = \begin{bmatrix} \alpha-\beta y^* & -\beta x^* \\ -\gamma y^* f'(x^*) & \delta-\gamma f(x^*) \end{bmatrix}$$

So that at (0,0): $$\begin{vmatrix} \alpha-\lambda & 0 \\ 0 & \delta-\gamma f(0)-\lambda \end{vmatrix} = 0$$

$$\Rightarrow \quad \lambda = \alpha, \quad \delta-\gamma f(0)$$

$$\Rightarrow \quad (0,0) \text{ is a saddle point.}$$

and at $(\tilde{x}, \frac{\alpha}{\beta})$: $\begin{vmatrix} \lambda & -\beta\tilde{x} \\ -\frac{\alpha\gamma}{\beta} f'(\tilde{x}) & -\lambda \end{vmatrix} = 0$

$$\Rightarrow \lambda = \pm i\sqrt{\alpha\gamma\tilde{x}f'(\tilde{x})} = \pm i\,\eta \quad \text{say.}$$

So that clearly system (2.3.1) has similarities to (2.2.2). The equilibrium point (0,0) is still a saddle point with the axes as separatrices, and $(\tilde{x}, \frac{\alpha}{\beta})$ is still structurally unstable. It is not difficult to see that whether it is a centre or not will depend on the nature of $f(x)$.

By using techniques given by Andronov et al. (1973b), we can calculate the third focal value, α_3, of the equilibrium point $(\tilde{x}, \frac{\alpha}{\beta})$ to establish sufficiency conditions for it being a multiple focus. Assume $f \in C^3$.

Set $\begin{aligned} u &= x - \tilde{x} \\ v &= y - \frac{\alpha}{\beta} \end{aligned}$

Hence system (2.3.1) becomes:

$$\begin{aligned} \frac{du}{dt} &= \beta v(u+\tilde{x}) \\ \frac{dv}{dt} &= (v+\frac{\alpha}{\beta})[\delta-\gamma f(u+\tilde{x})] \end{aligned} \qquad \ldots (2.3.3)$$

As we are concerned only with the nature of the trajectories near the origin of system (2.3.3), we can expand $f(u+\tilde{x})$ into a MacLaurin series:

$$f(u+\tilde{x}) = f(\tilde{x}) + f'(\tilde{x})u + \frac{1}{2}f''(\tilde{x})u^2 + \frac{1}{6}f'''(\tilde{x})u^3 + \ldots$$

Let $P_k(u,v)$ and $Q_k(u,v)$ be polynomials containing all terms of k^{th} degree in $\frac{du}{dt}$ and $\frac{dv}{dt}$ respectively. Hence we have:

$$\begin{aligned} P_2(u,v) &= \beta uv \\ P_3(u,v) &= 0 \\ Q_2(u,v) &= -\frac{\alpha\gamma}{2\beta}f''(\tilde{x})u^2 - \gamma f'(\tilde{x})uv \\ Q_3(u,v) &= -\frac{\alpha\gamma}{6\beta}f'''(\tilde{x})u^3 - \frac{\gamma}{2}f''(\tilde{x})u^2v \end{aligned} \qquad \ldots (2.3.4)$$

and using the coefficients in the equations (2.3.4), we obtain the following expression for the third focal value:

$$\begin{aligned} \alpha_3 &= \frac{\pi}{4\eta}\left[-\frac{\gamma}{2}f''(\tilde{x})\right] - \frac{\pi}{4\eta^2}\left[\frac{\alpha\gamma^2}{2\beta}f'(\tilde{x})f''(\tilde{x})\right] \\ &= -\frac{\pi\gamma f''(x)}{8\eta}\left[1+\frac{\alpha\gamma}{\beta\eta}f'(\tilde{x})\right] \end{aligned} \qquad \ldots (2.3.5)$$

If $\alpha_3 < 0$ then the origin of system (2.3.3) is a stable focus; if $\alpha_3 > 0$ then it is an unstable focus; and if $\alpha_3 = 0$ then higher focal values need to be considered (the equilibrium is a centre when all focal values are zero).

Since $f'(\tilde{x}) < 0$ and $\eta > 0$, we have:

$$\alpha_3 = 0 \Leftrightarrow \{f''(\tilde{x}) = 0 \quad \text{or} \quad f'(\tilde{x}) = -\frac{\beta\eta}{\alpha\gamma}\} \qquad \ldots (2.3.6)$$

There is no reason to expect f(x) to satisfy the particular qualities listed in (2.3.6), so that in general α_3 is more than likely non-zero, and the equilibrium a multiple focus. Its stability will depend on the details of f(x).

It is difficult to say whether the situation has genuinely been improved. True, the equilibrium is not neutrally stable in general, but a multiple focus is also structurally unstable, and has many similar bifurcation properties to that of a centre. Under small perturbations it is quite capable of becoming either stable or unstable regardless of its original state of stability.

Perhaps the heaviest criticism of the Lotka-Volterra model comes from the prolific pen of R.M. May [see, for example, May (1972, 1974a,b, 1976) and May and Oster (1976)], whose opinions can be gleaned from the following quotes (taken from the aforementioned references):

> "Structurally unstable models have no place in biology..."
>
> "...to regard the ... lynx and hare population oscillations as resulting from a Lotka-Volterra pure oscillation about a neutrally stable equilibrium point, which is to say having an amplitude determined by some environmental shock over one hundred years ago, is absurd."

Certainly the second criticism above (attacking the suggestion that the observed cyclic phenomena will depend only on the initial conditions) is valid if this model is to be employed as a direct mirror of reality. But this need not be the case. Furthermore, I feel that there is a place for structurally unstable models in biology, provided they are used purely as an indicator of what might be [see chapters 3, 6 and 7].

My own opinion of the current status of the Lotka-Volterra model is best summarized by Goel et al, (1971):

> "We are under the impression that the fall from favour occurred because of general notions about the omissions and oversimplifications, and not because calculations based on the model were in strong contradiction to observations."

3 GENERAL ANALYSIS

§3.1 Environmental Effects

Before entering into detailed discussions on general analysis of predator-prey systems, a few points concerning their surrounding environments should be mentioned. Firstly, to what degree do seasonal fluctuations affect the dynamics? The role that weather plays in limiting population density is felt to be small by many ecologists. They argue that since weather is not influenced by changes in population density, it cannot interact with a population in such a way as to produce a long term stabilizing effect on the population size. Nobody doubts the importance of weather in determining the potential productivity of a region over a long period of time; but it is usually regarded that any apparent stability of an ecosystem will be directly dependent on biological interactions.

Andrewartha and Birch (1954) objected to this viewpoint, citing several examples based on studies of insect populations in Australia. Their conclusions were held to be somewhat suspect, however, since they relied heavily on correlations between various components of the weather and fluctuations of population density. While it is possible for these fluctuations to reflect some of the observed changes in weather, correlations will not prove there is a direct causal relationship.

Even so, their suggestions are quite reasonable when applied to species with sufficiently small densities that predation and competition are not significant limiting factors. Should one of these species thrive and increase rapidly due to an excessive amount of good weather, competition and predation would become major inhibitors of further growth. Collier et al. (1973) refer to the California oak moth as a prime example. The number of caterpillars rises sharply after several exceptionally mild winters, but the resulting fierce competition for food allows only a small proportion to survive.

Most of the environmental changes that occur in a predator-prey system can be considered to be random in the sense that they are totally independent of the species densities. This leads us to the second, and fundamentally more important point.

We concluded in §2.1 that oscillations in the population densities were a natural part of the predator-prey interaction. If the mean densities of each species over a single oscillation are sufficiently large that density changes appear continuous, we can expect the random environmental fluctuations to have only small effects relative to these means. But the actual oscillating density can become very small, relative to the mean, before rising again. At its lowest ebb, the density may approach zero so closely as to be susceptible to extinction through these random fluctuations.

This is perhaps the biggest drawback of using deterministic models in ecology. The trajectory may approach either of the axes in an arbitrarily close fashion, yet still recover [see Figure 3.1.1]; whereas the stochastic model would assign an increasingly higher probability of extinction, the closer the trajectory was to the axis [see Figure 3.1.2].

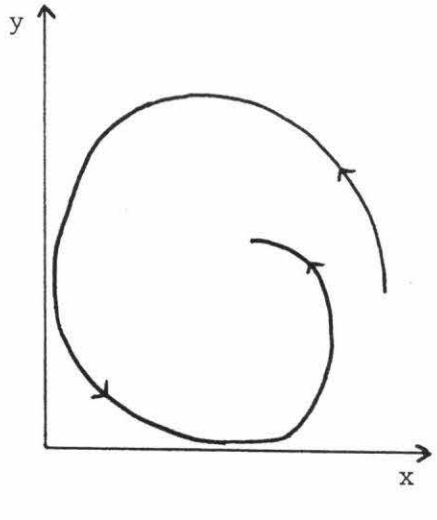


Figure 3.1.1

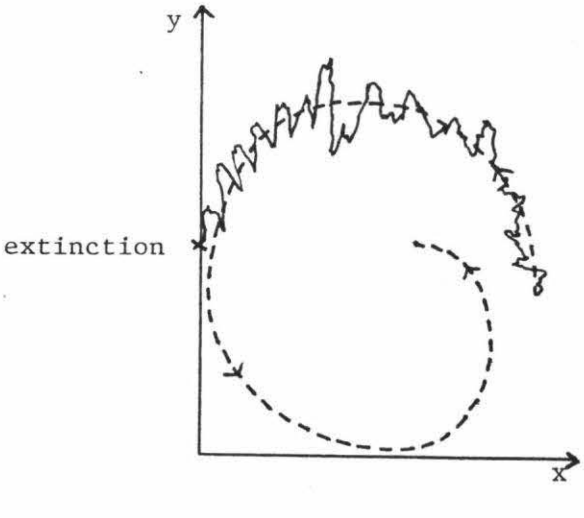


Figure 3.1.2

This effect was undoubtedly the cause of extinction in many of the laboratory experiments, simply by the fact that only small populations were used (in his work with paramecium, Gause (1934) found it necessary to continually add more of one or other species just to maintain the system through several oscillations).

For this reason, we define a system to be increasingly unstable the more likely the trajectories in E^0 are to approach close to either axis. Thus a factor which 'pushes' more trajectories closer to the axes is said to be destabilising; whereas a factor which 'draws' the trajectories further into E^0, away from the axes, is said to be stabilizing. When working with deterministic systems, the possibility of random extinction must be kept in mind at all times.

Brauer et al. (1976) introduced the concept of practical stability, where a trajectory of a system starting in E^0 at $t = 0$ is <u>practically stable</u> if its distance from either axis is never less than k for all $t \geq 0$, where k is some pre-determined positive constant.

Due to its stochastic nature, any system, no matter how stable, will have a positive probability of random extinction occurring. This suggests a value of k could be fixed for a given model so as to fix the likelihood of random extinction at a very low level. In this case, if every trajectory in E^0 has practical stability, then we say the system is practically stable. Note that practical stability cannot be determined by analytic means, since it is highly dependent on initial conditions. For a specific model, numerical computations could be made.

§3.2 Global Stability and the Analytic Approach

The purpose of this chapter is to study general qualitative results, either analytically or graphically, without referring to specific models. The advantages of this are two-fold; the risk of drawing conclusions based on the particulars of the equations rather than from the actual situation is minimized, and the results that are obtained will hopefully be relevant to most predator-prey systems.

Having discussed the simplest predator-prey model in the last chapter, we now jump to the other extreme and consider the general model:

$$\frac{dx}{dt} = P(x,y)$$
$$\frac{dy}{dt} = Q(x,y) \qquad \ldots (3.2.1)$$

Strictly speaking, the term 'general' is misleading, as there are important features of predator-prey dynamics which are not covered by (3.2.1):

(i) The system is autonomous, ignoring the possibility of time delays.

(ii) Spatial variation is neglected, the distribution of each species is assumed to be random throughout the environment.

(iii) The dynamics do not include stochastic variation.

The first two omissions are covered briefly in chapter 5, the last was discussed in the previous section. In the rest of this chapter, constraints are placed on (3.2.1) to establish a wide range of results.

Assuming the environment is closed to outward and inward migration, once the species density reaches zero, the species is extinct and the density remains at zero. If the prey became extinct, the predator population should decrease thereafter. This gives us the following conditions:

$$\begin{aligned} &\exists t_1 \geq 0: x(t_1) = 0 \Rightarrow x(t) = 0, \quad \frac{dy}{dt} < 0, \ \forall t > t_1 \\ &\exists t_2 \geq 0: y(t_2) = 0 \Rightarrow y(t) = 0 \qquad\qquad , \ \forall t > t_2 \end{aligned} \qquad \ldots (3.2.2)$$

With these conditions, (0,0) must be an equilibrium, and system (3.2.1) now takes the form:

$$\begin{aligned} \frac{dx}{dt} &= x\ F(x,y) \\ \frac{dy}{dt} &= y\ G(x,y) \end{aligned} \qquad \ldots (3.2.3)$$

A closed environment also suggests a limit to the population size of each species, though it is doubtful whether a least upper bound could ever be calculated. In terms of our model, this property is expressed by global stability:

A system is globally stable if and only if, for any initial community composition (x_0,y_0) in E at $t = 0$, the solution $(x(t),y(t))$ is bounded for all $t \geq 0$.

Furthermore, if there exists a unique equilibrium point (x^*,y^*) in E^0 such that $x(t) \to x^*$, $y(t) \to y^*$ as $t \to \infty$ for any solution $(x(t),y(t))$ in E^0, then we say (x^*,y^*) is a global attractor (or the equilibrium (x^*,y^*) is globally, asymptotically stable).

Kolmogorov (1936) was the first to consider system (3.2.3) and produced a set of sufficient conditions which would guarantee both the existence of one equilibrium point in E^0 (either a stable focus or an unstable focus surrounded by a stable limit cycle), and the global stability of the system. Although this result follows straightforwardly from the Poincaré-Bendixon theorem, Kolmogorov gave biological interpretations to the conditions required:

(i) Multiplication of prey is slowed by an increase in the number of predators. i.e. $\frac{\partial F}{\partial y} < 0$.

(ii) For any given constant ratio $\frac{x}{y}$, multiplication of prey is slowed down by an increase in both predator and prey numbers. i.e. $\frac{\partial F}{\partial S} < 0$ where S represents a straight line in E^0 through (0,0).

(iii) Prey multiply if predator and prey numbers are low i.e. $F(0,0) > 0$.

(iv) Prey cannot multiply if their numbers are sufficiently high, even if predators are totally absent. i.e. $\exists K > 0: F(K,0) = 0$ [Here K is called the carrying capacity].

(v) Prey cannot multiply if the predator numbers are sufficiently high. i.e. $\exists L > 0: F(0,L) = 0$.

(vi) Rate of increase of predators decreases with its own numbers. $\frac{\partial G}{\partial y} < 0$.

(vii) Predators cannot multiply if prey numbers are sufficiently low. i.e. $\exists J > 0: G(J,0) = 0$.

(viii) For any given constant ratio $\frac{x}{y}$, multiplication of predators increases as the prey and predator numbers increase. i.e. $\frac{\partial G}{\partial S} > 0$.

(ix) $J < K$, otherwise predators become extinct.

Apart from a brief mention in Minorsky (1962), this result remained largely unnoticed until resurrected by Rescigno and Richardson (1967) and Scudo (1971). May (1972) used Kolmogorov's result to infer that all 'sensible' predator-prey models should contain a stable limit cycle in E^0. Assuming the above result applies, May argues that if predator-prey oscillations have persisted, then the case of a globally stable focus with damped oscillations may be unrealistic. Thus using Kolmogorov's result and May's argument, we might expect the representative model of , say the hare/lynx ecosystem, to have a phase plane portrait similar to that of Figure 3.2.1.

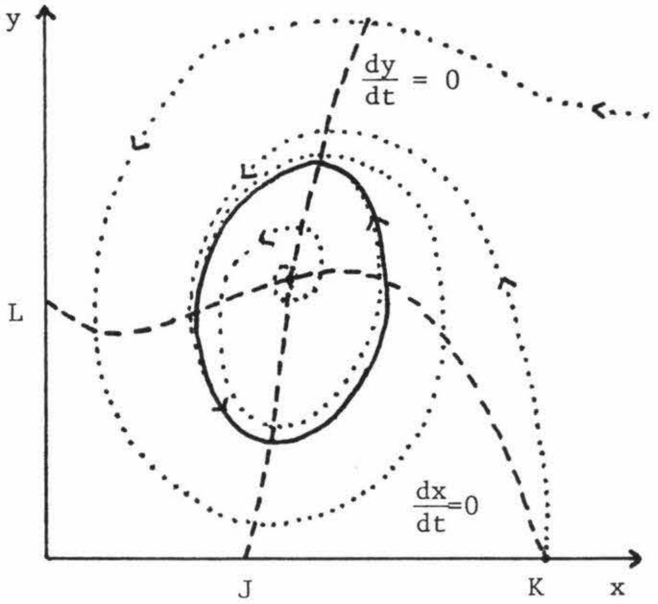


Figure 3.2.1

Expanding on these thoughts, May (1974a) noted that a model satisfying Kolmogorov's criteria was more likely to demonstrate limit cycle behaviour if the carrying capacity K was sufficiently large. This is an important observation, and is considered in more detail in §3.8.

However, there is a warning coupled with May's argument for the desirability of limit cycles in predator-prey models. The ratio between the predator's minimum density (y_{min}) and its mean density (y_{mean}) on the limit cycle is roughly of the order:

$$\frac{y_{min}}{y_{mean}} \sim e^{-a(K/\bar{x})^2} \qquad \ldots (3.2.4)$$

where a is a constant of order unity, and $\bar{x}$ is the overall mean prey density. Usually $K \gg \bar{x}$, which means the above ratio will be small; sometimes so small that y_{min} could come dangerously close to the x-axis. If this were the case, random environmental fluctuations could drive the predators to extinction. Thus a globally stable system in the deterministic sense will not necessarily ensure practical stability. Clearly the numerical values of the system parameters can be important as they will decide the amplitude of the limit cycle.

Kolmogorov's result can still be useful even when his criteria are not totally satisfied. For example, often the prey may find reproduction difficult at low densities if, say, they are unable to find mates This is known as the Allee effect, and results in the added condition $\frac{dx}{dt} < 0$ for small x. Clearly condition (iii) of Kolmogorov's criteria is not satisfied in this case, yet the result still holds for a restricted part of E^0 (x not small).

Albrecht et al. (1973) presented a model (which they admitted had no biological meaning) that satisfied the criteria, yet failed to show the expected qualitative behaviour. May replied that not only did their model have no biological relevance, but it was structurally unstable. But while the authors seem to have missed May's point, their example did demonstrate that the result needed tightening up analytically. Thus Albrecht et al. (1974) restated Kolmogorov's sufficiency conditions and proved some results:

$$\left.\begin{array}{ll}
\text{(a)} & \exists K > 0: (x-K)\,F(x,0) < 0, \quad \forall x \geq 0: x \neq K \\
\text{(b)} & \exists L > 0: (y-L)\,F(0,y) < 0, \quad \forall y \geq 0: y \neq L \\
\text{(c)} & \exists J > 0: (x-J)\,G(x,0) > 0, \quad \forall x \geq 0: x \neq J \\
\text{(d)} & \frac{\partial F}{\partial y} < 0 \quad \text{in } E^0 \\
\text{(e)} & \frac{\partial G}{\partial y} \leq 0 \quad \text{in } E^0 \\
\text{(f)} & x \cdot \frac{\partial G}{\partial x} + y \cdot \frac{\partial G}{\partial y} > 0, \quad \forall (x,y) \in E^0 \\
\text{(g)} & x \cdot \frac{\partial F}{\partial x} + y \cdot \frac{\partial F}{\partial y} < 0, \quad \forall (x,y) \in E^0 \\
\text{(h)} & J < K
\end{array}\right\} \quad \ldots (3.2.5)$$

<u>Theorem 3.2.1</u> If F, G satisfy all the conditions in (3.2.5) except (h), then all trajectories of (3.2.3) starting at (x_0,y_0) in E^0 approach (K,0) as $t \to \infty$. In other words, the predators become extinct.

<u>Theorem 3.2.2</u> If F, G satisfy all the conditions in (3.2.5), then there exists a unique equilibrium point (x^*,y^*) in E^0 such that

(1) if (x^*,y^*) is unstable, then there exists at least one periodic orbit in E^0.

(2) if (x^*,y^*) is stable, then it is a global attractor.

Corollary If F, G satisfy (3.2.5) and (x^*,y^*) is unstable, then there exists an outermost periodic orbit that is semistable from the outside and an innermost periodic orbit that is semistable from the inside. Thus if there is only one periodic orbit, it must be stable.

Freedman (1975) went one step further and analysed the following system:

$$\begin{aligned} \frac{dx}{dt} &= x\,\bar{F}(x,y,\varepsilon) \\ \frac{dy}{dt} &= y\,\bar{G}(x,y,\varepsilon) \end{aligned} \qquad \ldots (3.2.6)$$

where ε is very small, and $\bar{F}(x,y,0) \equiv F(x,y)$; $\bar{G}(x,y,0) \equiv G(x,y)$.

System (3.2.6) represents (3.2.3) in a perturbed state, where the perturbation may be the result of random variation in the system parameters. Assuming $F, G \in C^2$ and that there exists at least one equilibrium point $(x^*,y^*) \in E^0$ of the unperturbed system (3.2.3), Freedman used standard linearization techniques to establish the following.

Let (x',y') be the perturbed equilibrium point of (3.2.6) corresponding to (x^*,y^*) when $\varepsilon = 0$. We define

$$\begin{aligned} \eta(\varepsilon) &= \left.\frac{\partial\bar{F}}{\partial x}\right|_{(x',y',\varepsilon)}; \quad \lambda(\varepsilon) = \left.\frac{\partial\bar{F}}{\partial y}\right|_{(x',y',\varepsilon)}; \\ \mu(\varepsilon) &= \frac{\partial\bar{G}}{\partial x}_{(x',y',\varepsilon)}; \quad \upsilon(\varepsilon) = \left.\frac{\partial\bar{G}}{\partial y}\right|_{(x',y',\varepsilon)} \end{aligned} \qquad \ldots (3.2.7)$$

Shifting the equilibrium to the origin using the transformation $u = x - x'$; $v = y - y'$, system (3.2.6) can be rewritten in standard linearized form giving

$$\begin{aligned} \frac{du}{dt} &= x'\,\eta(\varepsilon)u + x'\lambda(\varepsilon)v + \tilde{F}(u,v,\varepsilon) \\ \frac{dv}{dt} &= y'\,\mu(\varepsilon)u + y'\upsilon(\varepsilon)v + \tilde{G}(u,v,\varepsilon) \end{aligned} \qquad \ldots (3.2.8)$$

When $|\Delta(0,0)| \neq 0$, Freedman was able to give a complete local analysis of the equilibrium point in (3.2.8) up to order ε, for sufficiently small ε. When $|\Delta(0,0)| = 0$, standard methods broke down, and other techniques, requiring further conditions, were used. Finally two sets of sufficiency conditions were given for a limit cycle to appear in (3.2.6). Both are based on the use of Lyapunov functions and the Poincaré-Bendixon theorem. As they are similar, only one need be outlined here.

Define $V(u,v) = \frac{1}{2}\,[y'\mu(\varepsilon)u^2 - x'\lambda(\varepsilon)v^2]$

$$W(u,v) = x'y'\,[\eta(\varepsilon)\mu(\varepsilon)u^2 - \lambda(\varepsilon)\nu(\varepsilon)v^2] + y'\mu(\varepsilon)u\,\tilde{F}(u,v) - x'\lambda(\varepsilon)v\,\tilde{G}(u,v)$$

Let Γ_k be the closed curve defined by $V(u,v) = k > 0$.

Theorem 3.2.3 Let $\mu(\varepsilon) > 0$, $\lambda(\varepsilon) < 0$ for sufficiently small $\varepsilon > 0$. If $\bar{F}$, $\bar{G}$ satisfy (i) (x',y') is an unstable focus.

and (ii) $\exists k > 0$: $\Gamma_k \subset \{(u,v): u > -x',\ v > -y'\}$ and $W(u,v) < 0$, $\forall (u,v) \in \Gamma_k$.

Then there exists a limit cycle of (3.2.8) about the origin inside Γ_k.

A similar theorem holds when $\mu(\varepsilon) < 0$ and $\lambda(\varepsilon) > 0$.

Bulmer (1976) noted that some of Kolmogorov's criteria would be difficult to justify biologically, such as (ii) and (viii). Furthermore, there is nothing relating the growth rate of the predator with the predation rate. So a modified set of conditions was presented:

$$\left.\begin{array}{l} \frac{\partial F}{\partial y} < 0;\ \frac{\partial G}{\partial x} > 0;\ \left.\frac{\partial F}{\partial x}\right|_{y=0} < 0;\ \frac{\partial G}{\partial y} \le 0 \\ \exists L,J,K > 0:\quad F(0,L) = 0;\quad F(K,0) = 0;\quad G(J,0) = 0;\quad K > J \\ \frac{dy}{dt} \le \alpha[x\,F(x,0) - x\,F(x,y) - \mu y]\ ;\quad \alpha,\ \mu > 0 \end{array}\right\} \quad \ldots (3.2.9)$$

The last inequality states that predators can only increase by converting prey into predators. This upper bound on $\frac{dy}{dt}$ was obtained by setting

α = maximum assimilation efficiency for converting prey into predator.

μ = minimum value of a factor covering all energy requirements and predator mortality.

$[x\,F(x,0) - x\,F(x,y)]$ = number of prey consumed in unit time by predators.

As a result, the prey isocline $F(x,y) = 0$ need not conform to a simple shape. Thus an odd number (≥ 1) of equilibrium points appear in E^0, alternating between saddle points, and nodes or foci. Nevertheless, the system remains globally stable.

Hastings (1978a) provided sufficient conditions for an equilibrium point $(x^*,y^*) \in E^0$ to be a global attractor in system (3.2.3).

Theorem 3.2.4 If there exists a unique, locally stable equilibrium point in E^0 and

(i) $\frac{\partial F}{\partial x} < 0$ in E^0

(ii) $\exists$ constant $\alpha < 0$: $\frac{\partial G}{\partial y} \leq \alpha$

(iii) $\exists K < 0$: $F(x,0)(K-x) > 0$, $\forall x \geq 0$: $x \neq K$

then the equilibrium point is globally stable in E^0.

Perhaps the most significant advancement since Kolmogorov's original result came from Brauer (1979) who successfully dispensed with some of Kolmogorov's conditions, while preserving the global stability in E^0 for an even wider class of systems than those given by (3.2.3). Consider

$$\begin{aligned} \frac{dx}{dt} &= x\,F(x,y) - A \\ \frac{dy}{dt} &= y\,G(x,y) - B \end{aligned} \qquad \ldots\ (3.2.10)$$

where $A, B \in \mathbb{R}$ and the following conditions hold in E^0:

$$\frac{\partial F}{\partial y} < 0; \quad \frac{\partial G}{\partial x} > 0; \quad \frac{\partial G}{\partial y} \leq 0; \quad \exists J > 0: G(J,0) = 0 \qquad \ldots\ (3.2.11)$$

Since $\frac{\partial F}{\partial y} \neq 0$, the prey isocline $x\,F(x,y) = A$ defines y as a single-valued function of x, $\Phi(x)$, which will be positive for all x such that $0 \leq \alpha(A) \leq x \leq \beta(A)$, where $\alpha(A)$ and $\beta(A)$ define where the prey isocline crosses the x-axis.

Theorem 3.2.5 Suppose that conditions (3.2.11) hold for system (3.2.10). Furthermore, if $\beta(A) = \infty$, then we also assume that $x\,F(x,y) - A$ and $\Phi(x)$ are bounded above. Then every trajectory starting in E^0 for $t = 0$ either reaches one of the co-ordinate axes in finite time, or remains in a bounded subset of E^0 for all $t \geq 0$.

Note that $\beta(0)$ is equivalent to the carrying capacity, and that if $\alpha(0)$ is positive, then there is an Allee effect in the prey dynamics. The significance of the constants A, B are discussed in §3.9.

§3.3 Graphical Analysis

In the last section, various desirable qualities of a predator-prey model were established (global stability, limit cycles, etc.), and conditions were imposed on the equations of (3.2.3) to produce them. However, it is possible to discuss the qualitative behaviour of a system without considering the equations at all. Thus conclusions drawn will not be artifacts of the exact form of any particular set of equations.

The method, referred to as graphical analysis, was first devised and applied to predator-prey systems by Rosenzweig and MacArthur (1963). Consider the general system given by

$$\frac{dx}{dt} = P(x,y)$$
$$\frac{dy}{dt} = Q(x,y) \qquad \ldots (3.3.1)$$

By considering the shapes of the curves L_x and L_y, representing the zero-isoclines $P(x,y) = 0$ and $Q(x,y) = 0$ respectively, the authors were able to infer the local properties of the equilibria, where L_x and L_y intersected.

The shapes of these isoclines were established in the following manner. If there were no predators ($y=0$), we would expect the prey to be unable to increase either above the carrying capacity K, or below the value A, representing the Allee effect. As the number of predators increase, so we would expect the prey to ultimately start decreasing in numbers. Thus L_x can be pictured most simply as a parabolic-like hump, as in Figure 3.3.1. Note that if the Allee effect was not present ($A=0$), L_x would intersect with the y-axis.

Now the greater than number of predators, the greater the number of prey necessary for the predator density to increase. Thus L_y will have a positive slope (though it is common to use the extreme case where L_y is a vertical straight line). At some point, predator increase must be curtailed by limiting factors other than prey density, such as space. Ultimately, even for large prey densities, L_y would asymptotically approach this ceiling as $x \to \infty$, and become horizontal [see Figure 3.3.1].

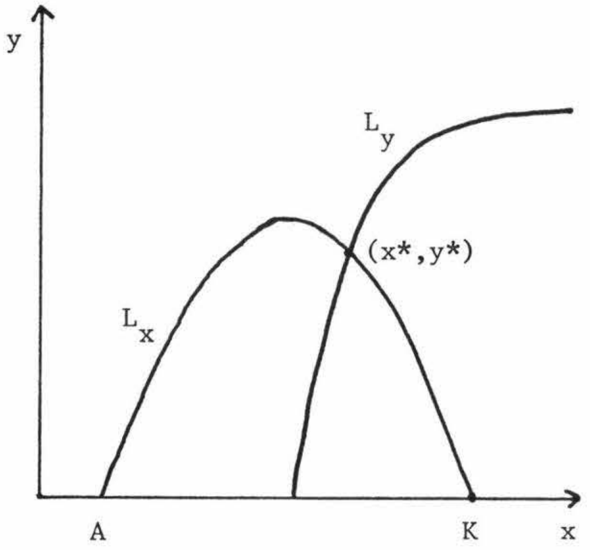


Figure 3.3.1

Rosenzweig and MacArthur demonstrated that the equilibrium point (x^*,y^*) is stable if L_y intersects L_x on the right-hand side of the hump, and unstable if on the left-hand side. Furthermore, (x^*,y^*) will be a focus if L_y has positive slope at this point, and a node if L_y is horizontal at this point.

The form of the isoclines can be varied to take other effects into account. For example, if the prey have a fixed number of refuges available where they can be considered safe from predation, then their survival can be virtually guaranteed. That the existence of the refuges provides a stabilizing mechanism for the predator-prey dynamics, was argued graphically by MacArthur (1970). If the equilibrium is unstable, and L_x rises sharply on the left [see Figure 3.3.2], then there will be a stable limit cycle surrounding (x^*,y^*). But the higher the number of refuges available, the larger the 'safe zone', and hence the more practically stable the system becomes. MacArthur also noted that the horizontal part of L_y may also drive the trajectories winding into a limit cycle, under certain conditions.

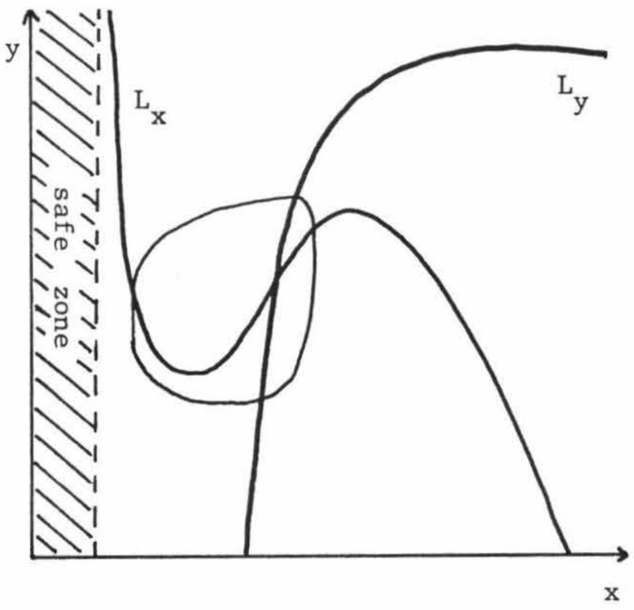


Figure 3.3.2

Graphical analysis has the additional advantage of using experimental data directly to obtain estimates for the isoclines. The technique was demonstrated by Rosenzweig (1969), using data from the experiments of Huffaker (1958), and by Maly (1969) using his own experimental data.

Working with *Paramecium* and the predatory rotifer *Asplanchna*, Maly observed the interactions over short time intervals with a variety of species compositions. The direction of change of density for each species was plotted at each composition, and the shape of the isoclines were established using statistical smoothing techniques. The prey isocline for the experiment is reproduced in Figure 3.3.3, where the arrows give the direction of change, and the circles indicate no significant change over the short time period.

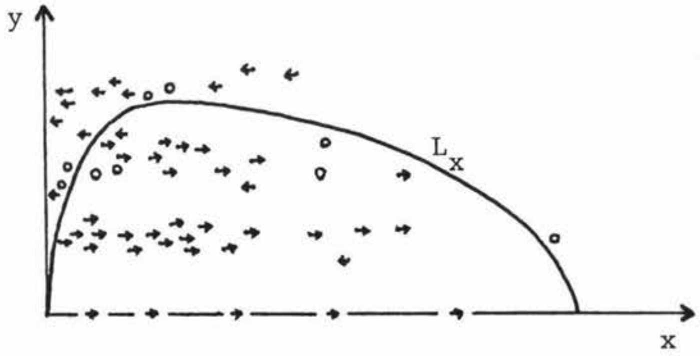


Figure 3.3.3

The original arguments of Rosenzweig and MacArthur (1963) in favour of a humped prey isocline are supported by empirical evidence such as Maly's, and Rosenzweig (1969) sought to determine just how general this property is. As the carrying capacity K is approached, the slope of L_x must become negative, so the question is really whether L_x has a positive slope at lower prey densities or not.

Many stability results in the last section required L_x to have a negative slope throughout which tallies with Rosenzweig's comment that the possibility of extinction becomes far greater if L_x does have a positive slope at low prey densities. If the predators are able to reproduce successfully at low prey densities then the curve L_y will be close to the y-axis and the chances of an unstable equilibrium point are high.

Strebel and Goel (1973) outlined some of the dangers that may arise while using this intuitively appealing technique of transforming experimental data into a deterministic model. To begin with, graphical analysis depends heavily on the fact that each specific community composition (or each point (x,y) in E) has a unique direction vector associated with it in the phase plane. However knowing only the population density of a given species, one has no indication of the age distribution or the sex ratio within that density. Clearly a drastic change in either of these factors may significantly alter the direction and magnitude of the vector in the phase space without numerically altering the actual population density. To use this method then, it will be necessary to allow the populations to achieve some sort of stable age and sex distribution, and Strebel and Goel suggest allowing one complete cycle of interaction to occur before recording the data for the purposes of estimating the isocline shapes. It is for this reason that Rosenzweig's arguments in favour of a humped prey isocline are not conclusive, as they are based on experiments which involved unstable age distributions. The short-term observations of Maly's work would not have allowed for any internal stabilization within each species.

A test was proposed to discover whether this effect remained significant in a given set of data. The direction vectors were plotted and the trajectory interpolated in a smooth fashion from these points. If the trajectory crosses itself significantly then clearly the uniqueness of the direction vectors has been violated and the earlier data needs to be ignored. The isoclines can then be estimated by connecting all the points where the trajectories are either vertical or horizontal.

Further problems arise at low densities of either species, since stochastic fluctuations may cause erratic results in these areas. We are concerned with the interaction between the prey and predator isoclines, so that the scales along the x and y axes will need to be normalized in such a way that x and y are measured on equivalent scales based on the average values of the prey and predator populations.

Strebel and Goel used these modifications to generate isoclines, using data from Huffaker (1958) and Huffaker et al. (1963), [Figures 3.3.4 and 3.3.5 respectively]. They concluded that the data from the former were insufficient for any sensible graphical analysis, whereas the results from the latter appear far more reasonable.

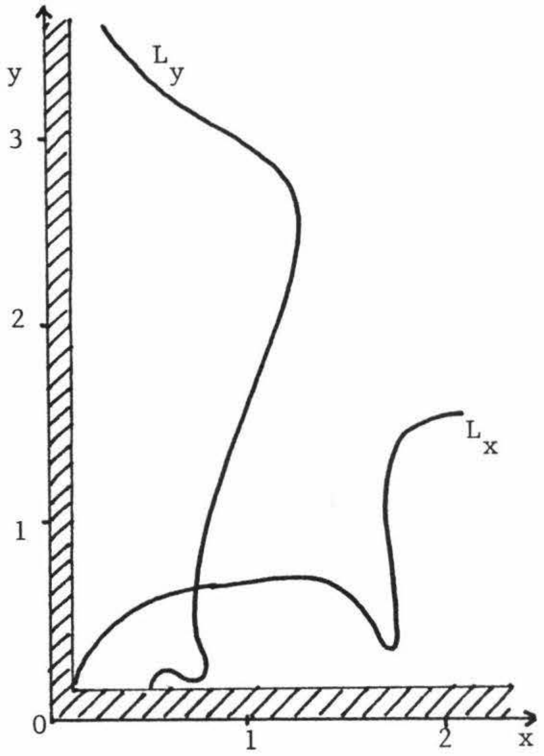


Figure 3.3.4

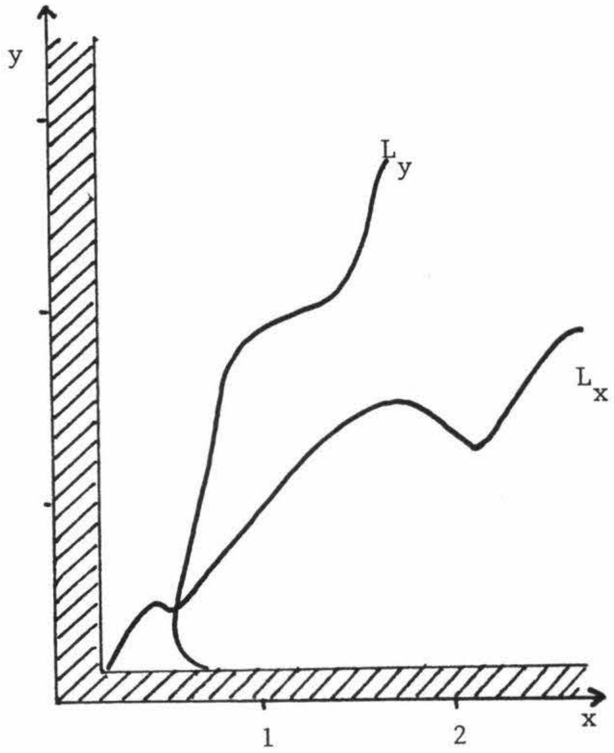


Figure 3.3.5

Once the isoclines have been obtained from experimental data, the equations of the system can be expressed (by varying appropriate parameters) to fit the curves. The equations will not be unique, but we can include the additional constraint that each term of the equation have some biological meaning. Strebel and Goel found that the following generalization of the Lotka-Volterra model will fit a variety of isocline shapes, through variation of the parameters ε and μ.

$$\begin{aligned} \frac{dx}{dt} &= \alpha\, x(1-\frac{x}{K_1}) - \beta\, x^{\varepsilon}\, y^{\mu} \\ \frac{dy}{dt} &= -\gamma y(1-\frac{y}{K_2}) + \delta\, x^{\varepsilon}\, y^{\mu} \end{aligned} \qquad \ldots\ (3.3.2)$$

Having determined the shape of the isoclines, how much can one infer about the local behaviour of the trajectories near an equilibrium? Vandermeer (1973a) made a systematic study of this question, using tangents to the isoclines at the equilibrium point (x^*,y^*), where the isoclines intersect. Let $T(L_x)$ and $T(L_y)$ be these tangents to the prey and predator isoclines respectively. Vandermeer made the following definitions. Let $\varepsilon > 0$ be arbitrarily small.

If for L_x, $\left.\frac{dx}{dt}\right|_{x=x^*+\varepsilon} < 0$; $\left.\frac{dx}{dt}\right|_{x=x^*-\varepsilon} > 0$

then we say $T(L_x)$ is stable.

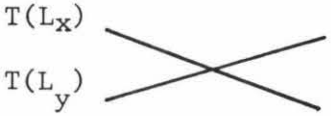
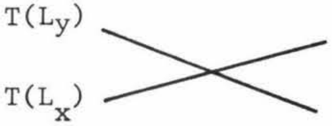
If for L_x, $\left.\frac{dx}{dt}\right|_{x=x^*+\varepsilon} > 0$; $\left.\frac{dx}{dt}\right|_{x=x^*-\varepsilon} < 0$

then we say $T(L_x)$ is unstable.

If $T(L_x)$ is not stable or unstable, we say it is metastable.

Similar definitions are made for $T(L_y)$. In general, one is unlikely to come across metastable tangents when working with isoclines in predator-prey systems. For the rest, we are now in a position to classify the structurally stable configurations around (x^*,y^*) in the table on the following page.

Specifying whether oscillations occur or not in Cases 3a,b; 4ab; 2c; 5c is difficult, since it depends on the magnitude of the angle between the two tangents. However we can say that as the acute angle between the tangents becomes larger, the trajectories become more oscillatory in nature.

Case	Tangents	(a) Both Tangents Stable	(b) Both Tangents Unstable	(c) $T(L_x)$ stable, $T(L_y)$ unstable
1.		st. focus	unst. focus	saddle pt.
2.		saddle pt.	saddle pt.	st./unst. node/focus
3.		st. node/focus	unst. node/focus	saddle pt.
4.		st. node/focus	unst. node/focus	saddle pt.
5.		saddle pt.	saddle pt.	st./unst. node/focus
6.		st. focus	unst. focus	saddle pt.

§3.4 Curvature Analysis

The analytical and graphical methods outlined in the previous two sections are complementary in the sense that the former provides the mathematical justification for the illustrative results of the latter. Traditionally, when studying models of predator-prey systems using differential equations, a judicious combination of these two approaches is used.

Using straightforward linear analysis will almost always yield an accurate picture of trajectory behaviour near an equilibrium point. However, systematic methods for determining global stability or the existence of limit cycles, seem to be as elusive as ever, and hence the analytic approach seems limited.

Assimacopoulos and Evans (1979) have established a new, systematic method for analysing predator-prey models based on the actual curvature of the trajectories. It is hoped that such difficulties as global stability, or the calculation of bifurcation points, can be made easier in many cases by using this approach. Because of its novelty, this paper is discussed in some detail.

Consider the system (3.3.1):

$$\dot{x} = \frac{dx}{dt} = P(x,y)$$
$$\dot{y} = \frac{dy}{dt} = Q(x,y)$$

We define the curvature of the trajectories as:

$$k = \frac{\dot{x}\,\ddot{y} - \dot{y}\,\ddot{x}}{(\dot{x}^2+\dot{y}^2)^{3/2}} \qquad \dots (3.4.1)$$

The properties of this function can be used to determine much of the qualitative behaviour of the system. If the trajectory through a point M(x,y) in E has zero-curvature, then M is either an inflection point of this trajectory, or an equilibrium point of the system.

At this point the authors make the first of several unfortunate errors in their paper. They claim a trajectory will be convex or concave (as t increases) at a point $M(x,y) \in E$ towards the origin, if k_0 is negative or positive respectively, where k_0 is given by:

$$k_0 = \dot{x}\,\ddot{y} - \dot{y}\,\ddot{x} \qquad \dots (3.4.2)$$

Yet a spiral winding into an equilibrium point will have constant sign curvature, but will change alternately from convex to concave, with respect to the origin. Fortunately, their definition is not essential to their argument.

Now the equation $k_0 = 0$ will define the lines of zero curvature. This will be a curve with (without) contact to the trajectories of the system where $\dot{k}_0 = 0$ ($\dot{k}_0 \neq 0$) at the points where $k_0 = 0$ is defined. Thus the real branches of zero curvature will be either loci of the trajectories inflection points (when they have no contact) or actual trajectories of the system (when they have contact).

At this point, we digress to point out another error in their work. In an example demonstrating the procedure of this approach, phase portraits of a particular predator-prey model were presented. The trajectories (dotted lines) and the line of zero curvature (solid line) were presented as in Figure 3.4.1.

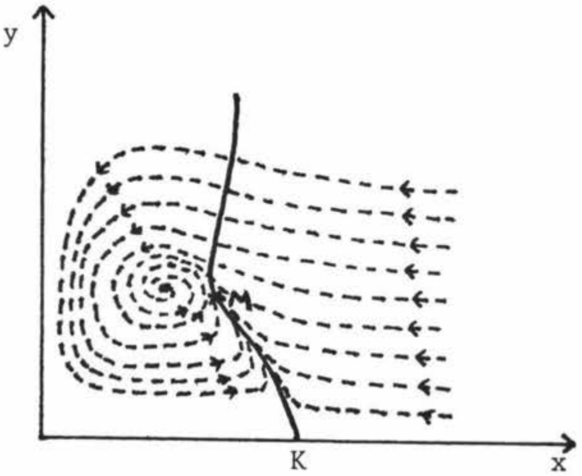


Figure 3.4.1

The authors suggested that the arc segment extending from the saddle point (K,0) to some point M further up the line of zero curvature coincided with the curve $\dot{k}_0 = 0$ and thus was a curve with contact; also coinciding with a segment of the separatrix extending from the saddle point (K,0) to M.

One suspects this is not true, based on the fact that each point on the line of zero curvature represents either an inflection point or an equilibrium point. This suggests that an arc with contact making up part of the line of zero curvature would need to be either a straight line or a locus of equilibrium points. Clearly neither is the case for this example.

It is not difficult to prove the authors' suggestion is false, and this is done in the Appendix. Their conclusion was based on numerical phase portraits of this system, which were not sufficiently precise to illustrate what is actually happening.

In fact, the line of zero curvature comes very close to the separatrix S, and only coincides with it at the saddle point (K,0), as in Figure 3.4.2.

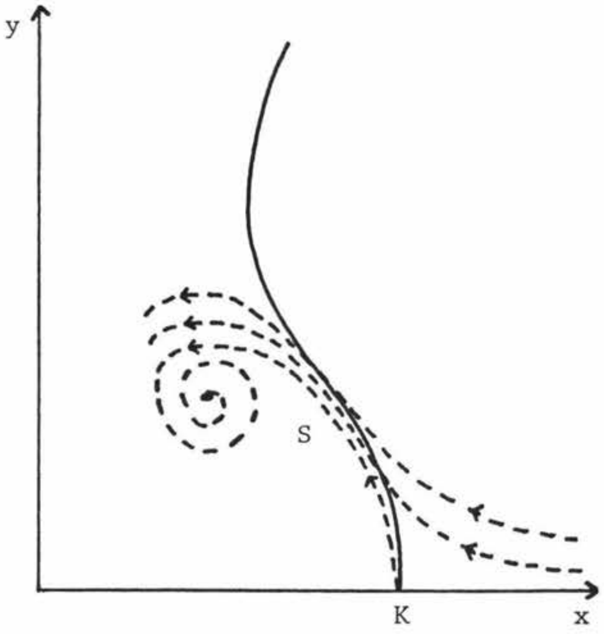


Figure 3.4.2

This will not affect the theoretical results of the paper, but it does emphasize the dangers of drawing analytical conclusions from numerical results. It seems certain then, that an arc segment of the line of zero-curvature will be an arc with contact only if it is linear [see, for example, the x and y axes in Figure 3.4.1].

The line of zero curvature will partition the phase plane into regions of fixed sign curvature, so that using this as an arc without contact, a theorem of Andronov et al. (1973a) can be employed to establish the existence of global stability.

Theorem 3.3.1 - Let M(x,y) be a point on the line of zero curvature, where it is an arc without contact. If $\dot{k}_0 > 0$ (< 0) at M, then the trajectory passing through M does so from the region where $k_0 < 0$ (> 0) to the region where $k_0 > 0$ (< 0).

Furthermore, the nature of the equilibrium points can also be established from the expressions for k_0 and $\dot{k}_0$. We present here, the following criteria:

(i) A necessary condition for an equilibrium point to be a saddle point or a node is that the line of zero curvature has real branches at this point.

(ii) The equilibrium is a saddle point if (i) holds, and if the curvature k, is not a monotonic function of x and y within any small neighbourhood of it, or within each sector formed by the real branches of k_0.

(iii) An equilibrium is a node if (i) holds and if the curvature k (or zero curvature k_0)is a monotonic function of x and y within any small neighbourhood of it, and within each sector formed by the real branches of k_0. The node will be stable (unstable) if the signs of k_0 and $\dot{k}_0$ are opposite (same) in the neighbourhood.

(iv) A sufficient condition for an equilibrium to be a focus or a centre is for the zero curvature not to have real branches in a sufficiently small neighbourhood of the equilibrium point. Thus, if the zero curvature does have real branches, they will be curves outside a small neighbourhood of the equilibrium.

(v) If (iv) holds and if $\dot{k}_0$ is sign definite, then the equilibrium will be a focus. It is unstable (stable) if the signs of k_0 and $\dot{k}_0$ are the same (opposite) in the neighbourhood.

(vi) If $\dot{k}_0$ is identically zero at every point in the region, then the equilibrium is a centre.

Clearly the criteria above may or may not be of practical use, depending on the complexity of k_0 and $\dot{k}_0$ for any particular system. As with the standard linear techniques, these criteria are not helpful when the system is structually unstable in a neighbourhood of the equilibrium point, since sufficient conditions for a centre or a multiple focus are not given. Note that the usefulness of (vi) is limited, as it is difficult to imagine any closed paths other than circles satisfying this criterion.

For example, looking at the Lotka-Volterra model we have:

$$k_0 = xy[\delta xR^2+\beta yS^2]$$

$$\dot{k}_0 = xy\,[\,\gamma R^2(3S+R) + \alpha S^2(3R+S)]$$

where $R(y) = \alpha - \beta y$ and $S(x) = \delta x - \gamma$

$k_0 = 0$ only has $x = 0$, $y = 0$ and the point $(\frac{\gamma}{\delta},\frac{\alpha}{\beta})$ as solutions. Hence criterion (iv) is satisfied for the entire region E^0. In this case, no more information can be gained using curvature analysis than the other standard methods; but this will not always be the case, as demonstrated by the model given in the authors' paper.

§3.5 The Growth Rate and Intraspecfic Competition

The growth rate of a species is defined as its death rate subtracted from its birth rate. The specific birth and death rates will depend on environmental and biological factors, and thus vary with time. However we can put an upperbound on the birth rate, expressed as the maximum fecundity (potential reproductivity), and a lower bound on the death rate, by establishing an ideal environment where there is no predation or starvation. Given these, we can define an inherent property of the species in question, the intrinsic growth rate, as the maximum possible growth rate for a population with a stable age distribution.

Tanner (1975) used simulation and analytical methods on two models incorporating intrinsic growth rates as well as predation and starvation factors, to formulate the following hypothesis:

> "Either a stable prey population possesses strong self-limitation... or the intrinsic growth rate of the prey species is less than that of the predator species."

When a species density increases to the point where the individuals start competing for food, we refer to this effect as intraspecific competition (or mutual interference). If the level of intraspecific competition is sufficiently high that the growth rate becomes zero, then the species is said to be saturated. Thus, by 'self-limitation', we mean the species population levels are controlled by saturation, rather than predation as in the case of the prey [see §3.8].

Tanner tested his hypothesis by comparing the intrinsic growth rates of both species for eight different natural predator-prey systems. Two of the species were known to be self-limited, and in both cases, the prey intrinsic growth rate was higher than that of the predator. Five cases were known to have little self-limitation, and in all of these the prey had the lower intrinsic growth rate. Finally, in the notorious snowshoe hare/lynx system referred to in Chapter 2, the intrinsic growth rates are approximately equal, and little is known about the controlling mechanism. Based on this data, Tanner has shown his hypothesis to be robust, yet little has been done to follow this up in any further detail.

Field observations indicate that a species population is typically composed of well-nourished individuals, with little sign of food deprivation. This suggests that the effects of mutual interference are not so much shared out amongst the population, but rather tend to favour some classes of individuals by weakening others. Jones (1979) discusses this in some detail.

Internal forces such as intraspecific competition generate a 'displacement pressure' within the species population. The individuals whose survival chances have been heavily reduced, become 'displaced' individuals, while those who have a high probability of survival become 'established' individuals. The age structure of the species may provide some of this displacement pressure, where the very young or very old may be classed as displaced. The chances of survival will increase with time for the very young however, so that those who survive will become established.

Alternatively, the species could be partitioned into hierarchical groups, where those high on the pecking order will be the most established. Perhaps there may be a certain number of refuges available to the prey, in which case the displaced would be those not currently occupying them. Even being successful at reproduction could be considered as the important favourable quality.

In all cases, it is clear that as the population increases, so will the number of displaced individuals. Whether or not this will always be significant in terms of both actual numbers and general stability of the system must depend on the details of the predator-prey system, to some degree.

Consider the prey growth rate, $j(x)$. The simplest approach involves constant birth and death rates, giving $j(x) = \alpha > 0$ for $x > 0$, as with the Lotka-Volterra model. This may not be too unreasonable if the prey species is primarily predation-controlled.

When linear growth does not seem adequate, a higher order term to allow for intraspecific competition is often added, giving the growth term:

$$f(x) = x\,j(x) = x(a - bx), \quad a,b > 0 \qquad \ldots (3.5.1)$$

Known as the logistic equation of growth, it can also be written in a form to include the carrying capacity K [see §3.8]. This gives the simplistic growth curve in Figure 3.5.1. If the system includes an Allee effect, then the curve intersects the x-axis to the right of the origin, as in Figure 3.5.2. Other growth expressions can be found in May(1974a).

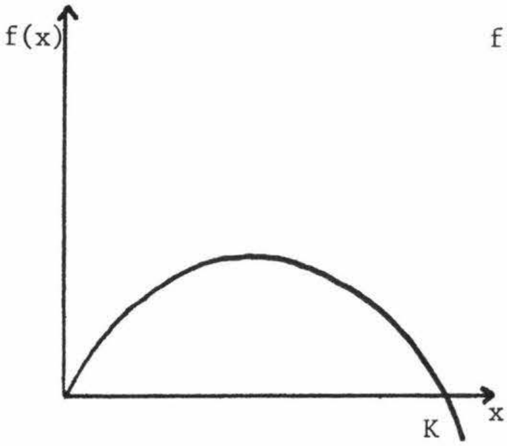


Figure 3.5.1

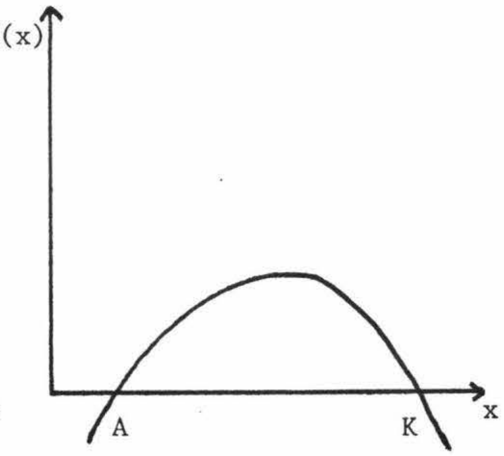


Figure 3.5.2

Now the linear term for prey growth is usually positive, corresponding with the birth rate; prey deaths are expressed by the predation response and the non-linear intraspecific competition terms. Conversely, the predator linear growth term is negative, corresponding to the death rate, and its birth rate will be associated with the predation term.

§3.6 The Predator Response to Prey Density

Prey are hunted down and killed by predators in an endless variety of ways depending on the species involved. For this reason, it would be convenient to discuss the qualitative aspects of predation without referring to specific factors. It has been observed that the actual number of prey killed by predation within unit time (termed the total response), depends largely on the prey density. On average then, we can refer to the number of prey killed per predator (known as the functional response), and get the following equation.

$$\{\text{Total response}\} = \{\text{Functional response}\} \times \{\text{Number of predators}\} \quad \ldots (3.6.1)$$

The unit time is usually short enough that there is no significant change in the number of predators. If there is a change in numbers, then we call this the numerical response.

The functional response can be determined empirically for many predator-prey systems. This involves keeping the prey density constant over short periods (thus ensuring a negligible numerical response) at various levels, and observing the predator feeding rate in each case. Holling (1959) classified the possible functional responses into types I, II and III given by Figures 3.6.1 - 3.6.3 respectively, where x and $g(x)$ represent the prey density and its corresponding functional response.

Type I

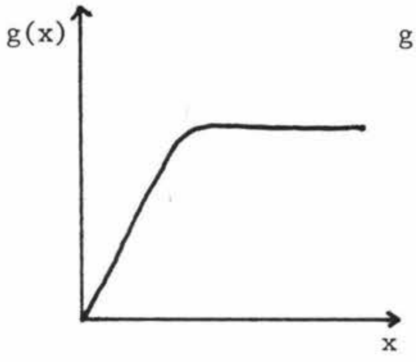


Figure 3.6.1

Type II

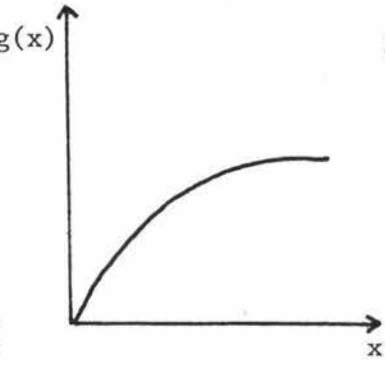


Figure 3.6.2

Type III

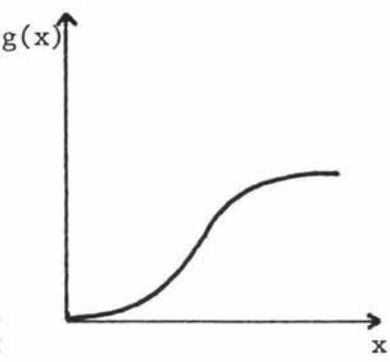


Figure 3.6.3

These response types are not really surprising, as we would expect the curves to be increasing at low prey densities, but levelling off at higher densities since a predator is obviously limited in how much it can eat in a short time interval. Since this paper appeared, experiments establishing functional responses for various predator-prey systems have been done, and the results have been collected by Murdoch and Oaten (1975) and Hassell (1978).

The type I response is generally not very common, and seems most suitable for aquatic invertebrates such as those feeding on plankton. The prey is devoured at a rate directly proportional to its density, until the predator becomes satiated.

The type II response is the most prevalent, particularly amongst invertebrates. The time required to catch, kill and eat the prey (the handling time) once it is sighted, is often long enough to significantly reduce the time available for hunting. The higher the prey density, the greater the number of sightings and hence more time spent in handling the prey. In effect, this modifies a type I response by reducing the number prey killed per predator at a particular prey density. So the vertical distance between the two curves will increase with prey density, and the type II curve will reach a lower plateau on the graph.

The type III response appears commonly with both vertebrates and invertebrates. There appears to be a wide choice of mechanisms that give rise to this sigmoid curve. For example, if the prey are patchily distributed, then the predation level may not rise very steeply at low prey densities since the patches may be hard to find. As the prey density increases however, the patch size becomes large enough that the predators aggregate in the patch area and a sharp increase in predation occurs.

If there are two species of prey available to the predator, only one particular species may be hunted until its numbers are so low that the predator 'switches' to the other species. Murdoch (1969) has found that this switching mechanism can also lead to a type III response.

Oaten and Murdoch (1975) note that the complicated nature of the relationship between the functional response and other components makes it difficult to establish whether it is stabilizing or not. This is supported by Hassell (1978), who had observed several species of predatory arthropods alter their responses from that of type III to type II when an alternative, preferred prey was used.

Readshaw (1973) classified the numerical response into two types: the reproductive response, and the aggregative response. With the former higher prey densities lead to a higher predator birth rate. The latter becomes apparent where the prey are patchily distributed. The predators rapidly increase in numbers in local areas where the prey population may be particularly dense. Because the aggregative response does not actually alter the overall predator population in the short term it is often incorporated into the functional response. An interesting application of the reproductive response appeared in a paper by Bell (1973), where a model of antibodies controlling bacteria in an infected animal's body was presented; the antibody numbers increasing dramatically when the invasion occurred [see §7.4].

Other, less important responses have also been referred to, the most significant being the developmental response [due to Murdoch (1971)]. More a long term factor, the size of individual predators may increase with prey density, to the point where they can consume more prey.

§3.7 Separation of Growth and Predation

We can now be a little more specific about the form of the equations in the model (3.2.3), by separating the growth and predation factors. For example, in his argument in favour of a humped prey isocline, Rosenzweig (1969) expressed the prey rate equation as

{rate of change of prey density} = {rate of prey growth, given no predators}
- {rate of predation}

or $$\frac{dx}{dt} = f(x) - g_1(x,y) \qquad \ldots (3.7.1)$$

Now, let g(x) be the functional response, so that the total response can be written as

$$g_1(x,y) = y \cdot g(x)$$

where $$\frac{dg}{dx} > 0, \quad \forall x \geq 0.$$

The advantages of equation (3.7.1) are clear, since both the growth f(x), and predation g(x), can be discussed graphically as well as analytically.

A similar division can be made with the predator rate equation, resulting in the system:

$$\begin{aligned}\frac{dx}{dt} &= f(x) - y\,g(x)\\ \frac{dy}{dt} &= -h(y) + \delta\,y\,g(x)\end{aligned} \qquad \dots\ (3.7.2)$$

where δ is the conversion rate of prey into predator. Note the marked similarity between this system and that of the Lotka-Volterra model.

To observe the effects of predation in a predator-prey system, the simplest case of (3.7.2) was considered by St. Amant (1970), where $f(x)$ and $h(y)$ were presented in linear form, giving the system

$$\begin{aligned}\frac{dx}{dt} &= \alpha x - y\,g(x)\\ \frac{dy}{dt} &= -\gamma y + \delta\,y\,g(x)\end{aligned} \qquad \dots\ (3.7.3)$$

The Lotka-Volterra model is included in this system, with $g(x) = x$, which is almost a type I response except that there is no levelling off at higher prey densities.

A more rigorous study of this system, along with general graphical considerations, was given by Oaten and Murdoch (1975). Let (x^*,y^*) be an equilibrium point in E^0, and define

$$r = \alpha\,[1 - \frac{\delta}{\gamma}\,x^*\,g'(x^*)]$$

Then using standard linearization techniques, we have

(i) oscillations near (x^*,y^*) occur if and only if $r^2 < 4\alpha\,\delta\,x^*g'(x^*)$ and furthermore

$$\text{if} \quad \begin{cases} r < 0 \text{ then } (x^*,y^*) \text{ is a stable focus}\\ r > 0 \text{ then } (x^*,y^*) \text{ is an unstable focus}\end{cases}$$

(ii) no oscillations near (x^*,y^*) occur when $r^2 \geq 4\alpha\,\delta\,x^*g'(x^*)$

$$\text{and if} \quad \begin{cases} r < 0 \text{ then } (x^*,y^*) \text{ is a stable node}\\ r > 0 \text{ then } (x^*,y^*) \text{ is an unstable node}\end{cases}$$

(iii) if $r = 0$, then (x^*,y^*) is a centre.

Note that at (x^*,y^*), $g(x^*) = \frac{\gamma}{\delta}$ so that

$$r < 0 \;\Leftrightarrow\; g'(x^*) > \frac{g(x^*)}{x^*} \;\Leftrightarrow\; (x^*,y^*) \text{ is stable} \qquad \dots\ (3.7.4)$$

From this condition we should be able to use the graph of the functional response to determine whether it is stabilizing or not near the equilibrium. Clearly (3.7.4) will hold for all values of x such that the tangent to the graph of g(x) at x will have a positive x-intercept. Figure 3.7.1 demonstrates that a type II response will not satisfy this criterion. On the other hand, for a type III response, Figure 3.7.2 indicates an interval $(0,x_m)$ such that all values of x contained in this interval satisfy (3.7.4).

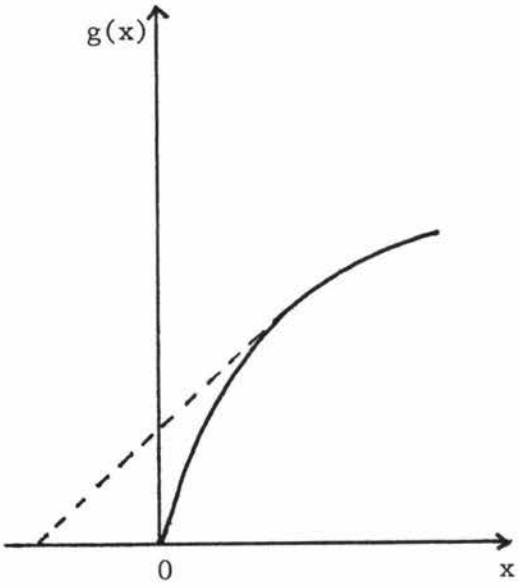


Figure 3.7.1

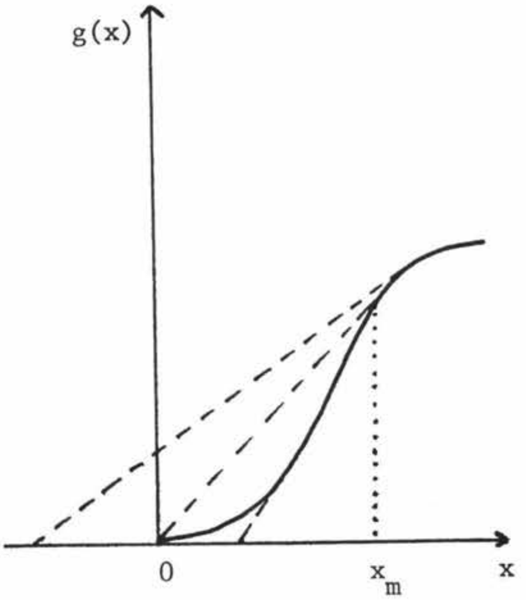


Figure 3.7.2

Predation is generally regarded to be 'stabilizing' at a particular prey density, if a greater than proportionate increase (decrease) in the rate of predation occurs for a given increase (decrease) in the prey density. If this is the case, then the magnitude of x_m can be taken as a measure of the tendency of the functional response to stabilize. Murdoch and Oaten (1975) used similar arguments to show that $g(x_m)$ and $\frac{x_m}{g(x_m)}$ can also be used as measures, and in fact the larger any of these values are, the more enhanced the stability will be.

Using these measures allows us to directly employ empirically determined curves, avoiding the need of prior knowledge of the parameters themselves. However these measures are only applicable for a type III response, since $x_m = 0$ for type I or type II responses.

Freedman (1976) considered another variation of system (3.7.2):

$$\frac{dx}{dt} = x\,j(x) - y\,g(x)$$
$$\frac{dy}{dt} = -\gamma y + \delta y\,g(x) \qquad \ldots (3.7.5)$$

where

$$\left.\begin{array}{ll} j(0) > 0; & j'(x) \leq 0 \quad \text{for} \quad x \geq 0 \\ \exists K > 0; & j(K) = 0 \\ g(0) = 0; & g'(x) > 0 \quad \text{for} \quad x \geq 0 \end{array}\right\} \qquad \ldots (3.7.6)$$

There are two trivial equilibria (0,0) and (K,0) representing saddle points, and the non-trivial equilibrium $P^* = (x^*,y^*)$ in E^0 defined by

$$g(x^*) = \frac{\gamma}{\delta}, \qquad \text{for } x^* < K$$
$$y^* = \frac{x^* j(x^*)}{g(x^*)}$$

Now system (3.7.2) is a special case of (3.7.5), and stability conditions can be found in a similar fashion.

$$\text{Set} \quad H(x^*) = x^* j'(x^*) + j(x^*) - \frac{x^* j(x^*) g'(x^*)}{g(x^*)} \qquad \ldots (3.7.7)$$

Thus $H(x^*) > 0 \Rightarrow P^*$ is unstable

$H(x^*) < 0 \Rightarrow P^*$ is stable

so that the value of $|H(x^*)|$ can be taken as a measure of the stability of the equilibrium.

By setting $x = K$, and noting $j(K) = 0$ we have

$$\left.\frac{dy}{dx}\right|_{x=K} = \frac{-\gamma + \delta\ g(K)}{-g(K)} < 0 \qquad \text{since} \quad g(K) > g(x^*) = \frac{\gamma}{\delta}$$

$$\text{and} \quad \left.\frac{dx}{dt}\right|_{x=K} = -y\ g(K) < 0$$

So the trajectories will pass through the line $x = K$ in the phase plane from right to left, with constant negative slope. Furthermore, any solution starting at the right of this line $(x > K)$ must cross this line in finite time. From here it is not difficult to see that the system must be globally stable in E^0, and Freedman proves the following.

Theorem 3.7.1 - If conditions (3.7.6) hold, then at least one of the following must be true for system (3.7.5):

(i) (x^*,y^*) is a stable equilibrium

(ii) there is a limit cycle around (x^*,y^*) which is stable from the outside, and which lies within the strip $\{(x,y)\colon 0 < x < K,\ y > 0\}$.

Armstrong (1976) developed a graphical method for studying yet another variation of system (3.7.2)

$$\left.\begin{aligned} \frac{dx}{dt} &= f(x) - y\,g(x) \\ \frac{dy}{dt} &= y\,k(x) \end{aligned}\right\} \qquad \ldots (3.7.8)$$

The method combined ideas from Rosenzweig (1969), where the prey growth rate $f(x)$ and the functional response $g(x)$ were compared, and from Oaten and Murdoch (1975), using intercepts of tangents to graphs of these functions. This system emphasizes the case where predators can be limited only by prey numbers.

The equilibrium (x^*,y^*), if it exists, satisfies

$$\begin{aligned} k(x^*) &= 0 \\ y^* &= f(x^*)/g(x^*) \end{aligned}$$

Armstrong made further restrictions: i) (x^*,y^*) is the unique equilibrium in E^0.

ii) $f(x)$, $g(x)$ are one-to-one.

iii) $k(0) < 0$; $\lim_{x\to\infty} k(x) > 0$.

iv) $g(x) > 0$.

As a result, local stability conditions can be established:

$$f'(x^*) - y^*g'(x^*) \begin{cases} < 0 \Rightarrow (x^*,y^*) \text{ is locally stable} \\ > 0 \Rightarrow (x^*,y^*) \text{ is locally unstable} \end{cases}$$

Graphically, these conditions can be interpret ed by using plots of $f(x)$ and $g(x)$ against x. Let a and b be the x-intercepts of the tangents to the graphs of $f(x)$ and $g(x)$ respectively, at $x = x^*$. Now it is only necessary to compare values of a, b and x^*:

$$\frac{1}{x^*-a} < \frac{1}{x^*-b} \Rightarrow (x^*,y^*) \text{ is locally stable}$$

$$\frac{1}{x^*-a} > \frac{1}{x^*-b} \Rightarrow (x^*,y^*) \text{ is locally unstable}$$

Note when $a = b$ this method cannot be used.

For example, in Figure 3.73 $f(x)$ has a standard logistic growth curve and $g(x)$ is of a Type II response. Here $b < a$ and hence the equilibrium will be locally unstable.

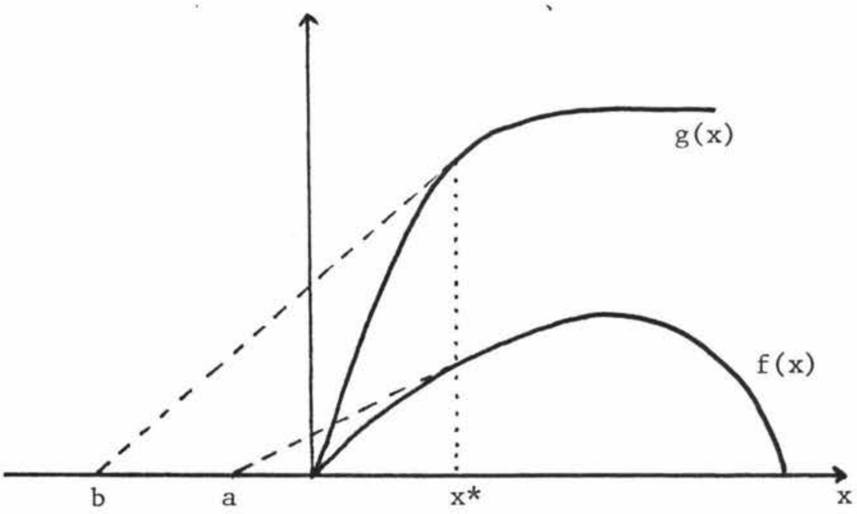


Figure 3.7.3

Armstrong feels this method should complement the graphical isocline method outlined in §3.3. If we wish to study the effects of varying the position of the predator isocline L_y while L_x is kept fixed, then the standard isocline method outlined in §3.3 seems best, especially as the shape of L_y is not too complex in general. When varying the prey growth rates or functional response however, Armstrong's graphical method may be more suitable.

Hsu (1978) presented a modification of Freedman's study on system (3.7.5) by including a prey density-dependent death rate for the predators:

$$\begin{aligned} \frac{dx}{dt} &= x\, j(x) - y\, g(x) \\ \frac{dy}{dt} &= y\, [-q(x) + \delta g(x)] \end{aligned} \qquad \ldots (3.7.9)$$

Alternatively, this system can be viewed as a special case of (3.7.8) where $k(x)$ has been divided into two components: the functional response

$g(x)$ with conversion rate δ, and the death rate $q(x)$. The following conditions were given:

(i) $j(0) > 0$; $\exists K > 0$: $j(K) = 0$; $(x-K)j(K) < 0$ for all $x \neq K$

(ii) $g(0) = 0$; $g'(x) > 0$ for $x \geq 0$

(iii) $q(0) > 0$; $q'(x) \leq 0$ for $x \geq 0$; $\lim_{x \to \infty} q(x) > 0$

Totally analogous to Freedman's arguments, Hsu demonstrates that the system will be globally stable in E^0. Furthermore, two theorems about the global stability of (x^*,y^*) are given.

Theorem 3.7.2 If $\left[\frac{xj(x)}{g(x)} - y^*\right]\left[x - x^*\right] \leq 0$ then (x^*,y^*) is globally stable in E^0.

In other words, (x^*,y^*) is globally stable when the prey isocline is above $y = y^*$ for $0 \leq x < x^*$ and below it for $x^* < x \leq K$. This is illustrated in Figure 3.7.4.

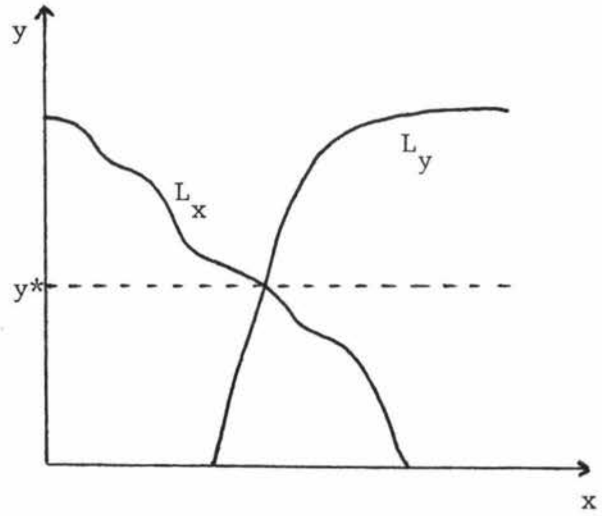


Figure 3.7.4

Theorem 3.7.3 If $\frac{d^2}{dx^2}\left[\frac{x\,j(x)}{g(x)}\right] < 0$ for $0 \leq x \leq K$, and (x^*,y^*) is stable, then (x^*,y^*) will be globally stable.

In other words, (x^*,y^*) will be globally stable if it is locally stable, and the prey isocline is humped.

Freedman (1979) modified his own system (3.7.5) to allow for density-dependence in the predator specific death rate, and a slightly more general intraspecific competition term:

$$\frac{dx}{dt} = x\,j(x) - y^m g(x)$$

$$\frac{dy}{dt} = -\gamma y + \delta y^m g(x) - y\,q(y) \qquad \ldots\ (3.7.10)$$

where m is the mutual interference constant, $0 < m \leq 1$.

δ is the biomass conversion constant.

$\gamma + q(y)$ is the predator death rate.

The conditions include those of (3.7.6.) and the following:

$$q(0) = 0, \quad \frac{dq}{dy} \geq 0 \quad \text{for } y \geq 0 \qquad \ldots\ (3.7.11)$$

Now on L_x, when $x = 0$, $y = \left[\frac{\alpha}{g'(0)}\right]^{\frac{1}{m}} > 0$, where $\alpha = j(0)$, and when $x = K$, $y = 0$.

Hence the prey isocline L_x intersects the x and y axes in E.

On L_y, when $y = 0$, $\begin{cases} x = 0 & \text{if } 0 < m < 1 \\ x = x_0 > 0 & \text{if } m = 1, \text{ with } g(x_0) = \frac{\gamma}{\delta}. \end{cases}$

Typical curves for L_x and L_y are given in Figure 3.7.5.

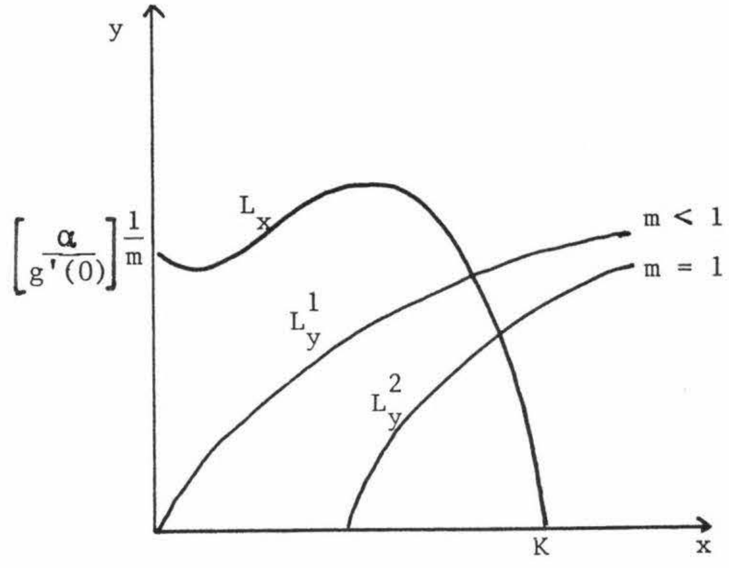


Figure 3.7.5

Clearly in all cases, an equilibrium point will exist in E^0 where $m < 1$. When $m = 1$, the additional constraint $x_0 < K$, is necessary to ensure the equilibrium point exists.

Again (0,0) and (K,0) are saddle points (standard linearization techniques establish this). Let the equilibrium in E^0 be $P^* = (x^*,y^*)$, and define:

$$\left.\begin{aligned} H &= x^* j'(x^*) + j(x^*) - y^{*m} g'(x^*) \\ R &= \delta(m-1)y^{*m-1} g(x^*) - y^* q'(y^*) \\ L &= HR + m\delta y^{*2m-1} g(x^*)\ g'(x^*) \end{aligned}\right\} \quad \ldots (3.7.12)$$

and so we have the following results.

(1) $H < 0 \Rightarrow P^*$ is asymptotically stable

(2) $H > 0,\ L > 0,\ H + R < 0 \Rightarrow P^*$ is asymptotically stable

(3) $H > 0,\ L > 0,\ H + R > 0 \Rightarrow P^*$ is unstable

(4) $H > 0,\ L < 0 \Rightarrow P^*$ is a saddle point

The unusual nature of case (4) arises when there is more than one equilibrium in E^0 [see Figure 3.7.6, for example].

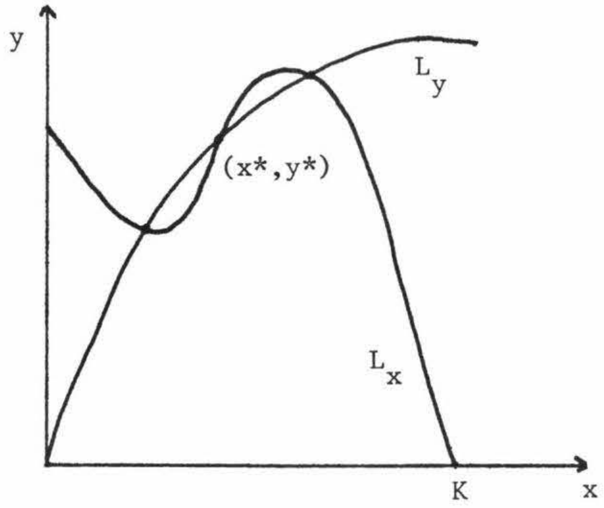


Figure 3.7.6

The critical point between stability and instability occurs when H is positive and sufficiently large that $H + R = 0$, where $R \leq 0$. Graphically, H becomes positive when P^* lies on a point of increase of L_x.

Based on this point, Freedman claims (without substantiation) that increasing either intraspecific competition or the predator death rate will stabilize the system. Certainly increasing the death rate will increase $q'(y^*)$, so that R will decrease, and the argument seems reasonable.

However, increasing intraspecific competition by decreasing m towards zero, presents a less clear situation since H will increase as R decreases. Therefore, consider

$$\frac{\partial}{\partial m}[H+R] = \delta\, g(x^*)\,[y^{*m-1}+(m-1)y^{*m-1}\log y^*] - y^{*m}g'(x^*)\log y^*$$

$$= y^{*m-1}\,[\delta\, g(x^*)(1+(m-1)\log y^*) - g'(x^*)y^*\log y^*]$$

Clearly for a sufficiently large value of y^*, m does not need to be very small to ensure that the partial derivative is negative. In this case, as m gets smaller, H + R will increase, so that the equilibrium point P^* is likely to be destabilized - in complete disagreement with Freedman's claim!

§3.8 Saturation and the Effects of Enrichment

Realistically we cannot assume that the prey food supply will be unlimited. Some authors have incorporated this fact into their models by admitting a third variable. There are a number of such models in the literature [see May (1974a)], particularly where carnivore-herbivore-plant systems are concerned. However if the prey food supply does not fluctuate significantly over time, it may be possible to relegate this to the set of environmental parameters.

The prey density is said to be saturated when it has grown to the pointwhere a shortage of food prevents any further growth. It is this saturation level, given there are no predators present, that we have defined as the carrying-capacity, K.

Both predation and saturation will have adverse effects on the prey growth rate; but does either factor, or a combination of both, actually control the prey population growth in some way? Undoubtedly any of these choices could find support through some existing predator-prey system, but we should heed the ecologist's warning that all is not always what it seems!

Originally it was argued that if there is an abundance of prey food which has not been completely consumed by prey, and if the prey density increases when predators are reduced in numbers, then the prey must be limited by predation. Ricklefs (1973) observes that this logic is not entirely valid, since an abundance of food does not necessarily imply that the prey are capable of utilizing it all. Furthermore, other limiting factors such as lack of space, or even behavioural changes may be present.

There is experimental evidence indicating that predation can be a major limiting factor, such as the work of Huffaker and Kennett (1956). Whether this is the case for most natural predator-prey systems, however, is not clear. For example, the plant-herbivore system of the Prickly-Pear/Cactus Moth in Australia is predation controlled, but this is far from evident unless the recent history behind this relationship is known. When introduced into Australia, the Prickly-Pear Cactus quickly became a large-scale pest throughout the country. A natural predator, the Cactus Moth, was finally introduced and within a few years the cactus was reduced to existence only at low density levels in isolated patches that the moth had failed to reach. As a result, the present situation gives absolutely no indication of the extent the Prickly-Pear is controlled by the moth.

The simplest prey-growth model incorporating K is the logistic growth function [see § 3.5]:

$$f(x) = \alpha x(1 - \frac{x}{K})$$

Other forms of f(x) incorporating the carrying-capacity are also used [see, for example, many of the models given in the next chapter].

The parameter K can take on special significance in resource management, where an overall increase in prey or predator numbers may be desirable. A predator-prey system is said to be enriched if the supply of prey food is increased; this is equivalent to increasing the value of K. Intuitively it seems evident that this is one way of increasing the average density of the prey (and hence the average density of the predator as well). However, in his controversial paper, Rosenzweig (1971) suggested that undesirable effects may also result from enrichment.

Noting the experimental results of Huffaker et al. (1963), where an observably stable predator-prey system was enriched with resulting extinction, Rosenzweig found that this destabilizing effect of enrichment may not be entirely unexpected. His arguments were based on graph theoretical techniques, where L_y is either vertical or near-vertical with positive slope for low values of y, and L_x is given the standard humped shape.

Using the theory developed in §3.3, it can be shown that the equilibrium point (x^*,y^*) will be a stable (unstable) focus if L_y intersects L_x to the right (left) of the hump peak (x_c,y_c). Changing the values of K will not affect L_y since the predator equation is independent of K.

But enriching the system by increasing K will very likely increase the values of x_c and y_c sufficiently that the stable equilibrium may become unstable, surrounded by a stable limit cycle [see Figures 3.8.1, 3.8.2 for the 'before and after' pictures].

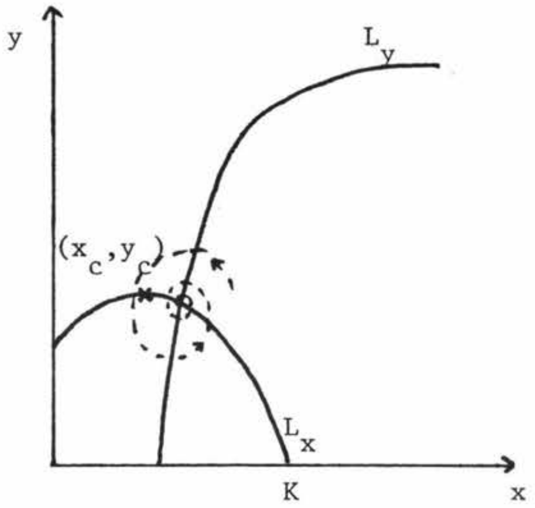


Figure 3.8.1

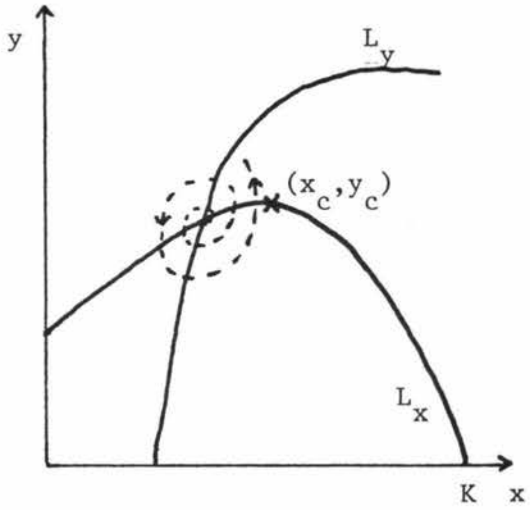


Figure 3.8.2

Rosenzweig suggests that as K increases further, the amplitude of the limit cycle may also increase, and thus raising the probability of extinction through random fluctuations. Yet there would be little danger of extinction if (x^*,y^*) was stable with a reasonable domain of attraction. Thus while yields for each species may increase, so might the dangers of a system collapse.

To find support for this 'paradox of enrichment' Rosenzweig considered six specific predator-prey models, and found in all cases that $\frac{\partial x_c}{\partial K} > 0$ (that is, the humped curve L_x moves to the right with enrichment).

McAllister et al. (1972) challenged this concept on experimental grounds, based on their work with nutrient enrichment in a lake to increase phytoplankton density, with the ultimate hope of boosting the salmon population. Their major criticisms included:

(i) Their enrichment program was successful, without altering the trophic stability or diversity in any way.

(ii) There are many mechanisms by which any instability caused by enrichment could be negated (for example, in this case salmon migrated before over-crowding could occur).

In reply, Rosenzweig stresses only the possibility of destabilization, so that ecosystem managers could be duly cautious. Criticism (i) seems perfectly reasonable if K is increased from K_1 to K_2 as in Figure 3.8.3, where $K_1 < K_2 < K_c$ (where K_c is the critical value of K_1 such that (x_c,y_c) coincides with (x^*,y^*)). Here we see an increase in the equilibrium values, but the equilibrium remains stable. Furthermore, if the predator satiation level is low, it is even possible that a value for K_c does not exist since the equilibrium point always remains to the right of (x_c,y_c), as in Figure 3.8.4.

Mechanisms preventing prey extinction, such as the existence of refuges, change the qualitative picture to begin with, as a limit cycle is very likely to be present for all values of K, and hence Rosenzweig's arguments would not be applicable anyway, as the equilibrium will always be unstable.

Gilpin (1972) presented an argument for the desirability of limit cycles in predator-prey models, independently of May (1974a) apparently. He noted that any model of the form (3.3.1) can only allow for extinction by having a trajectory intersect through one of the axes at an equilibrium point. This may be true deterministically, but it takes no account of stochastic fluctuations. For this reason, Gilpin's criticism of numerical extinction of a species in computer simulations, due to truncated density values, seems unreasonable.

Armstrong (1976) found that any model of the form (3.7.8) with logistic prey growth, exhibited this phenomenon when sufficiently enriched, regardless of the functional response type $g(x)$.

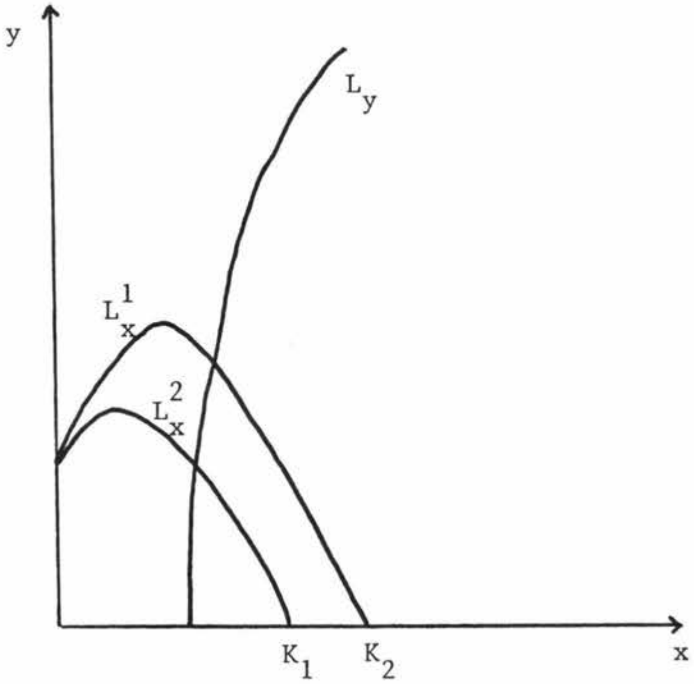


Figure 3.8.3

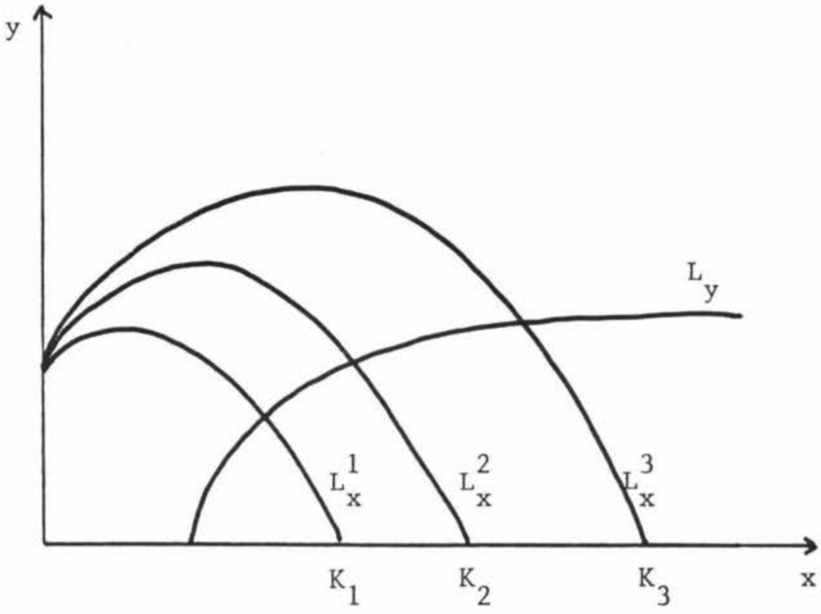


Figure 3.8.4

Freedman (1976) modified his general model (3.7.5) to ensure the prey growth function explicitly acknowledged the carrying capacity, by writing it as xj(x,K), where the following conditions were given, (with logistic growth in mind):

$$\left.\begin{array}{l} j(0,K) = \alpha > 0; \;\; j(K,K) = 0; \;\; \frac{\partial j}{\partial x}(x,K) \le 0; \\ \frac{\partial j}{\partial K}(x,K) \ge 0; \;\; \frac{\partial^2 j}{\partial x \partial K}(x,K) \ge 0 \;\; \text{for } x \ge 0 \end{array}\right\} \qquad \ldots (3.8.1)$$

Using these conditions in addition to those of (3.7.6), Freedman demonstrated that (x_c, y_c) will move to the right, and could possibly destabilize the equilibrium as Rosenzweig suggested. Hence assuming a value for K_c exists, it was found that as K passes through this value under enrichment, a limit cycle is thrown off from the equilibrium, and will in fact increase in amplitude as K increases further. This is a Hopf bifurcation process, and Freedman presented a criterion for the existence of such small-amplitude periodic solutions:

Given K_c exists, if

$$\frac{d}{dx}\left[\frac{x\,\frac{\partial^2 j}{\partial x^2}(x,K_c) + 2\frac{\partial j}{\partial x}(x,K_c) - y^*(K_c)\cdot\frac{d^2 g}{dx^2}(x)}{\delta\; g(x)\cdot\frac{dg}{dx}(x)}\right]_{x=x^*} < 0$$

then a stable limit cycle surrounding (x^*,y^*) exists for $K > K_c$.

Assuming logistic growth, Lin and Kahn (1976) also discussed the existence of limit cycles in the related system:

$$\begin{aligned} \frac{dx}{dt} &= \alpha\; x(1-\frac{x}{K}) - \beta y\; g(x) \\ \frac{dy}{dt} &= -\gamma y + \delta y\; g(x) \end{aligned} \qquad \ldots (3.8.2)$$

The bifurcation value was given by

$$K_c = x^* + \frac{\gamma x^*}{(\gamma - \delta x^* g'(x^*))} \qquad \ldots (3.8.3)$$

The authors used the averaging techniques of Krylov-Bogoliubov-Mitropolsky to establish a criterion for the existence of periodic solutions. However novel this approach may be, it was never made clear how the criterion could be readily applied. In addition, it only succeeds when system (3.8.2) displays weak nonlinearity and K is very close to K_c.

Kazarinoff and Van Den Driesche (1978) also discussed system (3.8.2), but from a more direct line of approach using Hopf bifurcation theory, following on from Freedman's work. They also presented criteria for the existence of periodic solutions, but their restrictions were far more relaxed than those of Lin and Kahn's above.

Furthermore, an estimate for the period of the resultant limit cycle for $K > K_c$ was included.

Let $\lambda = \pm iw$ be the eigenvalues of the system at $K = K_c$, where $w^2 = \beta\gamma\, y^*\, g'(x^*)$. Assume $g(x) \in C^3$.

$$\text{so } \left.\frac{\partial\lambda}{\partial K}\right|_{K=K_c} = x^* \left(-1 + \frac{\delta x^* g'(x^*)}{2\gamma}\right) - i\left(\frac{\delta {x^*}^2}{2w}\, g'(x^*)\right)$$

$$\text{Define:}\quad c_1 = \frac{1}{8}\left[\left(\frac{\alpha}{K_c} + \frac{\beta y^*}{2}\, g''(x^*)\right)\left(\frac{\delta}{\gamma}\, g'(x^*) + \frac{g''(x^*)}{g'(x^*)}\right) - \frac{\beta y^*}{2}\, g'''(x^*)\right]$$

$$\text{and}\qquad c_2 = \frac{1}{8w}\left[-\frac{4}{3}\left(\frac{\alpha}{K_c} + \frac{\beta y^*}{2}\, g''(x^*)\right)^2 - \frac{5\delta\alpha}{3K_c}\, g'(x^*) - \frac{5}{6}\,\beta\gamma y^*\, \frac{[g''(x^*)]^2}{g'(x^*)}\right.$$

$$- \frac{\delta^2\beta y^*}{3\gamma}\,[g'(x^*)]^3 - \frac{\beta\delta}{2}\, y^* g'(x^*) g''(x^*) - \frac{\delta^2}{3}\,[g'(x^*)]^2$$

$$\left. + \frac{\beta\gamma}{2}\, y^* g'''(x^*)\right]$$

$$e_2 = \frac{-c_1}{\mathrm{Re}\left[\left.\frac{\partial\lambda}{\partial K}\right|_{K=K_c}\right]}$$

Then the parameter $\tau_2 = \dfrac{-1}{w}\left(c_2 + \dfrac{\alpha}{K_c}\,\mathrm{Im}\left[\left.\dfrac{\partial\lambda}{\partial K}\right|_{K=K_c}\right]\right)$ gives the nonlinear correction term of the period of the limit cycle up to $O(\varepsilon^2)$ where ε is a sufficiently small parameter indexing the limit cycles through the relation

$$K = K_c\left(\frac{1}{1 + (\varepsilon^2 K_c e_2)/\alpha}\right)$$

giving the period $P(\varepsilon) = \dfrac{2\pi}{w}(1 + \varepsilon^2\tau_2) + O(\varepsilon^4)$

Note that there is no direct way of estimating how large ε may become with the results of the paper still remaining valid, so that given a particular value of ε, numerical computation will be necessary.

Brauer (1976) sought a more general approach towards enrichment by concentrating on the system (3.1.3), modified to stress the existence of the carrying-capacity:

$$\begin{aligned} \frac{dx}{dt} &= x\,F(x,y,K) \\ \frac{dy}{dt} &= y\,G(x,y) \end{aligned} \qquad \ldots (3.8.4)$$

Brauer provided plenty of analytic support to Rosenzweig's geometrical arguments on the effects of enrichment. Consider the following hypotheses on (3.8.4).

(i) For all $x, y, K > 0$, F, G, F_x, and their first-order partial derivatives are all continuous.

(ii) $F_K(x,y,K) > 0$; $F_y(x,y,K) < 0$. Thus L_x moves upward as K increases, and $F > 0$ (< 0) below (above) the curve L_x.

(iii) For each fixed K, the curve $F(x,y,K) = 0$ has a unique maximum $(x_c(K), y_c(K))$ where $x < K$, with $F_x(x_c,y_c,K) = 0$. Furthermore $F_{xx}(x,y,K) < 0$ to ensure (x_c,y_c) is a local maximum, and $F_K F_{xy} - F_{xK} F_y \geq 0$ guarantees (x_c,y_c) moving up and to the right as K increases.

(iv) $G_x(x,y) > 0$; $G_y(x,y) \leq 0$. Thus the predator isocline L_y will have a positive derivative (possibly infinite) everywhere.

(v) $F_x G_y - F_y G_x > 0$ to ensure that the two isoclines L_x and L_y are never tangent, and to allow for the possibility of a stable equilibrium in E^0 for some values of K.

(vi) K is sufficiently large for an equilibrium point $(x^*(K), y^*(K))$ to exist in E^0.

<u>Theorem 3.8.1</u> If conditions (i) to (vi) hold, then $y^*(K)$ is increasing and $x^*(K)$ is non-decreasing.

Clearly $x^*(K)$ will be strictly increasing if L_y has a positive, non-vertical slope throughout; that is, if there is mutual interference amongst the predators.

Theorem 3.8.2 If conditions (i) to (vi) hold then the equilibrium (x^*,y^*) is

$$\begin{cases} \text{asymptotically stable if } x^*F_x(x^*,y^*,K) + y^*G_y(x^*,y^*) < 0 \\ \text{unstable if } x^*F_x(x^*,y^*,K) + y^*G_y(x^*,y^*) > 0 \end{cases}$$

As we have seen in this section, as K increases, a bifurcation may take place causing a stable equilibrium to become unstable, surrounded by a stable limit cycle. Brauer relates this to another analytic form of Kolmogorov's Theorem.

Theorem 3.8.3 If conditions (i)-(vi) hold, and if $x F_x + y F_y < 0$ and $x G_x + y G_y > 0$, then (3.8.4) has either a stable equilibrium point or a stable limit cycle in E^0.

It seems reasonable to enquire further into the nature of $G(x,y)$, and what effect its properties may have on this phenomenon. Up to now, most analytic expressions for $G(x,y)$ have been independent of y. Thus consider the condition:

(vii) $G_y(x,y) \equiv 0$. That is, L_y is the vertical line $x = J$, say.

Theorem 3.8.4 Let $F(x,y,K)$ satisfy the conditions (i)-(iii) and $G(x,y)$ satisfy (vii), with $G(x,y) < 0$ (> 0) if $x < J$ $(> J)$. Therefore, if

$$\lim_{k\to\infty} F_x(J,y^*(K),K) \begin{cases} > 0, & \text{then } (x^*,y^*) \text{ is unstable for sufficiently large K.} \\ < 0, & \text{then } (x^*,y^*) \text{ is stable for all K.} \end{cases}$$

Thus to obtain the critical value K_c, if it exists, we need only solve the equations $F(J,y,K) = 0$ and $F_x(J,y,K) = 0$, eliminating y in the process, giving K_c as a function of $J = x^*$. Even if K_c cannot be expressed explicitly, the limit in theorem 3.8.4 could still prove useful.

Brauer notes that things are less clear when mutual interference amongst predators is included (when condition (vii) does not hold).

Theorem 3.8.5 - If conditions (i)-(vi) hold and if

$$\lim_{k\to\infty} \{x^*(K)\ F_x(x^*(K),y^*(K),K) + y^*(K)\ G_y(x^*(K),y^*(K))\} > 0$$

then the equilibrium becomes unstable for sufficiently large K.

In this case, finding the value of K_c may be cumbersome, and Brauer suggests that finding conditions under which Theorem 3.8.5 is satisfied may be the next best thing. This can be done by calculating

$\lim_{K\to\infty} x^*(K)$, $\lim_{K\to\infty} y^*(K)$ and substituting into the expression: $x\, F_x(x,y,K) + y\, G_y(x,y)$. Note that if the conditions to Theorem 3.8.5 are not satisfied, this does not mean that $(x^*(x),y^*(K))$ is stable for all K.

In conclusion, Brauer found that even though stability is more likely to be preserved under enrichment when mutual interference is present (as was argued graphically by Rosenweig), the results become far more dependent on the details of the model. Thus the degree of destabilization rests heavily, in this case, on the parameter values of the system.

Finally, we note that in their paper on curvature analysis of predator-prey systems, Assimacopoulos and Evans (1979) demonstrated the usefulness of their method by studying the effects of enrichment on a particular model previously studied numerically by Gilpin (1972) and analytically by Brauer (1976). In all cases the same value of K_c was determined for a given set of parameters, but the method of Assimacopoulos and Evans easily required the least effort.

In general, given a system of type (3.8.4), the value of K_c, if it exists, can be calculated in the following way. The stability of the equilibrium depends on the relative signs of k_0 and $\acute{k}_0$ [see §3.4] in a small neighbourhood (x^*,y^*). So that if k_0 is of a fixed sign in this region, one needs only to look at the sign of $\acute{k}_0$ along L_y in this neighbourhood. If sufficient conditions on x^* and y^* can be obtained to ensure $\acute{k}_0$ is of the right sign, then substituting these values into the prey isocline equation will yield the value for K_c.

§3.9 The Effects of Harvesting and Stocking

From a resource management point of view, increasing the yield of the desired species is important. In the last section, enrichment appeared to be a successful method of achieving this, provided it was not carried to extremes. There are two questions which should now be considered. Could the yields be increased more directly by stocking the predator-prey system with either species? What effects will the harvesting of the desired species have on the system?

Volterra briefly considered the problem using the Lotka-Volterra model. But it wasn't until Brauer and Sanchez (1975) incorporated constant harvesting rates in one-species growth models and two-species competition models, that anything like a general approach was considered. Not surprisingly, this harvesting rate ultimately destabilized the systems when set sufficiently high. More importantly, they found a critical value of this parameter which represented the transition from stability to instability. As we shall see, such bifurcations are common in predator-prey systems with constant harvesting rates.

To instigate initially simple investigations, stocking and harvesting rates have been kept constant, though some models with proportional harvesting have also been considered. It is questionable whether any resource management system would favour higher order stocking and harvesting rates, when so little is understood of the complexities of such policies.

Freedman (1976) modified his system (3.7.5) to allow for constant stocking of prey:

$$\frac{dx}{dt} = x\,j(x) - y\,g(x) + A$$
$$\frac{dy}{dt} = -\gamma y + \delta\, y\, g(x) \qquad \ldots\ (3.9.1)$$

with real constant $A > 0$. We assume conditions given by (3.7.6) still hold so that the equilibrium point $P^* = (x^*,y^*)$ in E^0 is given by

$$g(x^*) = \frac{\gamma}{\delta}; \quad x^* < K$$
$$y^* = \frac{x^* j(x^*) + A}{g(x^*)}$$

and analogous to system (3.5.8), the stability of (x^*,y^*) is determined by the function:

$$H(x^*) = x^*\,j'(x^*) + j(x^*) - \frac{[x^* j(x^*) g'(x^*) + A\, g'(x^*)]}{g(x^*)}$$

$$\text{with} \quad \begin{cases} H(x^*) > 0 \Rightarrow (x^*,y^*) \text{ is unstable} \\ H(x^*) < 0 \Rightarrow (x^*,y^*) \text{ is stable} \end{cases}$$

Clearly an increase in A will decrease $H(x^*)$. Thus increasing the stocking rate tends to be stabilizing, avoiding the dangers that appear with enrichment.

Brauer, Soudack and Jarosch (1976) modified the more general system (3.2.3) to include a constant predator harvesting rate:

$$\frac{dx}{dt} = x\,F(x,y)$$
$$\frac{dy}{dt} = y\,G(x,y) - B \qquad \ldots\ (3.9.2)$$

with real constant $B \geq 0$.

Conditions previously discussed by Brauer (1976) [see §3.7] are given:

$$\frac{\partial F}{\partial y} < 0; \quad \frac{\partial G}{\partial x} > 0; \quad \frac{\partial G}{\partial y} \leq 0 \quad \text{in } E^0 \qquad \ldots (3.9.3)$$

and

$$\frac{\partial F}{\partial x}\frac{\partial G}{\partial y} - \frac{\partial F}{\partial y}\frac{\partial G}{\partial x} > 0 \quad \text{in } E^0 \qquad \ldots (3.9.4)$$

The authors assume that there is a unique equilibrium point (x^*,y^*) in E^0 when $B = 0$. Then the implicit function theorem ensures that this equilibrium will depend continuously on the parameter B. Isoclines are given by $F(x,y) = 0$ (L_x) and $y\,g(x,y) = B$ (L_y), where L_y has the curves $y = 0$ and $g(x,y) = 0$ as asymptotes.

We note that the equilibrium point $P^* = (x^*(B),y^*(B))$ continues to exist in E^0 as B increases, until $B = B_c$, where B_c (assuming it exists) is defined by: $|\Delta(x^*(B_c),y^*(B_c))| = 0$. This equilibrium disappears altogether for $B > B_c$, following from the fact that condition (3.9.4) is equivalent to $|\Delta(x^*(B),y^*(B))| > 0$, and the predators becomes extinct in finite time.

The authors demonstrated that Kolmogorov's Theorem can still be applied, but only in a restricted neighbourhood of P*, bounded by the y-axis and a horizontal line $y = \varepsilon$, where ε is sufficiently large that the intersection of L_x and $y = \varepsilon$ is to the left of the intersection of L_y and $y = \varepsilon$. For $B < B_c$, such an ε can always be found.

The character of P* will depend on the details of F and G, but it can be shown that it will never be a saddle point. One other critical case occurs at $B = B_s$ defined by

$$x^*(B_s)\,F_x(x^*(B_s),y^*(B_s)) + y^*(B_s)\,G_y(x^*(B_s),y^*(B_s)) + G(x^*(B_s),y^*(B_s)) = 0.$$

This bifurcation value only becomes important when $0 \leq B_s \leq B_c$. Whether P* is a centre or a multiple focus when $B = B_s$ will depend on the higher order terms of F and G (the authors claim P* will be a focus, but their reasoning is erroneous).

Without a clearer picture of the nature of the phase plane, it is difficult to conclude anything with certainty. A tentative suggestion that increasing B will decrease the stability in E^0 to the point where extinction is guaranteed in finite time at $B = B_c$ was made, but it is difficult to be sure whether this would always be the case. Three models were simulated, and a more interesting phenomenon was discovered. In some cases, increases in predator harvesting tended to stabilize any instabilities resulting from an increase in enrichment. The implications of this are clear, and such phenomena bear further investigation.

A clearer exposition of trajectory behaviour in system (3.9.1) was given by Brauer and Soudack (1979 a) , expanding on their earlier work. This included dispensing with condition (3.9.4), since Brauer (1979) demonstrated that solutions will never become unbounded in E^0, for all $t \geq 0$, using only those conditions given by (3.9.3) [see §3.2].

Complex cases such as there being more than one limit cycle in E^0, or more than one equilibrium point in E^0 when $B = 0$ are not considered by the authors, in order to gain a better understanding of what qualitative changes are involved. Figures 3.9.1-3.9.4 demonstrate how the zero-isoclines evolve with increasing B. The equilibrium point (0,0) in Figure 3.8.1 disappears from E for $B > 0$, while the saddle point at (K,0) remains a saddle point $[=(\tilde{x}(B),\tilde{y}(B))$, say] for $B > 0$, and travels up the fixed curve L_x. At $B = B_c$, the curves L_x and L_y are only touching [Figure 3.9.3]; and thereis no equilibrium for $B > B_c$ [Figure 3.9.4].

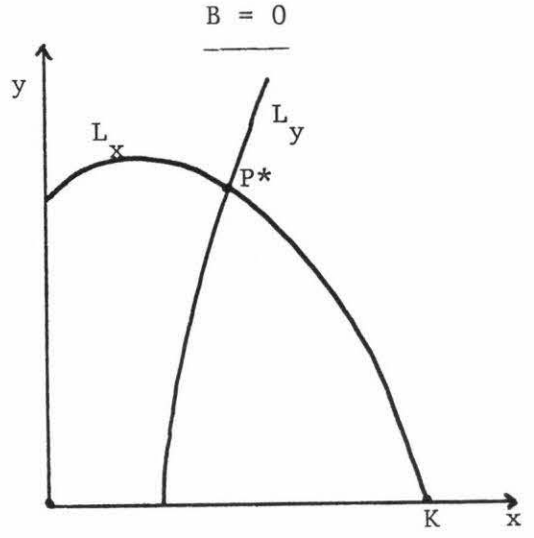


Figure 3.9.1

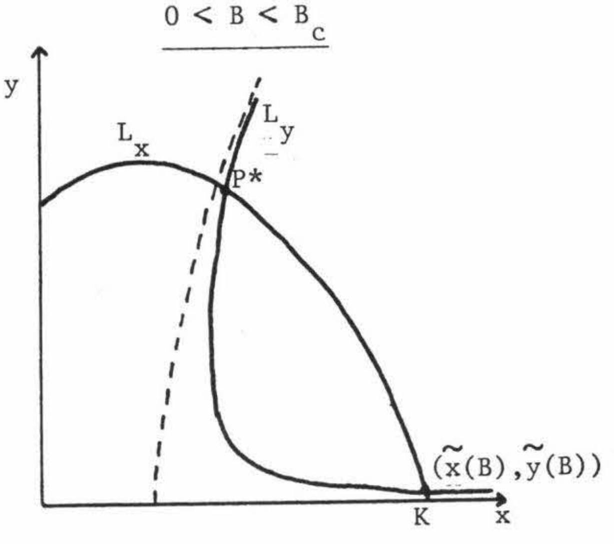


Figure 3.9.2

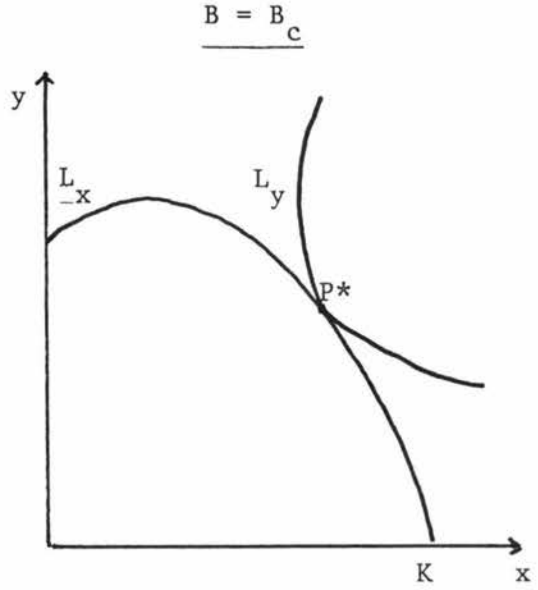


Figure 3.9.3

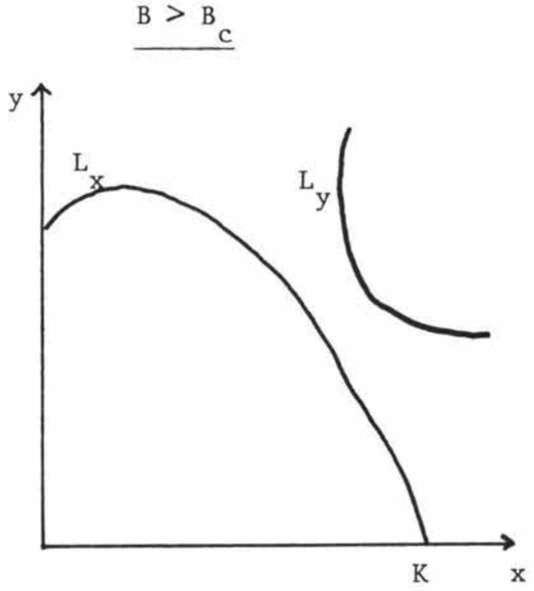


Figure 3.9.4

B_c can be calculated by maximizing $B(x) = \Phi(x)\ G(x,\Phi(x))$ over $0 \leq x \leq K$, where $y = \Phi(x)$ is given by the curve $F(x,y) = 0$.

The authors concentrate on estimating the region of asymptotic stability (for either a stable equilibrium point or a stable limit cycle). To this end it is necessary to determine the behaviour of the separatrices to the saddle point $(\tilde{x}(B),\tilde{y}(B))$. They were able to classify the phase portraits into three classes. Figures 3.9.5 and 3.9.6 deal with Case 1, where the region of asymptotic stability has shaded edges. Case 2 in Figure 3.9.7 has a separatrix loop (a structurally unstable pathway), and Case 3 in Figures 3.9.8 and 3.9.9 involves virtually certain predator extinction.

Case 1a

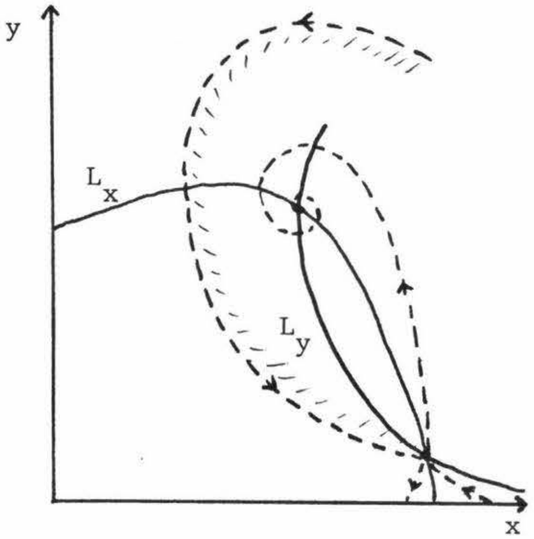


Figure 3.9.5

Case 1b

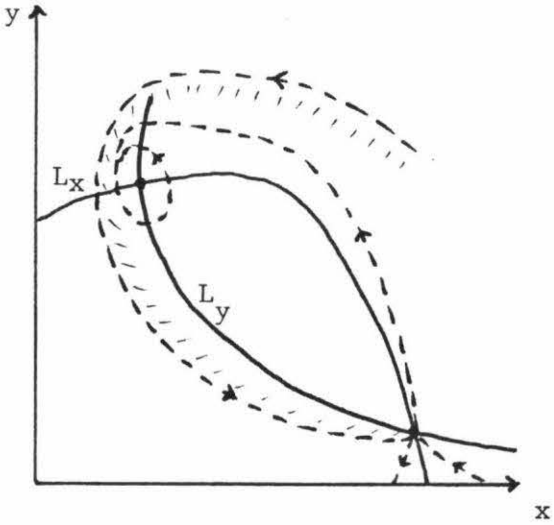


Figure 3.9.6

Case 2

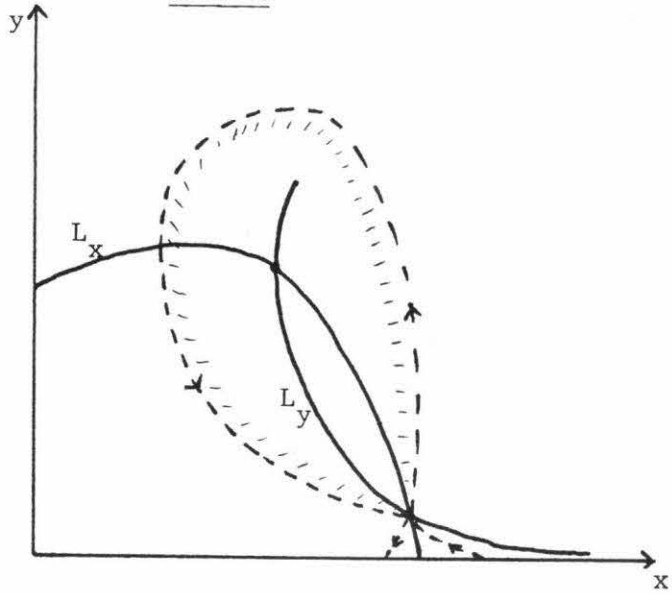


Figure 3.9.7

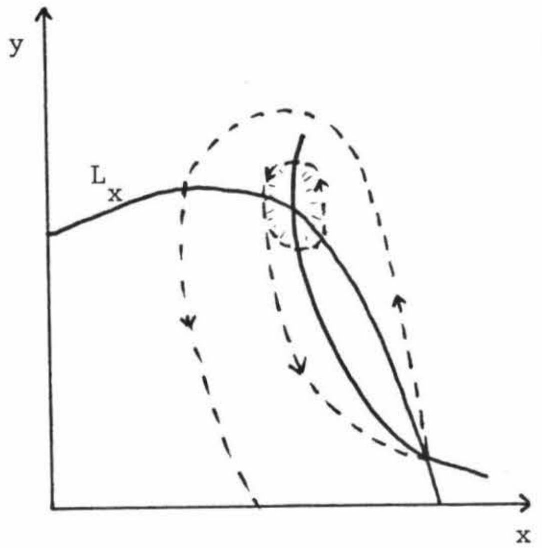


Figure 3.9.8

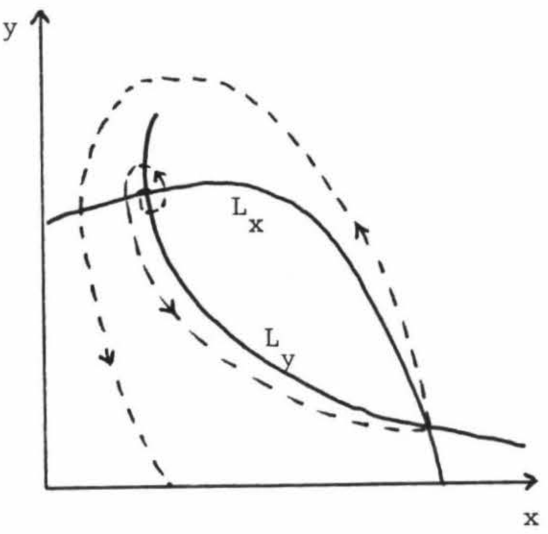


Figure 3.9.9

All other possible cases guarantee predator extinction in finite time. When B is close to 0, the phase portraits will be as in cases 1a or 1b. When B is slightly less than B_c, cases 3a or 3b will be present.

Based on these observations and simulations of particular models, the authors speculate about what can be expected as B increases from zero. Let B_r represent the unique value of B giving rise to case 2. Then we have:

$$\begin{cases} 0 < B < B_r & \text{Cases 1a, 1b can occur.} \\ B = B_r & \text{Case 2 will occur.} \\ B_r < B < B_c & \text{Cases 3a, 3b can occur.} \end{cases}$$

Clearly then, in a resource management system, harvesting rates must be kept below values of B_r, rather than just B_c as predicted originally. To estimate the value of B_r, it is necessary to use numerical methods on a particular model to pin down the transition phase between case 1 and case 3. Note that limit cycle behaviour will depend on the local stability of P*, which in turn will depend on the locality of P* with respect to the hump of L_x.

The next situation to be considered is constant harvesting of the prey. Brauer and Soudack (1979 b) approached this in much the same manner, though a few differences did appear in the results. Consider the following system:

$$\begin{aligned} \frac{dx}{dt} &= x\,F(x,y) - A \\ \frac{dy}{dt} &= y\,G(x,y) \end{aligned} \qquad \ldots\ (3.9.5)$$

where the real constant $A \geq 0$. We assume that conditions given by (3.9.3) hold, and that $P^* = (x^*(A), y^*(A))$ is a unique equilibrium point in E^0.

Let $y = \Phi(x)$ be defined by the curve $F(x,y) = 0$. Then there exists a constant α such that $\Phi(x) \geq 0$ for all $x: 0 \leq \alpha \leq x \leq K$. When $\alpha > 0$, the Allee effect is present in the system. Most models tend to set $\alpha = 0$, so that there exists a constant $L \geq 0$ such that $F(0,L) = 0$. Finally we note that there exists constant $J > 0$ such that $G(J,0) = 0$, with $J < K$.

Now as A increases, L_x moves down, so that there exists a critical value A_c such that $(x^*(A_c), y^*(A_c)) = (J,0)$, as demonstrated in Figures 3.9.10-3.9.12 for $\alpha = 0$, and Figures 3.9.13-3.9.15 for $\alpha > 0$.

Note that the isocline $x\,F(x,y) = A$ defines the modified function $y = \Phi_A(s)$ which will be positive for all x such that $0 \leq \alpha(A) \leq x \leq \beta(A) \leq K$, where $\alpha(0) = \alpha$ and $\beta(0) = K$.

Now for $0 \leq A \leq A_c$, $G(\alpha(A),0) < 0$ and $G(\beta(A),0) > 0$, so that there will be two equilibria on the x-axis: $P_\alpha = (\alpha(A),0)$ and $P_\beta = (\beta(A),0)$, which will both remain saddle points for $0 \leq A \leq A_c$.

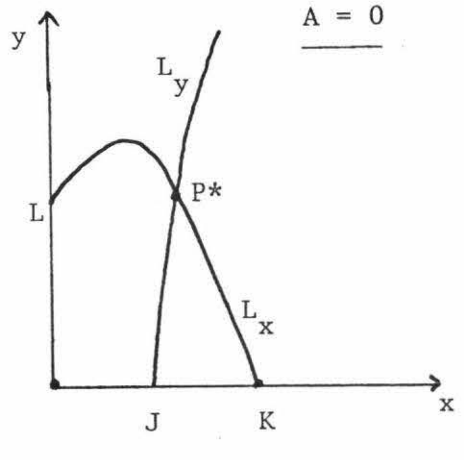


Figure 3.9.10

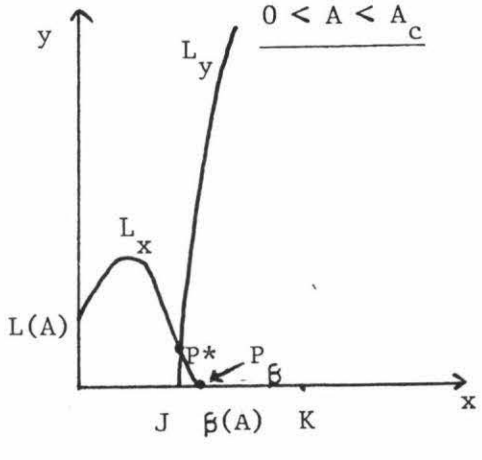


Figure 3.9.11

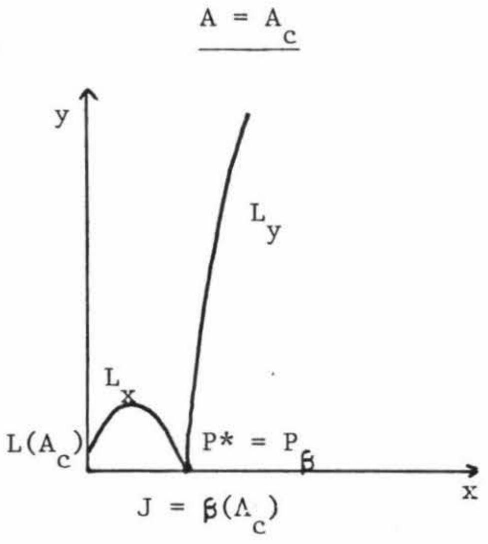

$A = A_c$

Figure 3.9.12

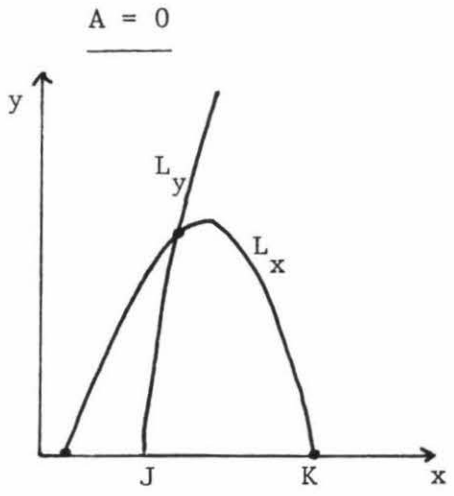

$A = 0$

Figure 3.9.13

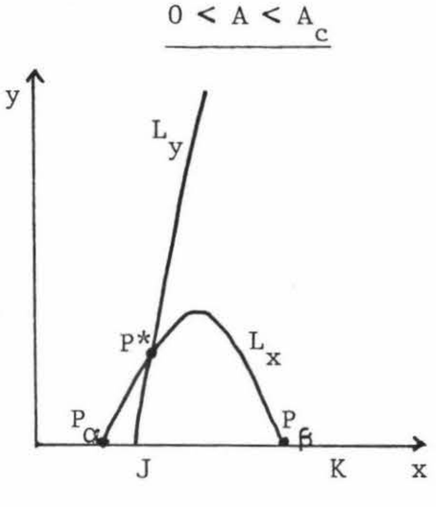

$0 < A < A_c$

Figure 3.9.14

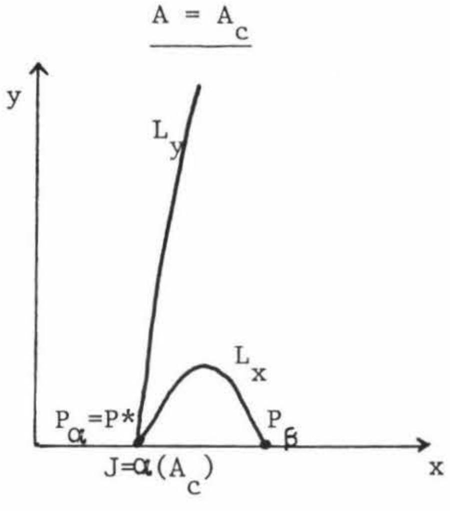

$A = A_c$

Figure 3.9.15

Once again we use the separatrices of the two saddle points P_α and P_β to determine the qualitative nature of the system in E^0, and estimate the regions of asymptotic stability. We shall only consider the cases where $\alpha > 0$, as the qualitative behaviour in E^0 does not change significantly for $\alpha = 0$ since P_α lies on the negative x-axis with its separatrix still reaching into E^0.

Once again there are three cases to consider, with case 2 representing the transition from case 1 to case 3 as A increases. Figures 3.9.16-3.9.20 give the following cases:

Case 1a

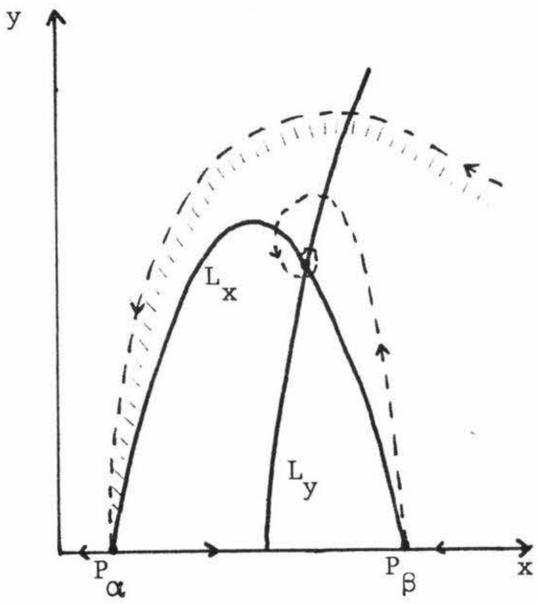


Figure 3.9.16

Case 1b

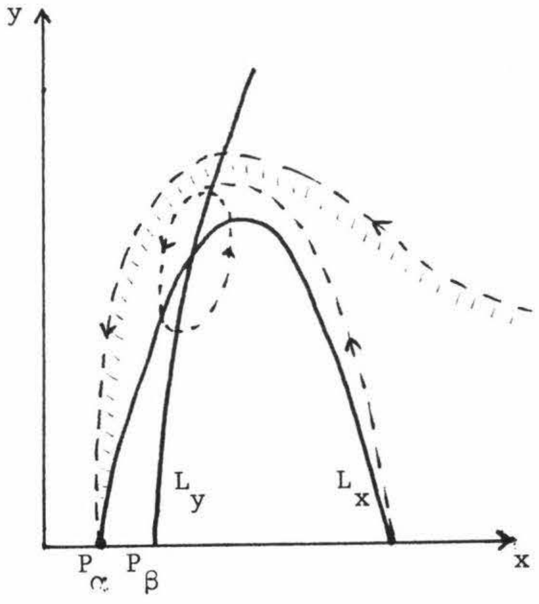


Figure 3.9.17

Case 2

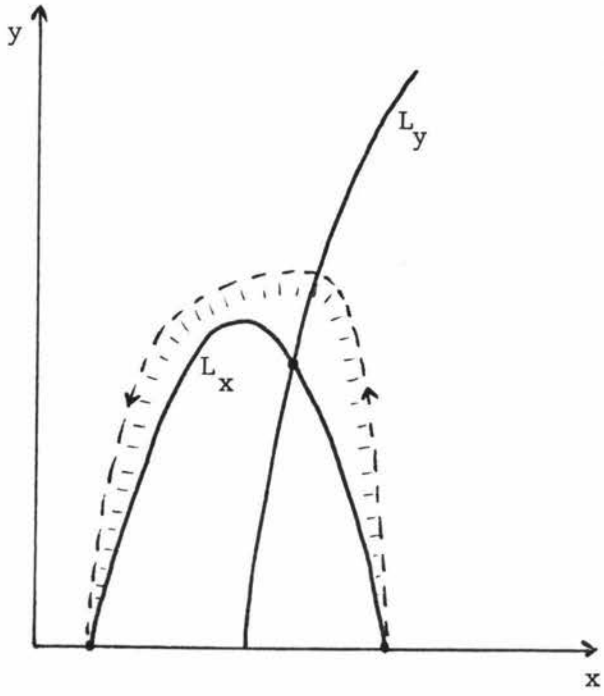


Figure 3.9.18

Case 3a

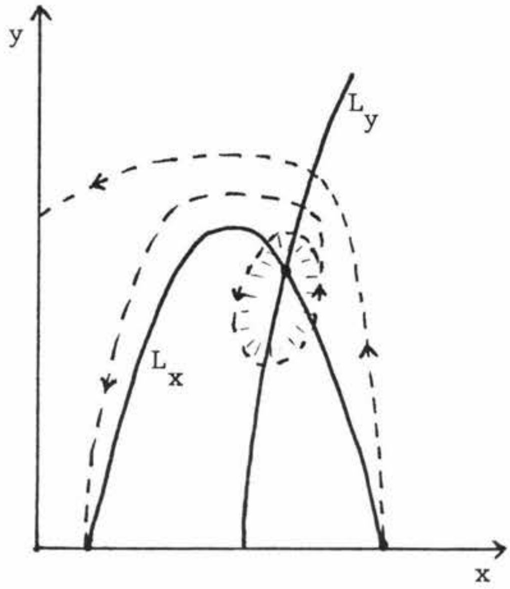


Figure 3.9.19

Case 3b

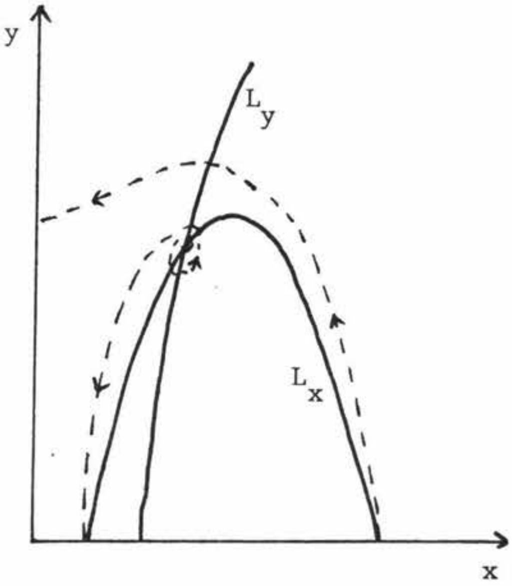


Figure 3.9.20

The authors determined that the following four transitions were possible as A increases from zero to A_c:

I. 1a

II. 1b $\rightarrow$ 2 $\rightarrow$ 3b

III. 1a $\rightarrow$ 1b $\rightarrow$ 2 $\rightarrow$ 3b

IV. 1a $\rightarrow$ 2 $\rightarrow$ 3a $\rightarrow$ 3b

As expected, the region of asymptotic stability decreases and may even disappear before A reaches A_c. Let A_r represent the value of A resulting in case 2.

Now there may also be a critical value of A representing the transition from stability to instability of the equilibrium point P* (when coinciding with the peak of the hump of L_x). If it exists, let this value of A be A_s. The following can be stated:

For II, III, IV; there exists an $A_r < A_c$ such that case 2 appears.

For III, IV; there exists an $A_s < A_c$ such that P* becomes unstable, with $A_s < A_r$ for III, and $A_s > A_r$ for IV.

Brauer and Soudack (1979 c) also considered the more complex situation where both species were being stocked at constant rates. Consider the following system:

$$\begin{aligned} \frac{dx}{dt} &= x\,F(x,y) + A \quad (A \geq 0) \\ \frac{dy}{dt} &= y\,G(x,y) + B \quad (B \geq 0) \end{aligned} \qquad \ldots (3.9.6)$$

with the usual conditions given by (3.9.3). Again, situations involving more than one limit cycle or extra equilibria other than $P^* = (x^*,y^*)$ in E^0 for $A = B = 0$ shall be ignored. The parameters α, J, K, L are as defined previously, and we have three possibilities: (i) $\alpha > 0$ (Allee effect); (ii) $\alpha = 0$, $L = \infty$ (certain number of prey guaranteed survival); (iii) $\alpha = 0$, $L < \infty$ (standard for most models).

To determine the behaviour of system (3.9.6), it will be necessary to split it up into parts. To begin with, we consider prey stocking only:

<u>Set B = 0</u>. As A increases, L_x moves up. There will be two equilibria in E for $\alpha = 0$, as in Figure 3.9.21 and either four, three or two equilibria in E for $\alpha > 0$, decreasing in number as A increases, as in Figure 3.9.22.

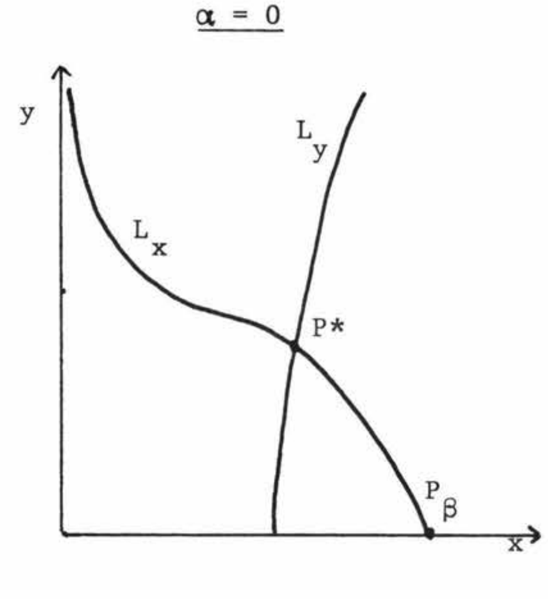


Figure 3.9.21

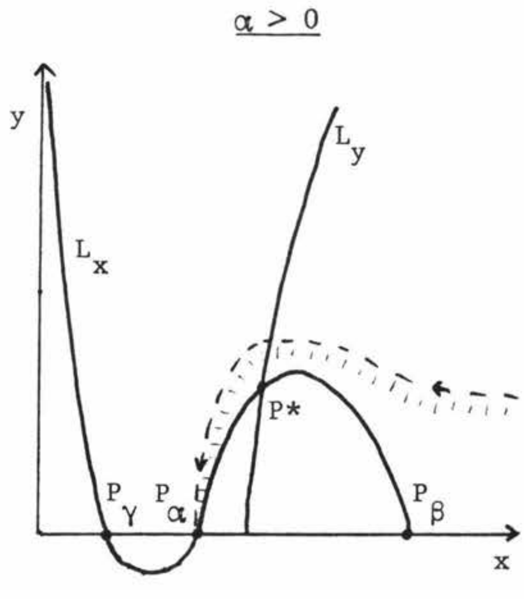


Figure 3.9.22

For $\alpha = 0$, if P* is unstable, then increasing A stabilizes it. For $\alpha > 0$, P_γ will be a stable node, P_α and P_β will be saddle points. In this case, increasing A is still stabilizing, but only for the domain of attraction of P*, the boundary of which is given by the separatrix of P_α given in Figure 3.9.22 [the broken line]. The rest of E^0 is the domain of attraction of P_α, resulting in predator extinction. As A increases further, P_γ and P_α coalesce at $A = A_c$, say, so that for $A > A_c$, the qualitative picture is similar to that of the case for $\alpha = 0$.

Set A = 0. As B increases, L_y moves up and further to the left of the original L_y when B = 0. The number of equilibria present depends on which of the three cases for α and L hold, as demonstrated in Figures 3.9.23-3.9.25.

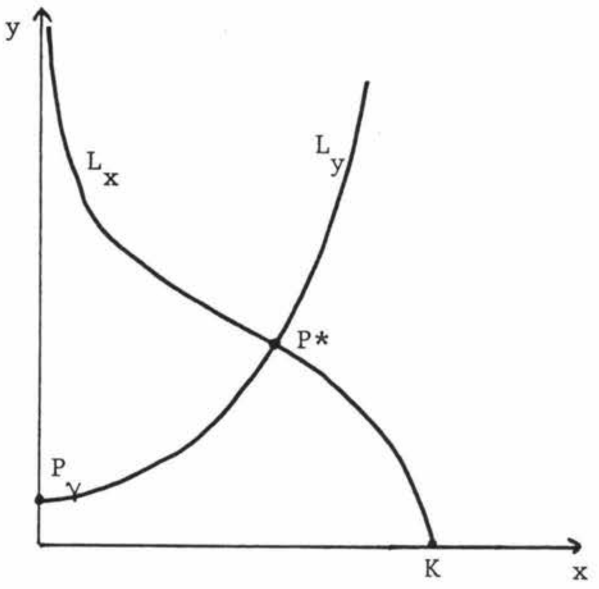

$\alpha = 0,\ L = \infty$

Figure 3.9.23

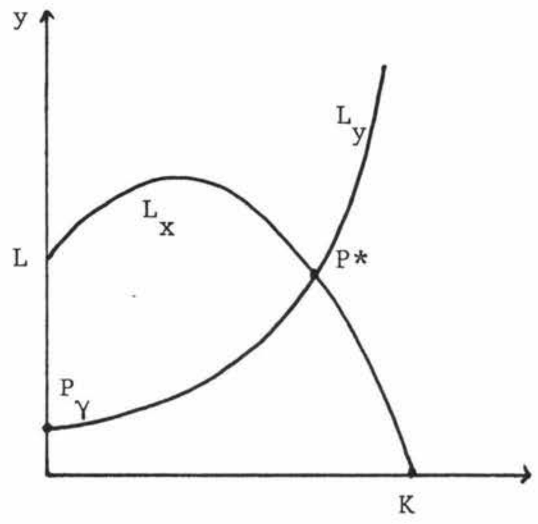

$\alpha = 0,\ L < \infty$

Figure 3.9.24

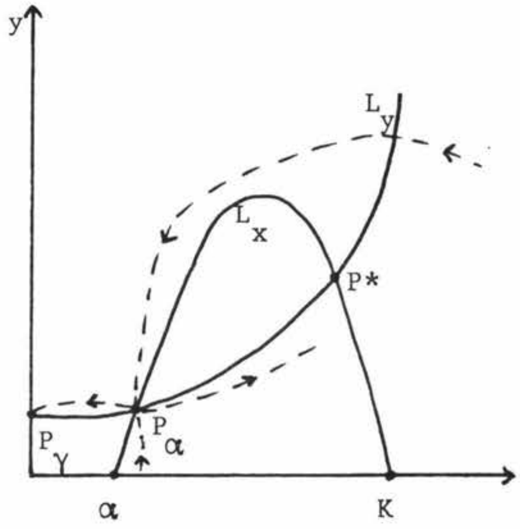

$\alpha > 0$

Figure 3.9.25

For $\alpha = 0$, $L = \infty$, P_γ is a saddle point and P* is globally stable in E^0. However we note that as B becomes large. P* comes dangerously close to the y-axis, and subsequently may result in prey extinction due to random environmental fluctuations.

For $\alpha = 0$, $L < \infty$, P_γ is still a saddle point, and the system is globally stable, tending either to a stable equilibrium P*, or a stable limit cycle surrounding P*. However there exists a critical rate $B_c > 0$ such that P_γ coincides with (0,L), and two possibilities occur. If the slope of L_y is greater than or equal to that of L_x when $B = B_c$, then P* and P_γ coalesce. For $B > B_c$ the equilibrium point P_γ becomes a globally stable node while P* disappears, thus guaranteeing prey extinction.

Should the slope of L_y be less than that of L_x at $B = B_c$, then P* will still lie in E^0. As B increases further, a new equilibrium point P_α appears, which will be a saddle point [see Figure 3.9.26].

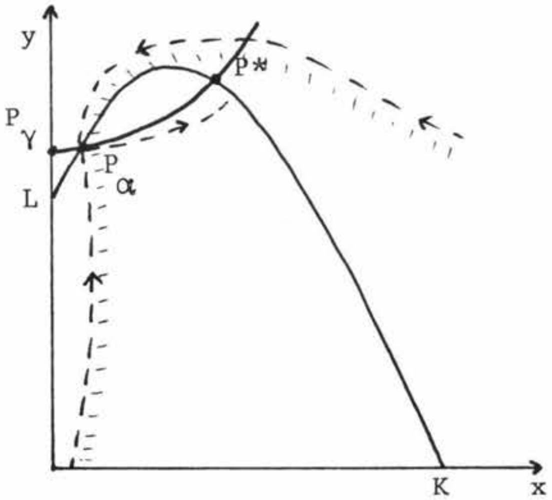


Figure 3.9.26

The shaded region indicates the area of stability for P* (or a limit cycle around P*). The rest of E^0 is the region of stability for the stable node P_γ. As B increases even further, another critical value B_s, is reached where P_α and P* coalesce, and disappear when $B > B_s$, thus ensuring prey extinction.

Now we consider the combined stocking of both prey and predator, with both A and B positive. When $\alpha = 0$, both P_γ and P_β disappear from E, and the situation is much like that of the phase portraits in Figures 3.9.23, 3.9.24 and 3.9.26. Thus P* is either globally stable, or there is a globally stable limit cycle surrounding P* (here we use "globally stable" in the usual sense, but any trajectories which leave the first quadrant E by crossing one of the axes in finite time are considered to terminate there). Should the rates of stocking be set too high, again P* becomes perilously close to the y-axis.

The situation is similar to past discussions for $\alpha > 0$ as well, with the notable exception of the case where A is sufficiently small that L_y intersects with L_x three times, giving rise to equilibrium points P_γ, P_α and P*, all in E^0. As illustrated by Figure 3.9.27 there are two regions of stability separated by the separatrices of the saddle point P_α. Thus P* (or a stable limit cycle surrounding P*) will be one attractor, and the stable equilibrium point P_γ will be the other.

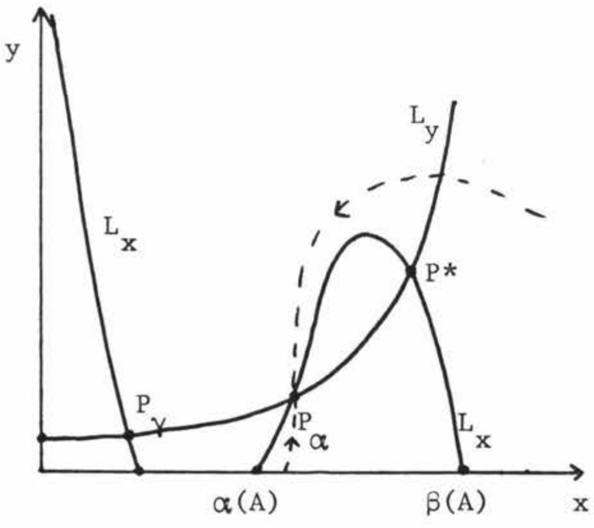


Figure 3.9.27

In general, the authors concluded that increasing A tended to stabilize the system and increased the average number of predators, while increasing B tended to promote prey extinction.

Before going on to discuss proportional harvesting rates, we should comment on the fact that systems with constant harvesting or stocking rates will not satisfy the conditions given by (3.2.2). This is a valid criticism of the above models as one would expect a reasonable model to take into account the dynamics of the system if one of the species became extinct, yet the authors above gloss over this point.

One way round this would be to define $x = 0$ and $y = 0$ as solutions to the system in question. This would lead to discontinuous behaviour near the axes; but is this unecessarily unreasonable when dealing with population models? Populations tend to behave continuously only when the numbers are sufficiently high. Near the axes, erratic behaviour is expected, and if we use Strebel and Goel's method [see §3.3] of taking into account random environmental fluctuations, these discontinuities need not bother us at all. It would still be necessary to take into account the qualitative behaviour of the original system on the axes, anyway.

Brauer and Soudack (1978) briefly considered proportional harvesting rates as applied to the predator (most of their paper being concerned with simulation studies of specific models). Consider the following system:

$$\begin{aligned}\frac{dx}{dt} &= x\,F(x,y)\\ \frac{dy}{dt} &= y\,G(x,y) - By, \quad B \geq 0\end{aligned} \qquad \ldots\ (3.9.7)$$

The authors assumed conditions given by (3.9.3) and (3.9.4) held, and further assumed that there was a unique equilibrium point P^* in E^0 when $B = 0$. The carrying capacity, K was defined in the usual way:

$$\exists K > 0: \quad F(K,0) = 0.$$

As B increases from zero, $P^* = (x^*(B),y^*(B))$ tended to move to the right along L_x. Thus the critical value of B where P^* coalesces with $(K,0)$ is defined by $B_c = G(K,0)$. The other critical value, B_r, signifying a stability change in P^*, is defined by

$$x^*(B_r)\ F_x(x^*(B_r),y^*(B_r)) + y^*(B_r)\ G_y(x^*(B_r),y^*(B_r)) = 0$$

When comparing this with constant harvesting rates, the authors concluded that proportional harvesting would be preferable, as it was not as prone to sudden qualitative changes in the system resulting in extinction. It is also worth noting that in both cases nutrient enrichment (i.e. increasing K) allowed for higher safe harvesting rates.

Knolle (1976) considered a Lotka-Volterra model, modified to include logistic prey growth and a time-delayed functional response [see § 5.1] for the predators. With this system, a harvesting function was included in the predator equation, expressed as a function of time only.

$$\begin{aligned} \frac{dx}{dt} &= x(\alpha-\beta y-ax) \\ \frac{dy}{dt} &= -\gamma y + \delta\int_0^r x(t-s)y(t-s)d\mu(s) + p(t) \end{aligned} \qquad \ldots (3.9.8)$$

Where p(t) is the periodic forcing term representing harvesting (for $p(t) \leq 0$) or stocking (for $p(t) \geq 0$).

Sufficient conditions for the existence of a positive periodic solution was given, as well as a lower bound for its period.

Applications of such recent work in this section are understandably few, but the first attempt to optimize the proportional harvesting rates in a system (keeping in mind the bounds set by practical stability) was made by Legovic et al. (1979). This, and other considerations of applications are discussed in chapter 7.

§3.10 The Effects of Natural Selection

Previously we considered what might be observed if a predator-prey system had its basic structure interfered with through enrichment, stocking and harvesting. Of less immediate practical importance is the question of the ultimate fate of the system if left alone. This would be of more theoretical interest to ecological geneticists than to any resource management system, primarily because evolutionary change in large populations are extremely slow relative to ecological change. Nevertheless, the exploitative nature of the predator-prey interaction, considered by many to be basically destabilizing, has sparked off frequent debate as to whether the system would eventually collapse or not under the influences of natural selection.

Rosenzweig and MacArthur (1963) first considered this problem using the graphical method they had developed. To predict the effects evolution would have on the zero-isoclines of the system, they presented the following argument. At a given prey density, a predator which can maintain itself and produce enough offspring to replace itself is defined to be more fit than a predator which is unable to kill sufficient prey to accomplish this. Thus natural selection should improve the predator's ability to find, catch and kill the prey. That is, we would expect the predator isocline L_y to drift to the left with evolutionary time. Assuming Rosenzweig's arguments for a 'hump' in the prey isocline L_x are reasonable, this shift to the left of L_y is likely to be destabilizing in the long run. Under increased predation, L_x would drift downwards.

Naturally the prey also improve their chances of survival through natural selection. How these improvements occur will depend on the major limiting factors of prey growth. Hence if predation is the dominating factor, we would expect the predators to find it increasingly difficult to catch and kill the prey, thus shifting L_y back to the right, and L_x upwards.

Furthermore, better utilization of prey caught for full nutritional value would move L_y to the left, but would not affect L_x since the actual predation rate would be unaffected by this. Similarly the prey utilizing their food would push L_x up.

We finish up then with what appears to be a fairly balanced continuous set of changes through evolution. The fact that these changes continue to take place is not doubted, but to what degree they are balanced remains unanswered. Rosenzweig (1973) sought to investigate this further by considering the above effects on specific models. All had a vertical predator isocline, $x = J$ and a humped prey isocline. Each model also included at least one parameter, e say, which was directly related to the hunting ability of the predator. In each case it was found that $\frac{\partial J}{\partial e} < 0$, indicating that evolution forced the predator isocline L_y to the left. To prove destabilization, one must be sure that the peak (x_c, y_c) of the hump in L_x is not also moving to the left. This condition was indeed satisfied, as $\frac{\partial x_c}{\partial e} > 0$ for each model. We note in passing that Rosenzweig's arguments depend on L_y being vertical - if it is not, then the changes in J may not necessarily reflect the changes in the rest of L_y.

By similar analysis on the effects of natural selection of prey, it was found that K tended to increase, as expected. In general it was postulated that there may exist a coevolutionary steady state (CSS) for which both species would evolve in such a way as to cancel out each other's adverse effects. Rosenzweig determined that this CSS would still exist even when such evolutionary pressures as genetic mutation and group selection were included.

The existence of a CSS says nothing about its stability in the evolutionary sense. Does the system approach this steady state? If so, under what conditions, and in what manner? It seems generally accepted that if the predator and prey species can successfully survive upon initial contact within an environment, then natural selection tends to stabilize the interaction; thus driving it towards the CSS. However the increasingly finely-tuned and specialized techniques for survival suggest there is a danger that this delicate balance may become over-sensitive.

Slobodkin (1974) notes that predation techniques are never likely to become 'perfect' anyway, in the sense that the predators usually concentrate on the very old or very young prey, and thus ensure that the fittest individuals survive. This mechanism guarantees the persistence of the predator-prey system with evolutionary time.

The somewhat controversial concept of group selection has produced another possible mechanism for the observed persistence. Gilpin (1975) feels that the overall balance is tipped slightly in the predator's favour, and that given sufficient time, the predators would ultimately over-exploit the prey to extinction. He points out that most populations tend to be aggregative, whether due to behavioural or environmental causes, and that different patches may evolve slightly differently with time. Clearly some patches are more likely to survive than others, and some will be driven to extinction by the aforementioned mechanism. Yet those that are fitter and survive will have time to migrate to the empty patches before they too succumb. This effect has been termed group selection, and it clearly opposes the drift towards instability. Gilpin attempted to support this argument by considering the evolution of parameters of a specific model, using simulation.

Investigations of this CSS proceeded further when Schaffer and Rosenzweig (1978) determined that its existence actually depended critically on the relative generation times of the two species. If the prey have a shorter life span on average than that of the predator, the CSS should exist. Conversely, if the predator life span is shorter, the system is more likely to collapse. To test this strong hypothesis, the authors looked at most of the accepted predator-prey systems which appear to have persisted. Only one exception appeared, that of the lynx-hare cycle in

Canada. However, since there is great debate as to the extent that this can be considered a predator-prey oscillation [see §2.1], they feel justified in adhering to their conclusion.

Following this, Rosenzweig and Schaffer (1978) considered what effects natural (that is, long-term) enrichment in a predator-prey system would produce in conjunction with coevolution. If the natural enrichment was sufficiently slow to be in step with the evolutionary changes, they concluded that the destabilizing effects of enrichment would be nullified by the stabilizing influences of evolution. They stress, however, that this would not be the case with artificial (that is, short-term) enrichment.

4 MODELS

§4.1 Simple Extensions of the Lotka-Volterra Model

Having provided a general framework for predator-prey models in the previous chapter, we are now ready to consider particular models. To include every model presented over the last fifty years is beyond the scope of this exposition. Instead specific models will be selected and discussed and the basis for selection will fall on at least one of the following:

(i) to consider a class of similar models by considering a representative.

(ii) to demonstrate the building of a model based on the biological observations peculiar to that system.

(iii) to discuss those models which are popularly employed in real situations.

(iv) to include special features which may not have been dealt with fully (or at all) in the previous chapter.

Until Holling's work on functional responses appeared, most of the models tended to be straightforward modifications of the Lotka-Volterra model. A standard way of extending or improving an existing model is to add higher order terms.

Based on the discussions in chapter 3 on the effects of intraspecific competition for resources by the prey, it seems logical to replace the constant prey growth rate term in the Lotka-Volterra model with the logistic term, giving the following system (often referred to as the Volterra-Gause-Witt model):

$$\begin{aligned} \frac{dx}{dt} &= \alpha x \left(1-\frac{x}{K}\right) - \beta xy \\ \frac{dy}{dt} &= -\gamma y + \delta xy \end{aligned} \qquad \ldots (4.1.1)$$

Using standard analytic and graphical techniques outlined in the last chapter, it is easy to show that the unique equilibrium $P^* = (x^*,y^*) = (\frac{\gamma}{\delta}, \frac{\alpha}{\beta}(1-\frac{\gamma}{\delta K}))$ in E^0 will be a globally stable focus for $0 < \frac{\gamma}{\delta} < K$. The other equilibria at (0,0) and (K,0) are saddle points, as shown in Figure 4.1.1.

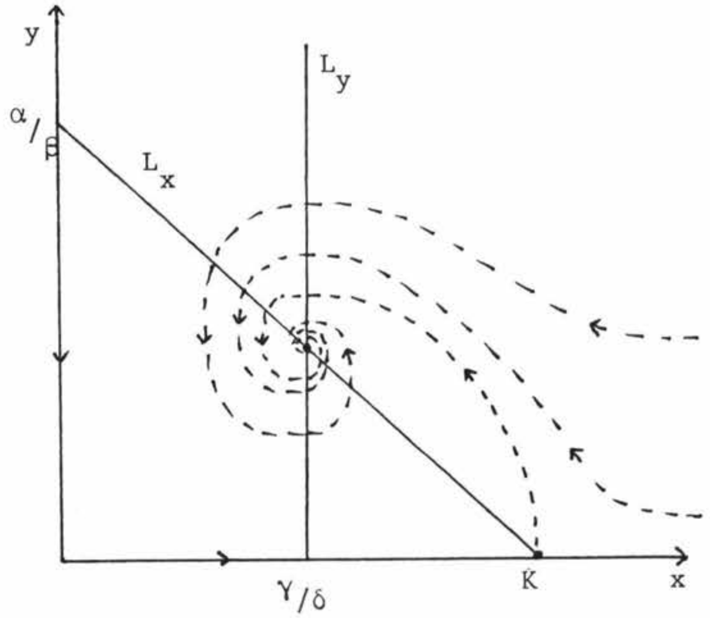


Figure 4.1.1

From this it seems reasonable to include an intraspecific competition term in the predator rate equation as well. Thus F(x,y) and G(x,y) in system (3.2.3) are taken to be general linear equations given in the following form:

$$\frac{dx}{dt} = x\ (\alpha - ax - \beta y)$$
$$\frac{dy}{dt} = y\ (-\gamma - by + \delta x) \qquad \ldots\ (4.1.2)$$

where all constants are real and positive.

Kilmer (1972) studied the structurally stable possibilities locally around P* in E^0, but was unable to describe any of the non-linear effects of the system. Walter (1974) proved that such a system will be globally stable in E and that where P* exists in E^0, it will be globally stable (thus dispelling any hope that limit cycle behaviour may occur). It is interesting to note that Walter used the positive definite Lyapunov function

$$V = \left[\frac{x^* e^{\frac{x}{x^*}}}{x}\right]^{\eta} \left[\frac{y^* e^{\frac{y}{y^*}}}{y}\right]^{\mu} - e^{\eta+\mu}$$

to prove the result, where $\eta = \frac{x^*}{\beta}$ and $\mu = \frac{y^*}{\delta}$.

Van der Vaart (1978) went one step further and considered the more general system of the form (4.1.2) with all the parameters taking any sign. With some fairly involved mathematics, it was proven that such a system will never exhibit limit cycle behaviour. Furthermore, it was shown that if P* in this system is a centre, only the case where it reduces to the Lotka-Volterra model is biologically plausible.

Gilpin (1974) added further higher order terms to produce the following system:

$$\begin{aligned} \frac{dx}{dt} &= x\ (\alpha+ax-bx^2-\beta y) \\ \frac{dy}{dt} &= y\ (-\gamma+cy-dy^2+\delta x) \end{aligned} \qquad \ldots\ (4.1.3)$$

where

$$\left.\begin{aligned} &\gamma,\ \beta,\ \delta,\ b,\ d > 0 \\ &c < \sqrt{4\gamma d} \\ &\text{Either } \{\alpha > 0\} \text{ or } \{\alpha \leq 0 \text{ and } a > \sqrt{-4\alpha b}\}^{*} \end{aligned}\right\} \ldots\ (4.1.4)$$

The parameters α, β, γ are as defined in the original equations (2.2.2). The parameter α is usually positive, but can be negative if the Allee effect is present, in which case the extra condition ensures prey growth in intermediate prey densities.

The parameters a and c represent social cooperation (when positive) or social conflict (when negative). With the former, a species may reap benefits from increasing numbers through better defences, easier location of sexual partners, or general resources; whereas the latter corresponds to inhibiting growth through territoriality, fighting over mates or plain lack of space.

The parameters b and d cover the effects of mutual interference through satiation. Note that the second condition in (4.1.4) ensures the predator isocline L_y does not intersect the y-axis.

The two zero-isoclines are both parabolas, whose vertices lie on the lines $y = c/2d$ and $x = a/2b$ [see Figure 4.1.2].

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* Correcting an error which appeared not only in this paper, but in a subsequent book of Gilpin's (1975) detailing the same analysis of the model.

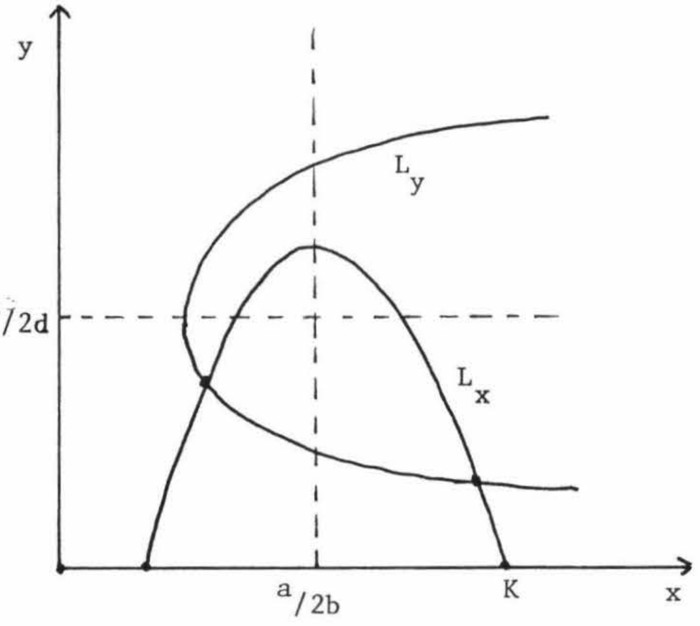

Figure 4.1.2

Since the last condition in (4.1.4) ensures that the vertex of L_x stays above the x-axis, there will be either two or three equilibria in E on the x-axis depending on whether $\alpha \geq 0$ or $\alpha < 0$ respectively. In a situation similar to the systems discussed in §3.9, the origin will be a saddle point with the axes as separatrices, and the point (K,0) will also be a saddle point. For $\alpha < 0$, the other equilibrium on the x-axis will either be a node or a saddle point.

In E^0, the number of equilibria will range between zero and four. Understandably, Gilpin made no attempt to classify the possible phase portraits in E^0, as the tremendous range of possibilities (some of them very complex), would prevent this. Instead, he presented a series of simulated phase portraits based on only one equilibrium point in E^0, to demonstrate the range.

§4.2 Models Incorporating a Functional Response

The models discussed in §4.1 did not really include any kind of functional response, as the predation interaction terms were linear without satiation. Many ecologists feel that the inclusion of a functional response in their models is imperative, though curiously enough there are not many in the literature which include this response in both the predator and prey equations. This seems particularly odd as a great deal of theory was developed to deal with such models [see §3.7], and in fact Holling's original work in this area was to account for changes in the predator's density due to changes in the prey density. Thus the predator-prey system could be modelled in the form:

$$\frac{dx}{dt} = f(x) - y\,g(x)$$
$$\frac{dy}{dt} = h(x,y) + \delta y\,g(x) \qquad \ldots (4.2.1)$$

where the term y g(x) represented what was lost by the prey, and gained by the predators through predation, with δ representing the appropriate conversion constant.

In the following we shall present some of the more common responses of each type and look at several models, where the response either appears in both equations (i.e. of the type given by (4.2.1)), or where it appears only in the prey equation (as is often the case!).

The number of times a type I response would have been observed in real life would be exceeding small, as are not unexpectedly, the number of models with said response. Gruber (1976) modified the Lotka-Volterra model to include a type I response:

$$\frac{dx}{dt} = \alpha x - y\,g(x)$$
$$\frac{dy}{dt} = -\gamma y + \frac{\delta}{\beta}\,y\,g(x) \qquad \ldots (4.2.2)$$

where

$$g(x) = \begin{cases} \beta x, & \text{for } 0 \le x \le \frac{\mu}{\beta} \\ \mu, & \text{for } x \ge \frac{\mu}{\beta} \end{cases} \qquad \ldots (4.2.3)$$

To ensure the predators survive, we also require:

$$\mu > \frac{\beta\gamma}{\delta} \qquad \ldots (4.2.4)$$

Now this system can be dealt with graphically by splitting the phase plane into two parts, and 'gluing' the trajectories together.

Assuming condition (4.2.4) holds, the line $x = \frac{\mu}{\beta}$ will be further to the right of the equilibrium point $(\frac{\gamma}{\delta},\frac{\alpha}{\beta})$, so that the trajectories up to this line will be normal Lotka-Volterra ones, as in Figure 4.2.1.

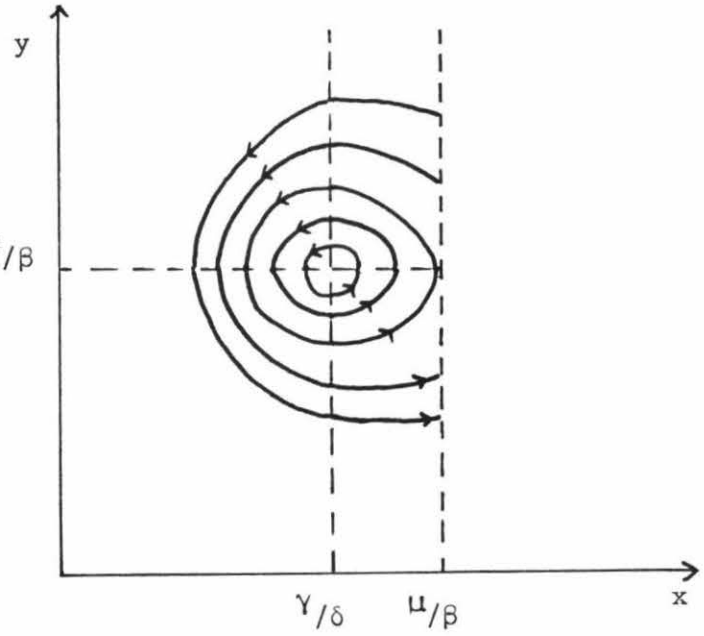

Figure 4.2.1

For $x \geq \frac{\mu}{\beta}$, system (4.2.2) becomes:

$$\frac{dx}{dt} = \alpha x - \mu y$$
$$\frac{dy}{dt} = ky \qquad \ldots (4.2.5)$$

where $k = \frac{\delta\mu}{\beta} - \gamma > 0$.

Now (4.2.5) has the following explicit solution:

$$x = \begin{cases} C\, y^{\frac{\alpha}{k}} - \frac{\mu y}{(k-\alpha)}\ , & \text{for } \alpha \neq k \\ C\, y - \frac{\mu y}{\alpha} \log y, & \text{for } \alpha = k \end{cases} \qquad \ldots (4.2.6)$$

where C is an arbitrary constant such that $C > 0$ for $k > \alpha$, and $C \in R$ for $k < \alpha$.

There are two possible results for this system depending on whether $k > \alpha$ or $k < \alpha$, as demonstrated by Figures 4.2.2 and 4.2.3 respectively. Note that the boundary line $y = \frac{\alpha-k}{\mu}\, x$ coincides with the x-axis when $k = \alpha$.

$\alpha < k$

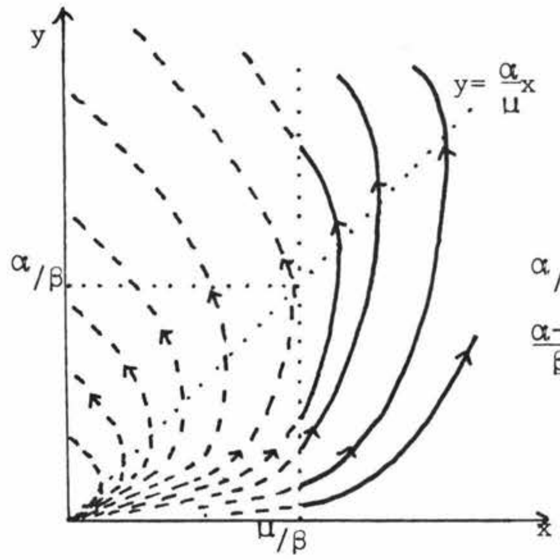

Figure 4.2.2

$\alpha > k$

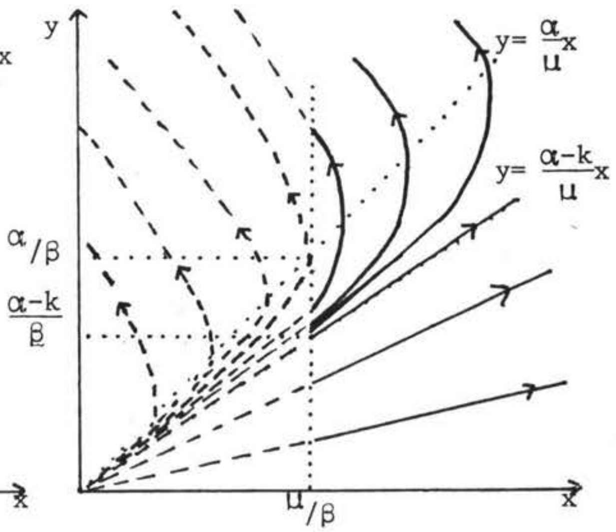

Figure 4.2.3

In terms of the parameter μ, the critical value occurs at $\mu_c = \frac{\beta}{\delta}(\alpha+\gamma)$. Hence there will be two different phase plane configurations depending on the parameter value μ, as shown in Figures 4.2.4 and 4.2.5, for $\mu > \mu_c$ and $\mu < \mu_c$ respectively.

$\mu > \mu_c$

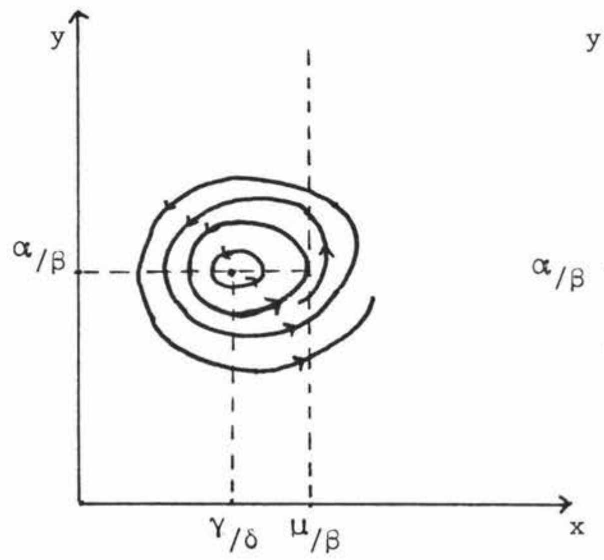

Figure 4.2.4

$\mu < \mu_c$

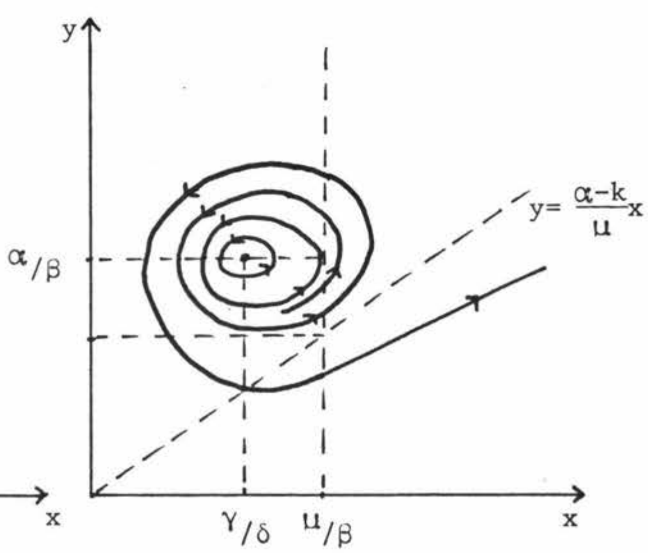

Figure 4.2.5

In conclusion, we see that for all initial populations (x_0,y_0) within the closed path passing through the point $(\frac{\mu}{\beta},\frac{\alpha}{\beta})$, the behaviour will be identical with that of the Lotka-Volterra model. If (x_0,y_0) lies outside this closed path, there are two possibilities:

(i) For $\mu > \frac{\beta}{\delta}(\alpha+\gamma)$, the trajectories will oscillate in an unstable fashion until they are sufficiently close to the axes that extinction will result.

(ii) For $\frac{\beta\gamma}{\delta} < \mu < \frac{\beta}{\delta}(\alpha+\gamma)$, trajectories will oscillate divergently as before until the line $y = \frac{\alpha-k}{\mu}x$ is crossed, where upon both x and y grow indefinitely with time. Though highly unrealistic, it is nevertheless an interesting and totally unexpected result. Either both the predator and prey prosper in numbers forever, or at least one of them become extinct!

Dubois (1979) used a similar system, complicated only by including logistic growth for the prey. Little detail of the model was provided, except to note that even such a simple system could present rich qualitative behaviour, such as two nested limit cycles surrounding a stable equilibrium point in E^0. The outer limit cycle is stable, and the inner one unstable.

In reality we are more concerned with type II and type III responses, for which there would be an endless array of mathematical representations. If the equations are to be tractable, then these representations must be simple, and thus there are three in common use for the type II response:

[Ivlev (1961)] $$g(x) = k\,[1-e^{-cx}] \qquad \ldots (4.2.7)$$

[Holling (1965)] $$g(x) = \frac{kx}{x+d} \qquad \ldots (4.2.8)$$

[Rosenzweig (1971)] $$g(x) = kx^g,\ 0 < g \leq 1 \qquad \ldots (4.2.9)$$

For example, Oster and Guckenheimer (1976) presented the following modification of the Lotka-Votlerra model, with logistic growth for the prey and the response given by (4.2.7):

$$\begin{aligned} \frac{dx}{dt} &= \alpha x(1-\frac{x}{K}) - \beta y(1-e^{-cx}) \\ \frac{dy}{dt} &= -\gamma y + \delta y(1-e^{-cx}) \end{aligned} \qquad \ldots (4.2.10)$$

where all parameters are positive. Using Freedman's results for systems of the form (3.7.5), we find this system is globally stable in E^0, and that the unique equilibrium point of E^0 is either stable or unstable with a stable limit cycle surrounding it. Similarly, using the fact that conditions (3.8.1) also hold, we can calculate the bifurcation value in terms of the carrying capacity K, where the limit cycle is thrown off from the equilibrium point via a Hopf bifurcation. Clearly these analytic results are vast improvements on the original work done by May (1972) and Gilpin (1972) on this model, as they used numerical integration to determine the existence of the limit cycle and to try and estimate the bifurcation value, without uncovering the underlying mechanism.

Others to use the type II response include Canale (1970), who found that this response seemed very suitable for modelling protozoa-bacteria predation systems. Rosenzweig (1971), followed by Brauer (1976), considered six different models, all using either (4.2.7) or (4.2.9) as the response for the prey equation. The predator equation for each model was given by

$$\frac{dy}{dt} = Ak\, y(e^{-cJ} - e^{-cx})$$

Shimazu et al. (1972) constructed the following model using logistic prey growth, a response given by (4.2.8), and a predator equation originally put forward by Leslie (1948):

$$\begin{aligned} \frac{dx}{dt} &= \alpha x(1-\frac{x}{K}) - \frac{\beta xy}{x+d} \\ \frac{dy}{dt} &= ry(1-\frac{y}{sx}) \end{aligned} \qquad \ldots \ (4.2.11)$$

where r, s > 0.

Using numerical integration, the authors found similar behaviour to that of system (4.2.10) provided oscillations could be assumed. Urabe (1974) came to similar conclusions using similar methods, whereas May (1974a) and Tanner (1975) demonstrated that, this, too was a Hopf bifurcation.

Goh (1978) proved a global stability theorem for the following generalized model with a response given by (4.2.8), though it is a pity that no biological interpretation for his result is readily apparent.

$$\frac{dx}{dt} = x\left[j(x) - \frac{ay}{1+wx}\right]$$
$$\frac{dy}{dt} = y\left[q(y) + \frac{eax}{1+wx}\right] \qquad \ldots (4.2.12)$$

Theorem 4.2.1 System (4.2.12) is globally stable in E^0 if there exists an equilibrium point $P^* = (x^*,y^*)$ in E^0 and if for all (x,y) in E^0 such that $(x,y) \neq (x^*,y^*)$;

$$(x-x^*)[j(x)-j(x^*)+aw\,S(x) \cdot y^*(x-x^*)] + (y-y^*)\left[\frac{1+wx^*}{e}\right][q(y)-q(y^*)] < 0$$

where $$S(x) = \frac{1}{(1+wx^*)(1+wx)}.$$

A more general approach towards such type II responses, was made by Lin and Kahn (1976) using Hopf bifurcation theory and non-linear correction techniques. Consider the following system:

$$\frac{dx}{dt} = \alpha x(1-\frac{x}{K}) - \beta y\ g(x)$$
$$\frac{dy}{dt} = -\gamma y + \delta y\ g(x) \qquad \ldots (4.2.13)$$

where $g(x)$ is given by each of the three expressions (4.2.7)-(4.2.9), resulting in three different models. The authors found that the general qualitative behaviour was the same in all three cases, similar to the previous models discussed. Furthermore, the model using a (4.2.7) response tended to be the most sensitive to parameter variation while the model using a (4.2.9) response was the least sensitive.

Of the type III responses, only the following seems to be in common use:

[Takahashi (1964)] $$g(x) = \frac{kx^2}{x^2+d^2} \qquad \ldots (4.2.14)$$

It must be remembered that most experimental modelling of predator-prey systems involves the use of type II responses (the work of Holling being a notable exception), so that the need for detailed studies with a type III response may not have been felt. Nevertheless, now that more general analytic techniques are appearing, it should not be difficult to broach this area in the near future.

§4.3 Prey Protection Through Refuges and Age Classes

As noted in the last chapter, guaranteeing the survival of a certain number of prey is a strong stabilizing mechanism provided the number is not so high as to starve the predators. For example, in §3.3 we discussed the prospect of a fixed number of refuges available in the environment providing safety from predation for any number of prey up to and including r, say. A graphical argument was used to demonstrate the stabilizing properties of this effect.

Maynard-Smith (1974) modified the Lotka-Volterra model to include this protection of prey:

$$\left.\begin{aligned}\frac{dx}{dt} &= \alpha x - \beta y(x-r)\\ \frac{dy}{dt} &= -\gamma y + \delta y(x-r)\end{aligned}\right\} , \quad r > 0 \qquad \ldots (4.3.1)$$

The phase plane for this system is given in Figure 4.3.1, with the old Lotka-Volterra zero-isoclines given as dashed lines.

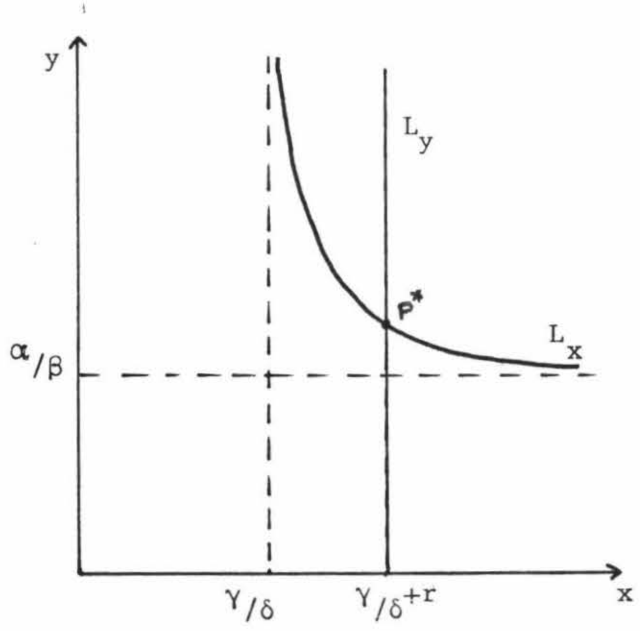

Figure 4.3.1

It is interesting to see that not only does the prey equilibrium value x* increase, but so does the predator equilibrium value y*. Further, system (4.3.1) is a special case of system (3.5.5), and it can be shown that the criterion of (3.5.6) always holds for all r > 0; hence P* will always be stable (either a focus or a node). From this, it is clear that the Lotka-Volterra system has been strongly stabilized through the inclusion of this protection factor.

St. Amant (1970) pointed out that the system (4.3.1) is reasonable provided the prey shelter in the refuges for a short time relative to their own average life expectancy; and that if $x > r$, then exactly r will be sheltered in any one given moment. A more realistic view might entail some of the prey settling down in these refuges, and perhaps even fighting off other prey from trying to shelter in the same place. Instead of remaining constant however, the prey population within the habitats would change, independently of the prey outside. Let x_1 and x_2 be the number of prey outside and inside the refuges respectively. Once the prey are established in the habitats, we assume that further inwards migration would be negligible. Setting r to be the expected number of prey in the refuges at any given time, St. Amant gives the model:

$$\begin{aligned} \frac{dx_1}{dt} &= \alpha x_1 - \beta x_1 y + \nu x_2 \\ \frac{dx_2}{dt} &= \mu(r-x_2) \qquad \qquad \ldots (4.3.2) \\ \frac{dy}{dt} &= -\gamma y + \delta x_1 y \end{aligned}$$

where $\mu > 0$ represents the overall growth rate (depending on how crowded or how sparse the shelters are); and $\nu > 0$ represents the rate of migration out of the refuges.

The second equation of (4.3.2) is almost an over-simplification, since inital values of x_2 less than r, remain less than r as $t \to \infty$ (and similarly for $x_2 > r$). Expecting the parameter μ to deal with births, deaths and outward migration from the refuges is perhaps expecting a bit much. A logistic growth equation might be more suitable.

The equilibrium point in E^0 for (4.3.2) is given by

$$P^* = (x_1^*, x_2^*, y^*) = \left(\frac{\gamma}{\delta}, r, \frac{\alpha\gamma+\nu r\delta}{\beta\gamma}\right)$$

and using standard linearization techniques:

$$\Delta(x_1^*, x_2^*, y^*) = \begin{bmatrix} -\frac{\nu\delta r}{\gamma} & \nu & -\frac{\beta\gamma}{\delta} \\ 0 & -\mu & 0 \\ \frac{\delta}{\beta\gamma}(\alpha\gamma+\delta\nu r) & 0 & 0 \end{bmatrix}$$

so that:

$$\operatorname{Det}(\Delta(P^*)-\lambda I) = \begin{vmatrix} -\frac{\nu\delta r}{\gamma}-\lambda & \nu & -\frac{\beta\gamma}{\delta} \\ 0 & -\mu-\lambda & 0 \\ \frac{\delta}{\beta\gamma}(\alpha\gamma+\delta\nu r) & 0 & -\lambda \end{vmatrix}$$

$$= -(\mu+\lambda)\begin{vmatrix} -\frac{\nu\delta r}{\gamma}-\lambda & -\frac{\beta\gamma}{\delta} \\ \frac{\delta}{\beta\gamma}(\alpha\gamma+\delta\nu r) & -\lambda \end{vmatrix}$$

$$= -(\mu+\lambda)[\lambda^2+\frac{\nu\delta r}{\gamma}\lambda+(\alpha\gamma+\delta\nu r)] = 0$$

$$\Rightarrow \lambda = -\mu \quad \text{or} \quad \lambda = \frac{1}{2}\left[-\frac{\nu\delta r}{\gamma} \pm \sqrt{(\frac{\nu\delta r}{\gamma})^2 - 4(\alpha\gamma+\delta\nu r)}\right]$$

Clearly all eigenvalues will either be negative or have negative real parts. Thus the equilibrium will be locally stable. This is not really surprising, since the rate equation for x_2 in system (4.3.2) can be solved directly, and the solution $x_2(t)$ can be put into the first rate equation, giving:

$$\frac{dx_1}{dt} = \alpha x_1 - \beta x_1 y + \nu x_2(t)$$
$$\frac{dy}{dt} = -\gamma y + \delta x_1 y \qquad \ldots (4.3.3)$$

This is just the Lotka-Volterra model with a stocking term verying with time. As we have seen in §3.9, stocking of prey in a prey-predator system tends to stabilize.

Another possible guarantee of survival for the prey arises if there exists some kind of invulnerable age class within the prey age structure (cf. the established individuals as opposed to the displaced ones, discussed in §3.5). The simplest partition of a species into age classes is based on ability to reproduce. Further subdivisions can be made on other relevant factors such as ability for defence from predation, but we shall restrict our studies to two classes.

Let A_1 = {all prey which are too young to reproduce, at a given time}
A_2 = {all prey not in A_1}

We are assuming that the number of prey which are too old to reproduce will be negligible, though this may not always be the case in a real system. Smith and Mead (1974) sought to investigate whether the inclusion of such a simple age structure into a Lotka-Volterra system would be stabilizing or not. They considered two possibilities; predators may either concentrate their attack on individuals of class A_1, or those of class A_2. In the first case, the young are likely to be more vulnerable due to their inability to defend themselves. The latter case may occur when the young are in some way protected, while the adults become open to predation (for example, many insects are safe as burrowing larvae, but fall prey to birds once they mature to flying adults).

No qualitative investigations of the following two models were made by the authors however - instead, simulation techniques were employed over a range of values and included stochastic effects on the parameters. They concluded that there did seem to be a link between age structure and stability.

With the following, standard linearization techniques about the internal equilibrium point P* were used in an attempt to determine more about the nature of this stability. Note that both models were incorrectly presented in this paper, both errors being very similar in nature. This leads me to wonder whether they were in fact coincidental misprints, or were instead actually used by the authors in their investigations (it can be shown that P* in both of the incorrect versions will always be stable!).

In the first case, the Lotka-Volterra model was modified to give (in corrected form):

$$\begin{aligned} \frac{dx_1}{dt} &= \alpha x_2 - x_1\,(\beta y+\mu) \\ \frac{dx_2}{dt} &= \mu x_1 - \nu x_2 \qquad \ldots (4.3.4) \\ \frac{dy}{dt} &= y(-\gamma + x_1) \end{aligned}$$

where x_1 = number of prey in A_1.

x_2 = number of prey in A_2.

$\mu > 0$ is the rate at which individuals in A_1 mature and join A_2.

$\nu > 0$ is the death rate of prey in A_2 (i.e. not from predation).

The Jacobian is given by

$$\Delta(x_1,x_2,y) = \begin{bmatrix} -\mu-\beta y & \alpha & -\beta x_1 \\ \mu & -\nu & 0 \\ \delta y & 0 & \delta x_1-\gamma \end{bmatrix}$$

and the equilibrium point in E^0, $P^* = (\frac{\gamma}{\delta}, \frac{\gamma\mu}{\delta\nu}, \frac{\mu}{\beta}[\frac{\alpha}{\nu} - 1])$. For the moment, we ignore the fact that $y^* < 0$ when $\alpha < \nu$ (the reason why is made clear in the discussion at the end of the analysis).

$$\left|\Delta(P^*)-\lambda I\right| = \begin{vmatrix} -\frac{\mu\alpha}{\nu}-\lambda & \alpha & -\frac{\beta\gamma}{\delta} \\ \mu & -\nu-\lambda & 0 \\ \frac{\delta\mu}{\beta}(\frac{\alpha}{\nu}-1) & 0 & -\lambda \end{vmatrix}$$

$$= \frac{\delta\mu}{\beta}(\frac{\alpha}{\nu} - 1)\begin{vmatrix} \alpha & -\frac{\beta\gamma}{\delta} \\ -(\nu+\lambda) & 0 \end{vmatrix} - \lambda\begin{vmatrix} -(\frac{\mu\alpha}{\nu}+\lambda) & \alpha \\ \mu & -(\nu+\lambda) \end{vmatrix}$$

$$= -\mu\gamma(\frac{\alpha}{\nu} - 1)(\nu+\lambda) - \lambda[(\frac{\mu\alpha}{\nu} + \lambda)(\nu+\lambda)-\mu\alpha] = 0$$

$$\Rightarrow \quad \lambda^3 + [\nu + \frac{\mu\alpha}{\nu}]\lambda^2 + [\mu\gamma(\frac{\alpha}{\nu} - 1)]\lambda + [\mu\gamma(\alpha-\nu)] = 0$$

$$\Rightarrow \quad \lambda^3 + c\lambda^2 + k\lambda + \nu k = 0 \qquad \ldots (4.3.5)$$

where $c = (\nu + \frac{\mu\alpha}{\nu})$, $k = \mu\gamma(\frac{\alpha}{\nu} - 1)$

We note that $c > 0$, and that k can take either sign, but we will not consider the case of $k = 0$ ($\alpha = \nu$) since two of the characteristic values of (4.3.5) become zero, and hence the non-linearities of the system need to be considered.

Thus, using Descartes' rule of signs on equation (4.3.5), we have five cases for the three roots, depending on the sign of k:

Case	Sign of k	Positive Roots	Negative Roots	Complex Roots
I	< 0	1	2	0
II	< 0	1	0	2
III	< 0	0	1	2
IV	> 0	0	3	0
V	> 0	0	1	2

Now let A be a real root of equation (4.3.5). Thus $(\lambda - A)$ will be a factor, which can be factored out through long division. The resultant quotient, $Q(\lambda)$, and remainder, R, are given by

$$\begin{aligned} Q(\lambda) &= \lambda^2 + (c+A)\lambda + [k + A(c+A)] \\ R &= \nu k + A\,[k + A(c+A)] \end{aligned} \qquad \ldots (4.3.6)$$

Since $(\lambda - A)$ is a factor of (4.3.5), we also have

$$(\lambda - A)Q(\lambda) = 0 \qquad \ldots(4.3.7)$$

$$R \equiv 0 \qquad \ldots(4.3.8)$$

and from (4.3.6) and (4.3.7) we have $Q(\lambda) = 0$

$$\Leftrightarrow \qquad \lambda = \frac{1}{2}\,[-(c+A) \pm \sqrt{D}] \qquad \ldots (4.3.9)$$

where $\qquad D = (c+A)^2 - 4[k+A(c+A)]$

and from (4.3.6) and (4.3.8) we have

$$k(\nu+A) + A^2(c+A) \equiv 0 \qquad \ldots (4.3.10)$$

Now, suppose case III was true. Hence $k < 0$, $A < 0$, $D < 0$. Clearly $A + c < 0$, otherwise D becomes positive. Thus the real parts of the complex roots will be positive, and so the equilibrium point P^* will be unstable in this case. Since cases I and II include a positive root, P^* will also be unstable for these cases. Hence if $k < 0$, then P^* is unstable; that is

$$\alpha < \nu \Rightarrow P^* \text{ is unstable} \qquad \ldots (4.3.11)$$

Now suppose case V was true. Hence $k > 0$, $A < 0$, $D < 0$. Since $c > \nu$, we have $A + c > A + \nu$. Thus if $A + c < 0$, then $A + \nu < 0$. But if the identity (4.3.10) is to hold, $(A+c)$ and $(A+\nu)$ must have opposite signs (with neither being zero). Thus $A + c > 0$, and the real parts of the complex roots will be negative, so that P^* will be stable in this case. Since P^* will also be stable for Case IV, we have the result:

$$\alpha > \nu \Rightarrow P^* \text{ is stable} \qquad \ldots (4.3.12)$$

Before discussing these results, let us consider the second model, based on predation of the adult prey, rather than the young:

$$
\begin{aligned}
\frac{dx_1}{dt} &= \alpha\, x_2 - \mu x_1 \\
\frac{dx_2}{dt} &= \mu\, x_1 - x_2\,(\beta y + \nu) \qquad \ldots\ (4.3.13) \\
\frac{dx}{dt} &= y(-\gamma + \delta x_2)
\end{aligned}
$$

Applying the same procedure:

$$\Delta(x_1,x_2,y) = \begin{bmatrix} -\mu & \alpha & 0 \\ \mu & -(\beta y+\nu) & -\beta x_2 \\ 0 & \delta y & \delta x_2-\gamma \end{bmatrix}$$

with $P^* = \left(\frac{\alpha\gamma}{\delta\mu},\ \frac{\gamma}{\delta},\ \frac{1}{\beta}(\alpha-\nu)\right).$

So that $|\Delta(P^*) - \lambda I| = 0$

$$\Rightarrow\ \lambda^3 + (\alpha+\mu)\lambda^2 + \gamma(\alpha-\nu)\lambda + \gamma\mu(\alpha-\nu) = 0$$

$$\Leftrightarrow\ \lambda^3 + c\lambda^2 + k\lambda + \mu k = 0 \qquad \ldots\ (4.3.14)$$

where $c = (\alpha+\mu),\quad k = \gamma(\alpha-\nu)$

Clearly the cases in the table will hold for this model, so that by letting A represent a root of (4.3.14), equation (4.3.9) will hold with the new value of c, and the identity (4.3.10) is modified to give:

$$k(\mu+A) + A^2(c+A) \equiv 0 \qquad \ldots\ (4.3.15)$$

Using (4.3.9) and (4.3.15), precisely the same arguments can be used to show that the results given by (4.3.11) and (4.3.12) hold for this model as well.

What conclusions can we draw from these results? To begin with, we are only concerned with the stability of P^* when x_1^*, x_2^* and y^* are all positive. Hence only result (4.3.12) matters for both models. However note that the bifurcation resulting in the change from stability to instability occurs at $y^* = 0$. Because of result (4.3.11) we can say that the stability of P^* increases with increasing $(\alpha-\nu)$. By shifting P^* further from the y-axis, increasing $(\alpha-\nu)$ also inproves the practical stability of each of the two systems.

Thus the larger the difference between the prey birth rate and the prey death rate (from causes other than predation), the more stable the system in both the stochastic and the deterministic sense of the word.

It is curious that the local stability of P^* remains totally independent of the predation factors (expressed by the parameters β and δ) for both models. It is difficult to say whether this would be an inherent property of the predator-prey system, or just a particular quirk of the models - arising because of the special properties of the Lotka-Volterra model, on which they were based.

Using simulation, the authors felt that the first model (4.3.4) tended to promote greater stability than that of the second model (4.3.13). Without considering the non-linear effects, it is obviously difficult to compare these two highly similar systems in the qualitative sense. However note that y^* in (4.3.4) differs from that of (4.3.13) by a factor of μ/ν, so that the stochastic stability due to random environmental fluctuations may be less in (4.3.13) if $\mu/\nu \gg 1$.

Of course, such discrete partitioning into age classes may not always be reasonable. One could consider continuous changes in age within a species by considering a variable time delay before the young reach reproductive maturity (this method can also be used for the discrete case by setting a fixed time delay). The use of time-delays preserves the two-variable population system, but at the cost of more intractable mathematics [see chapter 5].

By considering such variable time delays within a Lotka-Volterra model, Gurtin and Levine (1979) found that when predation was concentrated on the young, the system became destabilized. The authors feel that the instability is more likely to be due to the time-delay than the variable age structure. If this is true, then there need not be a direct contradiction to the results from models (4.3.4) and (4.3.13).

Two other points are worth mentioning here. One is that all the above models which include age structure [as pointed out by Murdoch and Oaten (1975)], tacitly assume that the age distribution is fairly stable. However this assumption is not too unreasonable if the ecosystem has persisted for several generations without having undergone any significant perturbations. The other point is that some ecologists are concerned about the size distribution of a species. As size and age are often (but not always!) highly correlated, this effect may be included into the age structure.

§ 4.4. Logarithmic Models

One of the more annoying features of the various models considered so far is their insolvability, even in the most simplistic cases.

This can be discouraging at times (constant use of numerical integration is not always convenient). However Coutlee and Jennrich (1968) successfully modified the Lotka-Volterra model in such a fashion as to allow for exact solutions, without altering the qualitative or biological features of the original modal in any significant way.

Consider the following system defined in E^0:

$$\frac{dx}{dt} = x\ (\alpha - \beta \log y) \qquad\qquad x,\ y > 0 \qquad\qquad \ldots\ (4.4.1)$$
$$\frac{dy}{dt} = y\ (-\gamma + \delta \log x)$$

Here the internal equilibrium point is given by $P^* = (x^*, y^*) = (e^{\gamma/\delta}, e^{\alpha/\beta})$. It is not difficult to show that this system has exact solutions given by:

$$x(t) = x^* \exp[c_1\sqrt{\delta}\ \cos\ (\sqrt{\beta\delta}\ t + c_2)] \qquad\qquad \ldots\ (4.4.2)$$
$$x(t) = y^* \exp[c_1\sqrt{\beta}\ \sin\ (\sqrt{\beta\delta}\ t + c_2)]$$

where c_1 and c_2 are arbitrary constants defined by the initial conditions. Clearly each trajectory in E^0 will be a periodic closed path, with frequency $w = \sqrt{\beta\delta}$, identical with that of the linearized Lotka-Volterra system. Further, we note that the zero-isoclines are still perpendicular with each other and parallel with the axes.

The only significant difference between the two models would be of a quantitative nature. That is, given a specific situation to be modelled, the two models will obviously yield different numerical values. However in keeping with the spirit of our aims outlined in chapter 1, quantitative disparities will be ignored for the present in the light of their qualitative similarities.

In retrospect, it is not difficult to see why this transformation provides such 'improvements'. Consider the general system (3.2.3):

$$\frac{dx}{dt} = x\ F(x,y)$$
$$\frac{dy}{dt} = y\ G(x,y)$$

For $x,y > 0$, this system can be transformed to:

$$\frac{d}{dt}(\log x) = F(x,y) \qquad\qquad \ldots\ (4.4.3)$$
$$\frac{d}{dt}(\log y) = G(x,y)$$

If F and G are linear polynomials in x and y, then a substitution of log x and log y in these expressions seems natural.

It is perhaps surprising that this paper has remained either forgotten or ignored since it appeared. The idea surfaced on two other occasions; Gomatam (1974) independently considered logarithmic predator-prey models, inspired by the single-species growth equation of Gompertz(1825) given by

$$\frac{dN}{dt} = N(a - b \log N)$$

He proceeded to repeat most of the analysis given by Coutlee and Jennrich, but he also included analysis of a model with mutual interference:

$$\begin{aligned} \frac{dx}{dt} &= x(\alpha - \beta \log y - a \log x) \\ \frac{dx}{dt} &= y\,(-\gamma + \delta \log x - b \log y) \end{aligned} \qquad \ldots(4.4.4)$$

where a, b > 0.

As with the corresponding system (4.1.2), this system's internal equilibrium point P^* is globally stable. The exact solutions are given by

$$\begin{aligned} x(t) &= x^* \exp\,[e^{-\frac{1}{2}(a+b)t} \{\frac{1}{\mu}\,(\eta c_1 - \beta c_2)\,\sin \mu t + c_1 \cos \mu t\}] \\ y(t) &= y^* \exp\,[e^{-\frac{1}{2}(a+b)t} \{\frac{1}{\mu}\,(\delta c_1 - \eta c_2)\,\sin \mu t + c_2 \cos \mu t\}] \end{aligned} \qquad \ldots(4.4.5)$$

where $\mu = +\sqrt{\beta\delta - \eta^2}$, $\eta = \frac{1}{2}(b-a)$, and c_1, c_2 are constants defined by the initial conditions.

Gomatam notes that logarithmic models may become more directly useful with n-species quadratic systems, since they too will yield exact solutions.

Neither of these papers considered the fact that logarithmic models do not allow for x or y becoming zero, and that difficulties arise if they even drop below 1 (where x and y are densities rather than actual population numbers). These difficulties need not be unduly worrisome however, as they can be handled in a fashion similar to that of the constant-harvesting models in §3.9.

On the other hand, Strickfaden and Lawrence (1975) presented the following model:

$$\begin{aligned} \frac{dx}{dt} &= x(j(x) - \beta y) \\ \frac{dy}{dt} &= y(-\gamma + \delta x) \end{aligned} \qquad \ldots (4.4.6)$$

where $j(x) = \alpha + a_1x + a_2x^2 - a_3x^3$.

The authors sought to 'approximate' this model with a logarithmic 'metamodel' given by

$$\begin{aligned} \frac{dx}{dt} &= x(k(x) - \beta \log y) \\ \frac{dy}{dt} &= y(-\gamma + \delta \log x) \end{aligned} \qquad \ldots (4.4.7)$$

where $k(x) = \alpha + a_1\log x + a_2\log^2 x - a_3\log^3 x$.

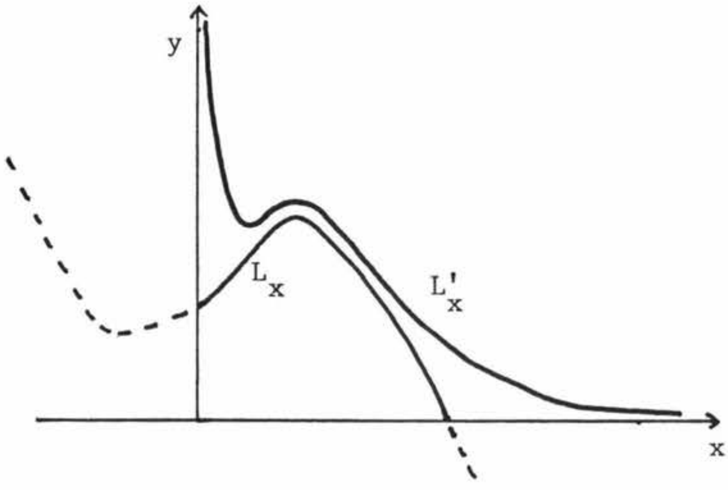

Figure 4.4.1

The prey zero isoclines L_x and L'_x for the models (4.4.6) and (4.4.7) respectively are given in Figure 4.4.1, and it is clear that the two isoclines could be closely matched, but only for a small range of intermediate values of x.

More importantly, the authors are trying to draw qualitative conclusions about (4.4.6) by using this approximation, which surely must be a dubious endeavour based on the shapes of L_x and L'_x. Any trajectories of (4.4.7) approximating either axis in E^0 must differ in nature from those of (4.4.6).

For example, moving the vertical predator isocline to the right will cause the equilibrium point to disappear in (4.4.6); but in (4.4.7), the equilibrium persists in E^0 indefinitely. The authors use numerical integration to demonstrate the existence of a limit cycle in (4.4.6) for an unspecified range of values of the parameters, then assume that this limit cycle will be approximated by a similar one appearing in (4.4.7), so that approximation to its amplitude and period can be made. Such results should be held a bit suspect until analytic support can be provided for these approximations.

§4.5 Stochastic Models

This area will only be covered briefly, though it should be stressed that this is not intended to belittle the importance of such an approach. In fact, most modellers would enthusiastically incorporate random changes in their deterministic models to try and obtain some sort of measure of the practical stability of the system, provided the mathematics did not become too intractable.

Unfortunately, even the simplest stochastic versions of predator-prey systems have proved to be beyond the reach of analytical study to any satisfactory degree. Bartlett (1957) demonstrated this with a stochastic formulation of the Lotka-Volterra model. The model is constructed by setting the probability of an event occurring to be proportional to the corresponding term in the RHS of the deterministic system. So for the Lotka-Volterra system given by (2.2.2) we have:

Event	Probability
$x \to x+1$	$C\alpha x$
$y \to y-1$	$C\gamma y$
$x \to x-1,\ y \to y+1$	$C\delta xy$
$x \to x-1,\ y \to y$	$C(\beta-\delta)xy$

where C is the scaling constant ensuring the probabilities sum to one.

Bartlett investigated this model using simulation, and found that populations often persisted through several oscillations of a well defined cycle, but then suddenly jumped into a different, less well-defined cycle, which was sufficiently erratic to result in extinction of one of the species. He concluded that random fluctuations can be considered destabilizing [in view of our discussions in §3.1, this is hardly surprising].

Jeffries (1974) investigated the stochastic version of the Lotka-Volterra system modified to include logistic growth for both species. In its deterministic form, we know that when such a model possesses a unique equilibrium point P^* in E^0, it will be globally stable. Upon simulating the stochastic model, a curious phenomenon appeared. The trajectories tended to wander in what appeared to be a cycle around P^*. Trajectories rarely meandered outside this cycle to any significant degree due to the strong stabilizing aspects of the non-linear terms in the original deterministic model. Alternatively, brief excursions inside the cycle towards P^* occurred occasionally, and these movements appeared almost random, until the trajectories wandered back into the oscillations again. As might be expected, initial displacements far from P^* frequently lead to the collapse of the system, as extinction resulted before the stabilizing influences could take effect. Jeffries aptly referred to these cycles as probabilistic limit cycles.

Independently, Bulmer (1976) demonstrated that this would be the case if stochastic variation was introduced to a stable equilibrium point, provided that stabilizing mechanism was not too weak.

Others to explore randomised deterministic models include Billard (1977), Smeach and Rust (1978), and Bécus (1979 a,b), though their work is rather mathematical in nature, and does not explore any possible biological implications. Attempts to invoke statistical mechanics into ecological modelling by Leigh (1968), Samuelson (1971), and Goel et. al. (1971) also suffer from this drawback.

§ 4.4 Other Models

Occasionally a modeller may wish to explore a particular facet of a system which requires an alternative mode of expression in the model equations. For example, up to now we have assumed that the fractional response of the predator to prey density is just that - a response totally dependent on prey density. However, De Angelis et. al. (1975) have raised the point that mutual interference amongst predators will not only affect the predator population density, but also their predation rate. What is being suggested, then, is that the total response will decrease through both the slow changes in predator density (numerical response) and through the faster changes in the predation rate (functional response). Thus, let us consider the functional response to be a function of both x and y. Consider the following model:

$$\frac{dx}{dt} = x[\alpha - ax - \frac{ky}{wx + y + d}]$$
$$\frac{dy}{dt} = y[-\gamma - by + \frac{ekx}{wx + y + d}] \qquad \ldots (4.6.1)$$

Generally this system displays a unique equilibrium point $P^* = (x^*, y^*) \in E^0$, though there are special cases where up to three equilibria can appear in E^0. Assume that P^* is unique, and set $b = 0$ for the time being. The authors used Kolmogorov's Theorem to investigate the model (in a commendably thorough fashion!).

To establish the stability properties of the system, the parameter k was chosen (others could have been used equally successfully) as the pivot around which the other parameters are varied to observe changes in the system. The following graphs were obtained:

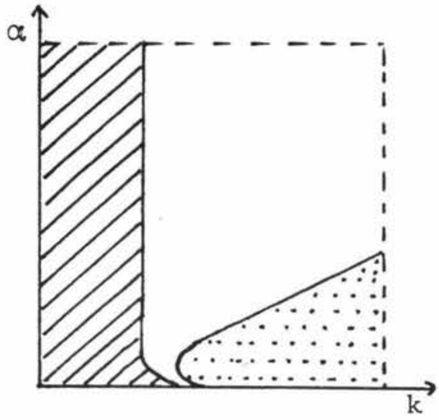

Figure 4.6.1

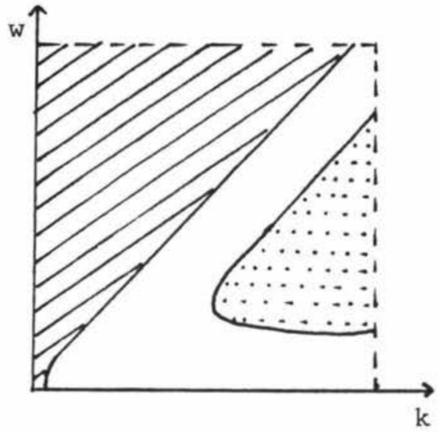

Figure 4.6.2

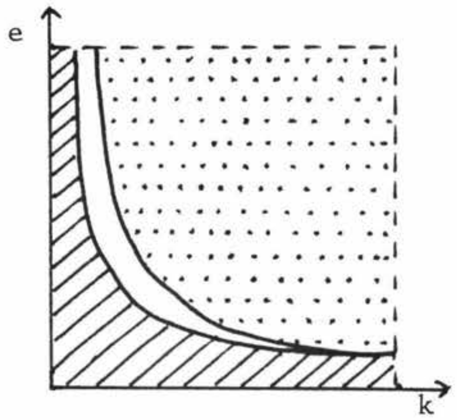

Figure 4.6.3

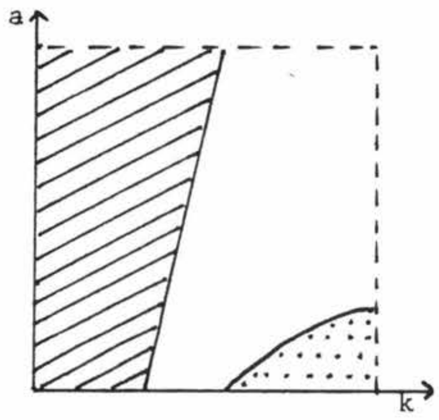

Figure 4.6.4

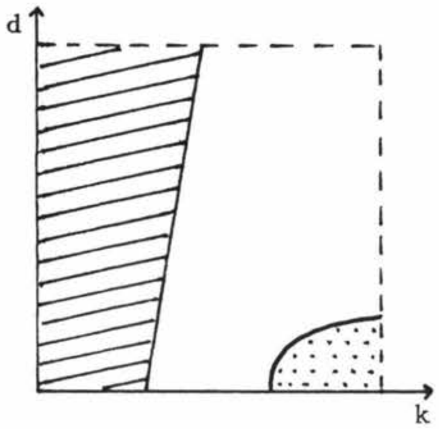

Figure 4.6.5

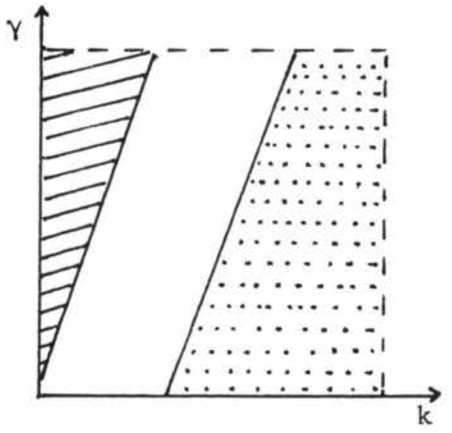

Figure 4.6.6

Throughout Figures 4.6.1 - 4.6.6, the cross-hatched areas indicate when the equilibrium point P^* does not lie in E^0, so that the predators are driven to extinction; the blank areas indicate when P^* is globally stable; and the dotted areas indicate when P^* is locally unstable, but surrounded by a stable limit cycle. Note that where two certain parameters are being varied as above, the others in the system are automatically fixed at certain values. Obviously if these values were altered, then the graphs above would also change.

The point that is being made here is the need for caution when performing sensitivity analysis with small perturbations in the parameters. For example, consider Figure 4.6.2. For k sufficiently large and fixed, we can vary w so that P^* is initially asymptotically stable (w very small), becomes unstable (w at an appropriate intermediate value), becomes stable again (w raised further), until finally w is sufficiently large that P^* disappears from E^0. Clearly a small perturbation in w will not tell us whether the result is stabilising or not overall.

De Angelis et. al. arrived at several conclusions:

(i) Increasing the feeding rate k tended to increase the range of other parameters for which a stable limit cycle exists.

(ii) The y term in the denominator of the functional response term is apparently the major stabilising influence, as far as the interactions between the two species goes.

(iii) In real life predator-prey systems, especially those involving insects, it is often true that $k \gg \alpha$. However, insect control by predation or density-dependent mortality would very likely stabilise such systems, preventing limit cycle behaviour.

(iv) Increasing b above zero, while ensuring that Kolmogorov's criteria are not satisfied any longer, was found to increase both the local stability of P* and the global stability of the system.

Finally the authors stress the point that there are a large number of parameter combinations still unconsidered for this model, and that perhaps more ecosystem models should be subjected to this rigorous sort of analysis.

Others to vary the traditional approach towards the functional response include Watt (1959), who modified both a type II and type III response.

$$\begin{aligned} &\text{type II:} && g(x,y) = k[1 - e^{-cxy^{1-b}}] \\ &\text{type III:} && g(x,y) = k[1 - e^{-cx^2y^{1-b}}] \end{aligned} \qquad \ldots (4.6.2)$$

where $0 < b < 1$.

Goswami and Lahiri (1979) modified the type II response given by (4.2.9) in a Lotka-Volterra model with logistic prey growth:

$$\begin{aligned} \frac{dx}{dt} &= \alpha x(1-x/k) - \beta x^m y^n \\ \frac{dy}{dt} &= -\gamma y + \delta x^m y^n \end{aligned} \qquad \ldots (4.6.3)$$

where $m, n > 0$. To ensure Kolmogorov's criteria were satisfied, further restrictions on these parameters were necessary:

$$n < 1, \ (m+n) > 1 \qquad \ldots (4.6.4)$$

As a result, it was found that a limit cycle solution existed for sufficiently large values of K. This is not entirely unexpected, since the prey isocline is humped and the predator isocline has positive slope.

Pearce (1970) argued that satiation may be present whether the prey density is large or not, depending on how high the relative predator density was. Hence a model was presented where the interaction terms were given as functions of the ratio $z = y/x$:

$$\begin{aligned} \frac{dx}{dt} &= x[j(x) - f(z)] \\ \frac{dy}{dt} &= y[k - g(z)] \end{aligned} \qquad \ldots (4.6.5)$$

where $j(x)$ is the natural prey growth rate, allowing for intraspecific competition.

k is the natural predator growth rate, given the prey are abundant.

f and g are positive, monotonically increasing functions, with $f(0) = 0$ and $g(0) = 0$.

Further assumptions are made:

$$f(z) = cz \text{ for small } z; \quad j(x) = \alpha \text{ for small } x \qquad \ldots (4.6.6)$$

where $c, \alpha > 0$ are constants.

Pearce proved that for sufficiently large x, oscillatory behaviour appeared in E^{θ}; whereas for smaller values of x, the populations either both died out or both increased.

It is a shame that this idea has not been followed up, and comparisons made with those models using more conventional functional responses. This essentially deterministic model is probably not well known, as it appeared in an applied statistical journal!

5 VARIATIONS ON TIME AND SPACE

§5.1 Time Delays

When a particular event occurs, the appropriate response by dependent variables may not appear immediately. That is, a certain response observed at present may be entirely (or partially) dependent on the state of the system at a certain time in the past. References to such time delays (or time lags) within ecosystem dynamics have already been made in past chapters.

Delays appear in a variety of ways. The most obvious examples appear through seasonal variation. Consider, say, a species which thrives only in summer, and lays eggs which keep throughout the winter, until next spring. Clearly the effects of particularly bad weather during egg laying will not be apparent until the next season. With such cases where the generations are non-overlapping, it is generally accepted that modelling with difference equations is preferred, and so need not concern us.

More directly related to predator-prey systems, delays occur within the act of predation in the sense that predators will not be hunting for prey while they are either handling the prey or when they have just devoured prey, as they probably will not be hungry. These delays can often be incorporated into the functional and numerical responses of the predators to prey density.

The most important delays occur through migration within a heterogenous environment, or as a direct result of the age distribution of either species. With the former, often significant time is spent in travelling from one patch to another [see §5.2] . With the latter, it is clear that for most species,a certain amount of time must elapse before reproductive abilities appear; and predators will require time to learn how to hunt.

The question of stability is not straightforward, particularly as the existence, persistence and magnitude of time delays in field studies have been difficult to determine. Cushing (1977b) suggested that delayed responses of a population to its own density are likely to be destabilizing. For example, if a food supply became seriously depleted, the population may continue to grow over the delay period until it is too late to preserve more than a small proportion of its population.

By contrast, delays involved in predation are generally considered stabilizing as they frequently allow the escape of other prey over the delay period.

Further qualifying is necessary, though, as Maly's(1969,1978) experiments suggest this type of delay tended to destabilize with respect to the predators.

Utida (1957) observed very regular oscillations in his experiments with the braconid wasp / boll weevil system. The wasp lays eggs in the weevil larvae, and the weevil is ultimately consumedby the larval wasp (although technically a host-parasite interaction, all the attributes of a predator-prey system were there as the weevil was actually killed by the wasp). Clearly this system has a built-in time lag as the effects on the adult population size of the weevils are not felt until the next generation. Utida noted that the amplitude of the oscillations depended more on the size of the delay than on anything else. Caswell (1972) also found this to be the case when simulating a three species model.

MacArthur (1970) argued for instability, using graphical analysis. Looking at the vector field close to an equilibrium point in E^o, the vectors will point in the direction they would have a pointed a time τ ago, where τ is the time delay. This may be enough to alter the stability, or at least increase the instability, of the equilibrium point.

There are a variety of ways in which a time lag can be introduced into a differential equation model. To begin with, there are two classes of delay:

(a) Discrete Lag - where τ is a fixed constant representing the lag, so that the equation will have the form:

$$\frac{d}{dt}[Z(t)] = F[Z(t), Z(t-\tau)]$$

(b) Continous Lag - where the effects are felt over all the values of Z on the interval from $(t-\tau)$ to t, so that the equation has the form:

$$\frac{d}{dt}[Z(t)] = F[\{Z(\theta): t-\tau \leq \theta \leq t\}]$$

Historically, it had been generally accepted that Hutchinson (1948) and Leslie (1948) were the first to include such time delays in equations modelling population dynamics. More recently, however, Scudo (1971) and Caswell (1972) pointed out that Volterra had worked extensively with such delays as early as 1931, and that these papers simply had not appeared in translation (this has since been rectified by Scudo and Ziegler (1978)).

Volterra modified his own predator-prey model to include a continuous delay in the following way:

$$\begin{aligned}\frac{dx}{dt} &= x(t)[\alpha - \beta y(t) - \int_{-\infty}^{t} F_1(t-s)y(s)\,ds] \\ \frac{dy}{dt} &= y(t)[-\gamma + \delta x(t) + \int_{-\infty}^{t} F_2(t-s)x(s)\,ds]\end{aligned} \qquad \ldots(5.1.1)$$

Thus the impact on each species of the entire past history of the other is expressed by the last terms of each equation.Clearly the limits of integration can be altered to τ to represent short 'memories' if desired.

Volterra was able to conclude, after extensive analysis (a great deal of theory on such integro-differential equations was developed by him), that system (5.1.1) has unique, positive solutions $x(t)$, $y(t)$ which will oscillate indefinitely when not resting on an equilibrium point. Furthermore, it was shown that no periodic solutions exist. Cushing (1977a) has shown that (5.1.1) is generally unstable (the equlibrium point in E^o is only stable in a special, structurally unstable case). It is also shown that even when the delay is small, the equilibrium remains unstable.

Wangersky and Cunningham (1957) appeared to have offered the first predator-prey model with a discrete lag incorporated into the differential equations:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x(t)[1 - x(t)/K] - \beta x(t)y(t) \\ \frac{dy}{dt} &= -\gamma y(t) + \delta x(t-\tau)y(t-\tau)\end{aligned} \qquad \ldots(5.1.2)$$

This is a Lotka-Volterra system with logistic prey growth and a fixed delay in the predator response to both the prey density and its own density. For low values of τ, the equilibrium point in E^o is stable, but as it increases , it becomes unstable. For still higher values of τ, limit cycles might appear. More comprehensive analysis of this model was given by Goel et al (1971).

May (1973) highlighted the dangers of considering only two-species models by comparing the effects of time lags in two- (herbivore plant and carnivore-herbivore) and three- (carnivore-herbivore-plant) species systems. If a two-species system has a potentially stabilizing negative feedback mechanism, which is applied with a time delay that is long relative to the natural time scale of the system, then an unstable situation can be expected. But by adding an extra trophic level, the system's time scale can be sufficiently lengthened that the feedback mechanism is now in a position to stabilize the system.

MacDonald (1976,1977) presented two convenient ways of expressing systems such as (5.1.1) as a set of three ordinary differential equations, which provided for easier bifurcation analysis. This method was expanded by Kapur and Khan (1978).

Arditi et al (1977) found qualitative behaviour similar to that of (5.1.2) when a discrete lag was introduced into the predator death rate.

Strebel and Goel (1973), after their discussion on deriving isoclines from experimental data,included a general method for detecting time delays in a system, with the aid of a general model.

Over the last five years there has been a tremendous surge in the number of papers on time delays in predator-prey systems. A great deal of these include highly involved mathematics, particularly from such authors as Cushing (1976 a,b,c; 1977 a,b,c,d), Leung (1976,1977,1979) and Bojadziev and Chan (1979), and one wonders whether this is not one area where the biologist's claim of lack of communication is justified. Yet the aim for a better understanding of such delays and their effects is laudable; it is almost as if this sudden interest is in response to Oster's (1974) cry a few years earlier:

> "Many ecologists, after paying lip service to the presence of time delays, promptly forget about them. I can't overemphasize what a pain they are, and what a mathematical Pandora's Box they open. They're there in biological systems alright, but mathematicians still don't know much about them."

§5.2 Spatial Heterogeneity And Migration

Until now it has been tacitly assumed that both species are randomly distributed throughout the environment (homogeneous).Thus predation was viewed as a process whereby a predator just happens to bump into its prey and subsequently the prey either escapes or is devoured, depending on the likelihood of capture. Unfortunately such a convenient viewpoint is highly unrealistic in general.

Homogeneous distributions may occur in special circumstances,such as microbial systems in liquid environments.Terrestrial environments, on the other hand, are inevitably patchy. As soil types and plant life vary on the surface, depending on the suitability of conditions, so will the dependent higher trophic levels. Thus temporal variation in the environment is more than likely to produce areas far more favourable to prey survival than others, and one can expect prey aggregation as a result. In this case we say the prey are patchily distributed throughout the environment (heterogeneous).

Variation within the environment is by no means the only source of prey aggregation. Social behaviour, perhaps for defence purposes, may also result in a preference for group structures.

As a result the predation process has to be viewed under a new light. No longer can the predators be satisfactorily viewed as randomly wandering particles hoping to run acrossfood along the way. They must hunt for their food, particularly as prey aggregation usually decreases the likelihood of being discovered (though Wiens (1976) points out that there are documented cases indicating that the prey patches only serve to make them more conspicuous). From this, and the observation that once predators have invaded a patch they may only be able to devour a limited number of prey, it is argued that spatial heterogeneity in prey is stabilizing - but this is not the whole story.

It is the degree of mobility which seems to have the greatest effect on stability in heterogeneous systems.Under pressures from increasing prey numbers within a patch, many prey would either spread further away from the core of the patch (along the lines of a diffusion process), or migrate to another patch, provided they were sufficiently mobile. Ecologists accept that there is a strong relationship between high mobility in prey relative to the predator, and stability of the system. Thus should predators invade a particular prey patch, some prey could escape, and others could return to reinhabit the patch once the predators have departed.

For example, Murdoch and Oaten (1975) cite the study made on mussels on pier pilings in Southern California. The mussels grow in clumps,and are periodically attacked by starfish which not only devour them, but weaken the mussel clump as a whole in the process. Storms or heavy swells will cause these weakened clumps to fall from the pilings, resulting in local extinction of the patch. However, there is a significant time lag before the starfish finally leaves the area where the clump once was, thus allowing time for regeneration of previously devastated clumps elsewhere.

It is the series of experiments conducted by Huffaker (1958) which actually provide some of the strongest evidence to date. In the first series, a set of trays of oranges was exposed. A species of mite which feeds on oranges was introduced into this environment. This series contained three experiments, one where the oranges were adjacent, one where they were randomly placed, and one where they were equally spaced. The mites survived in all three experiments, but thrived best when the oranges were adjacent.

When a predatious mite was introduced into the system, the prey were driven to extinction fairly quickly when the oranges were adjacent. The prey reached much higher numbers, however, and the system persisted longer when the oranges were not adjacent. This suggests that prey survival can be prolonged by decreasing predator mobility (even though prey mobility suffers as well), since it is the predators which must search out and find the prey.

Nevertheless, extinction always resulted, and no oscillations were observed. Huffaker increases the complexity by introducing a maze of vaseline barriers between the oranges, which could not be crossed by either mite. Finally, a means by which only the prey could transport themselves to other areas was incorporated into the system. As a result, this last arrangement produced a series of three predator-prey cycles over a period of eight months (previous to these alterations, none of the predator-prey systems in Huffaker's experiments had lasted longer than 32 days). Thus only in a heterogeneous environment, where the prey had greater mobility than the already highly efficient predators, was prey survival possible. The suggestion that heterogeneous environments are stabilizing should not be surprising since the fate of one patch will be independent of the other patches, and hence the probability of at least a few patches remaining should be high.

We have discussed how a patchy environment will undoubtedly lead to a patchy distribution of prey, but can we expect a similar response from the predators? Generally speaking, the answer is yes. Predators will often concentrate their attack in the denser prey patches. This behaviour is frequently referred to as the aggregative response to prey density, and is considered to generate a type III response in predation. Many feel that this is yet another stabilizing feature of heterogeneity, since the less populated patches do not receive the brunt of the attack.

St. Amant (1970) attempted to investigate the stabilizing potential of spatial heterogeneity by presenting a two-patch system, with inter-patch migration, using Lotka-Volterra systems for each patch:

$$\left.\begin{aligned}\frac{dx_1}{dt} &= \alpha_1 x_1 - \beta_1 x_1 y_1 + A x_2 \\ \frac{dy_1}{dt} &= -\gamma_1 y_1 + \delta_1 x_1 y_1 + B y_2\end{aligned}\right\}\text{ system 1}$$

$$\ldots(5.2.1)$$

$$\left.\begin{aligned}\frac{dx_2}{dt} &= \alpha_2 x_2 - \beta_2 x_2 y_2 + C x_1 \\ \frac{dy_2}{dt} &= -\gamma_2 y_2 + \delta_2 x_2 y_2 + D y_1\end{aligned}\right\}\text{ system 2}$$

where A,B,C and D are all positive parameters representing immigration (note that emigration has been included in the parameters α_1,α_2, γ_1 and γ_2). Assuming that an equilibrium point $P^* = (x_1^*, x_2^*, y_1^*, y_2^*)$ existed in E^o for (5.2.1), St. Amant was only able to suggest that migration was sufficient to ensure that P^* was stable.

Using simulation on a variety of models of the type given by (5.2.1) St. Amant concluded that it is the degree of migration that is crucial. System 1 and system 2 needed to oscillate out of phase, yet be sufficiently coupled by migration as to stabilize the system as a whole, even when small time lags were introduced.

Vandermeer (1973) presented a modelling approach far superior to that of St. Amant's in relation to spatial heterogeneity. The model looks at inter-patch migration over any number of patches, but without requiring details of the predator-prey dynamics.

Let p = proportion of habitats (patches) occupied by predators.
q = proportion of habitats occupied by prey.

Note that p + q may not equal one since some habitats will have both predators and prey and some may be empty.

Suppose we are given an environment where every habitat contains an inherently unstable predator-prey system; that is $p=q=1$ initially and each local system would tend to extinction in time, if there was no migration.

Let λ_1,λ_2 be the migration rates of predators and prey respectively.
μ_1,μ_2 be the extinction rates of predators and prey respectively.

Then the model is given by:

$$\begin{aligned} \frac{dp}{dt} &= \lambda_1 p(1-p) - \mu_1(1-q)p \\ \frac{dq}{dt} &= \lambda_2 q(1-q) - \mu_2 pq \end{aligned} \qquad \text{...(5.2.2)}$$

The extinction of predators is proportional to the number of habitats without prey; and the extinction of prey is proportional to the number of habitats with predators. The first term of each equation demonstrates the way in which the environment can become saturated.

The isoclines of the system are given by:

$$p = \frac{\lambda_1 - \mu_1}{\lambda_1} + \frac{\mu_1}{\lambda_1} q$$

$$p = \frac{\lambda_2}{\mu_2} - \frac{\lambda_2}{\mu_2} q$$

so that there are two possible outcomes. Either the isoclines intersect in E^o, giving a globally stable equilibrium, or they fail to intersect in E^o, and the prey (and hence the predators) become extinct.

Thus the condition for stability is given by:

$$\frac{\lambda_2}{\mu_2} + \frac{\mu_1}{\lambda_1} > 1 \qquad \text{...(5.2.3)}$$

In conclusion then, even where the predator-prey dynamics are unstable, within each patch, the system as a whole can be stable provided that:

(1) the predator migration rate is sufficiently small relative to the prey migration rate;

(2) the predator extinction rate is sufficiently large relative to the prey extinction rate.

Clearly the above results provide strong support to Huffaker's observations based on his experiments. Chewning (1975) was also inspired by these observations, and attempted to be as general as possible by providing a model which considered N habitats, each with its own internal predator-prey dynamics and inter-habitat migration rates.

Using standard linearization techniques and some linear algebra, some results under which stability of the system can be guaranteed, were provided. Unfortunately, no satisfactory biological interpretations of these highly mathematical results were included.

Hastings (1977) borrowed some of the best features of Vandermeer's approachand constructed a more comprehensive model under a structure defined by the following set of rules.

Consider a number of large, identical patches in the environment, where each patch can be in one of three states:

(1) An empty patch can be invaded only by prey, creating a prey patch.

(2) The patch remains in this state until it is invaded by a predator, and the new two-species patch is called a predator patch.

(3) Within each predator patch, it is assumed that the predator-prey dynamics are such that local extinction occurs after a set elimination time, recreating an empty patch.

(4) The invasion rate of the predator is assumed to be directly proportional to the number of patches it currently occupies.

(5) The invasion rate of the prey is taken as being proportional to the number of patches it currently occupies (the sum of predator and prey patches).

Note that while time spent within each patch is held to be important, travelling time from patch to patch is regarded as insignificant (all patches are acceeessible from all other patches).

The time scale is set by normalizing the elimination time to 1. Let x and y be the fraction of prey patches and predator patches respectively. The system can then be expressed by:

$$\frac{dx}{dt} = \alpha\,[1 - x(t) - y(t)][x(t) + y(t)] - \beta x(t)y(t)$$
$$\frac{dy}{dt} = \beta\,[x(t)y(t) - x(t-1)y(t-1)] \qquad \ldots(5.2.4)$$

where $0 \leq x \leq 1$, $0 \leq y \leq 1-x$, and $(x(t),y(t)) = (\Phi_1(t),\Phi_2(t))$ for $-1 \leq t \leq 0$ represent the initial conditions.

Along with the trivial equilibria (0,0) and (1,0), there will be a unique non-trivial equilibrium point P^*, provided $\beta > 1$. Standard linearization techniques were used to obtain the following results, outlined by Figure (5.2.1) (denoting the parameter space).

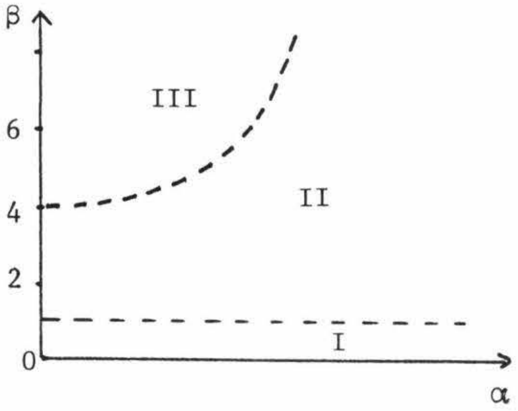

Figure 5.2.1

In region I, P^* does not exist and the predators are driven to extinction. In region II, P^* is locally stable; and in region III, P^* is locally unstable.

Hastings felt that if P^* is stable, then the assumption that the extinction time of predator patches is fixed is not critical, since the system could withstand minor fluctuations in this period.

The model allows for the extinction of predators, a feature omitted by Vandermeer's model. Numerical work indicates that solutions in region II will be globally stable, though nothing has been said about the existence of a limit cycle for solutions in region III. Hastings (1978b) modified system (5.2.4) very slightly (though results were similar), with the intention of investigating a three-species model.

So far we have assumed that a heterogeneous environment implies discrete patches of populations, where the only individuals to be found between patches are those migrating from one patch to another. However, we can go one step further, and promote space to the status of an independent variable along with time. Thus we are now more concerned with the effects of random dispersal of the species in the environment-often referred to as a diffusion process.

Skellam (1951) first developed the basics of the theory for random dispersion of biological populations by applying analytical expressions for molecular diffusion. It is only in the last decade that such an approach has been applied specifically to predator-prey systems. A brief précis of some of the advances made follows, though far more comprehensive surveys have been made by Levin (1976,1978), McMurtrie (1978) and Okubo (1980).

It has been suggested that aggregative behaviour can occur even in basically homogeneous environments. Segel and Jackson (1972) sought to investigate whether random dispersal could alter the stability of a spatially homogeneous equlibrium by comparing two models:

$$\begin{aligned} \frac{dx}{dt} &= \alpha x(1 - x/K) - \beta xy/(x+h) \\ \frac{dy}{dt} &= y(\delta x/(x+h) - \gamma - ay) \end{aligned} \qquad \ldots(5.2.5)$$

and

$$\begin{aligned} \frac{\partial x}{\partial t} &= \alpha x(1-x/K) - \beta xy/(x+h) + \mu\frac{\partial^2 x}{\partial u^2} \\ \frac{\partial y}{\partial t} &= y(\delta x/(x+h) - \gamma - ay) + \nu\frac{\partial^2 y}{\partial u^2} \end{aligned} \qquad \ldots(5.2.6)$$

where (5.2.6) varies in a one-dimensional environment with $0 \leq u \leq L$ and includes the reflective boundary conditions:

$$\frac{\partial}{\partial u}x(0,t) = \frac{\partial}{\partial u}x(L,t) = \frac{\partial}{\partial u}y(0,t) = \frac{\partial}{\partial u}y(L,t) = 0 \qquad \ldots(5.2.7)$$

It was demonstrated that (5.2.6) had a spatially homogeneous, stable equilibrium point, P_s^*, corresponding with the equilibrium point P^* in (5.2.5). But when predator mobility is greater than that of the prey, or when factors such as the Allee effect are introduced, it was discovered that P_s^* in system (5.2.6) becomes unstable, yet P^* in (5.2.5) remains stable.

Murray (1975) demonstrates that when random dispersal is incorporated into the Lotka-Volterra model, only spatially homogeneous equlibria are possible (though Jorné (1977) was able to produce a spatially heterogeneous equilibrium by including cross-diffusion - or random dispersal in two-dimensional space. This included the somewhat implausible assumption that the prey diffuse preferentially towards the predators, and that the predators in turn diffuse away from the prey!)

In general, we conclude that random dispersal is not likely to enhance the neighbourhood stability of interacting populations in a homogeneous environment. A more mathematically formidable problem arises on investigation of dispersal in a heterogenous environment. This is of particular interest with such systems as plankton in the ocean, where the populations are almost totally at the mercy of water movement (the diffusive process), yet can display an amazing degree of patchiness in their distributions (aggregative process). Dubois (1975,1979) and Steele (1974 a,b) have investigated such systems in detail.

Mathematical treatments of such complex systems have become increasingly common in recent times, both in the specific sense [see, for example, Chow and Tam (1976), Rothe (1976), Bhargava and Saxena (1977) and Laplante (1979) incorporating diffusion into simple predator-prey systems such as the Lotka-Volterra model], and in the general sense [Comins and Blatt (1974), Conway and Smoller (1977), Leung (1978) and Cohen et al (1979)].

6 MATHEMATICAL INTERLUDE

§ 6.1 Nonlinear Equations

Most of the results of the last three chapters have been based on the linearization of the models near the equilibria. Clearly the nonlinear effects become stronger the further the population densities stray from the critical points, and they may either reinforce the linear behaviour, or directly oppose it with varying degrees of strength. Further complications can occur if there are several other equilibria and saddle point separatrices in the area.

If we accept the arguments in favour of limit cycles representing the most realistic picture of stability in predator-prey systems, then some knowledge of the nonlinear effects in the model is clearly desirable. As there are no standard techniques available for nonlinear study as forceful as the corresponding linearization methods, modellers frequently use computer simulation to gain some insight into the dynamics.

Over the last ten years attempts have been made to improve the situation using methods originally designed for engineers and physicists. Usually they involve some type of correction factor which is added to the linearized solutions. Montroll (1972) considered general systems where the right-hand sides of the equations were quadratics, by solving the related logarithmic model [see §4.4] in its linear form, then using the solutions to improve the quantitative accuracy of the original model. The Lotka-Volterra model was explored in this fashion.

Grasman and Veling (1973) obtained an asymptotic formula for the period of a Lotka-Volterra system which proved to be accurate even for cycles far from the equilibrium point. Using a different approach, Frame (1974) provided explicit expressions for the solutions of this model in terms of a convergent trigonometric series (deriving an estimate of the sums using Bessel functions) and included the exact period of oscillation. Dutt and Ghosh (1975) applied the Krylov-Bogoliubov-Mitropolsky perturbation technique to the Lotka-Volterra model, obtaining first order corrections to the period. In a similar fashion, Dutt, Ghosh and Karmarkar (1975) applied first order corrections to the Volterra-Gause-Witt model (the Lotka-Volterra model with logistic prey growth). Dutt (1976) sought to improve on Frame's paper by also applying Hamilton-Jacobi theory.

All of the above papers have one thing in common - the application of fairly sophisticated mathematics to improve the quantitative accuracy of models which have long been regarded as qualitatively over-simplistic. For this, and other reasons, ecologists tend to, and quite rightly, criticise these mathematical exercises. Other examples include Varma (1977) and Willson (1980) where exact solutions to the Lotka-Volterra model are provided under the constraint that the prey birth rate and the predator death rate are identical!

This is not to say that improving the quantitative accuracy of such models is a totally futile exercise. Having established that, say, there exists a limit cycle in E^o for a certain model, obtaining estimates of where it might lie in the phase plane with respect to the axes would be important in establishing practical stability. De Angelis (1975) provides reasonably accurate estimate of a limit cycle for a variety of predator-prey systems, based on a cubic approximation of the prey isocline L_x (including the hump and prey protection at low densities).

Even a better understanding of the qualitative effects of non-linear terms can be developed by such techniques. Lin and Kahn (1976) and Brearly and Soudack (1979) used the averaging methods of Krylov-Bogoliubov-Mitropolsky to do this.

§ 6.2 The Lotka-Volterra Model Revisited

Before beginning, it is worth re-reading the quote given at the end of chapter 2. Interestingly, we have found [in chapters 3, 4 and 5] that for one of the most heavily criticised mathematical models in ecology, the Lotka-Volterra model remains extensively used in a variety of modified forms. Certainly it is the simplest of the predator-prey models, and lends itself nicely to the inclusion of other biologically relevant factors.

Let category A represent all the qualities a predator-prey model must include, and category B all those qualities such a model only might require. Given a predator-prey system then, category A of the representative model might include, say, an equilibrium point in E^o, oscillatory behaviour, and a saddle point at the origin with separatrices coinciding with the axes. Category B would include, in general, an endless variety of factors, all of which may, or may not be present in the system, in varying degrees. The Lotka-Volterra model has all the properties listed in A, but few of the optional ones in B.

There are other properties unique to this model. To my knowledge, no other conservative system has been used to model a predator-prey system. Thus we are even provided with a conserved energy constant H, as given in §2.2.

Is it possible that the Lotka-Volterra model represents some kind of foundation, on which all other predator-prey models can be built? In other words, can all other models be treated as perturbations (small or large) of this fundamental model? Clearly the related ecological question asks whether a predator-prey ecosystem can be interpreted as a classical system which has been perturbed through added complexities. Thus, the closeness of a predator-prey system to the classical version could be measured by establishing how close its representative model is to the Lotka-Volterra model.

There is the danger, of course, that we are attaching more credit to the model's flexibility than is really due. As perhaps a first step in support of the rather sweeping general outlook given above, this chapter will indicate just what the potential of a conservative system can be.

Instead of viewing the structurally stable configurations of a model as the rightful centre of our attention, we shall determine under what circumstances structural instabilities can occur. Bifurcation theory then allows us to establish what structurally stable systems lie nearby. This is outlined below.

The space of all dynamic systems representing predator-prey models can be partitioned into 'blocks' of structurally stable [S.S.] systems, whose boundaries consist of all the structurally unstable [S.U.] systems. It has been proven that the set of all S.S. systems is dense in the space of two-dimensional dynamic systems. Thus the probability of a S.U. system appearing in the real-world is zero. It can be viewed more as a transition stage, where a set of parameters defining an S.S. system can be varied in a way that drives the system across the boundary, resulting in a topologically different S.S. system (the transition is termed a bifurcation).

It is convenient to define D, the degree of structural instability of an S.U. system. D will be the largest positive integer k, if an arbitrarily small perturbation can result in a structurally unstable system of degree k-1. Furthermore, we define D=0 for S.S. systems; and it is possible for D to be infinite, or undefined. Using the analogy outlined above, S.U. systems with values of D greater than one can be viewed as lying on junctions of boundaries in the dynamic system space, so that different small perturbations can result in a variety of configurations. A more precise definition of D can be found in Andronov e. a. (1973 b).

Virtually all of the bifurcating systems encountered so far have $D = 1$. A prime example was the frequent appearance of the Hopf bifurcations in systems where enrichment increased the carrying capacity K past the bifurcation point $K = K_c$ [see Figure 6.2.1, representing a local part of the space of dynamic systems].

As K increases and the system is driven across the border in Figure 6.2.1, the actual pathway could be somewhat erratic. These small fluctuations are due exclusively to the stochastic nature of the environment.

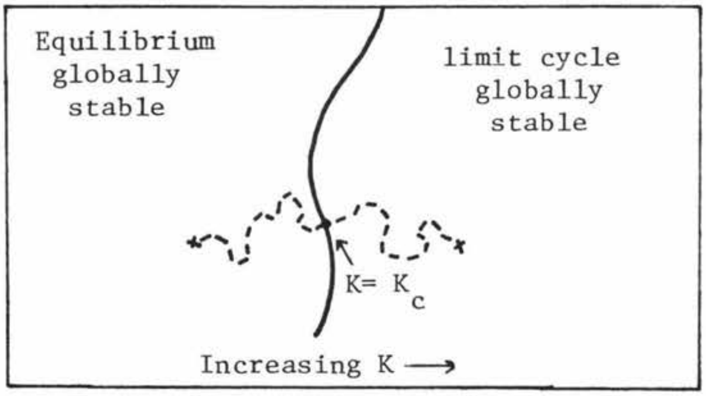

Figure 6.2.1

What, then, of systems with higher values of D? Is there any place for them in ecological modelling? Walker (1978) noted that the data for the lynx/show-shoe hare system indicated a jump from one apparently stable cycle, to another stable cycle with a smaller period. He suggested that more than one limit cycle may be present in its representative model, and that bifurcating systems with higher degrees of structural instability may produce such configurations.

Returning to the Lotka-Volterra model, we find that it does not have a degree of structural instability equal to one (such systems with $D = 1$ were classified by Andronov et. al). Little more about its value of D can be established, though one suspects that it is very high indeed. In effect, this means that an immense range of predator-prey models may lie close to the Lotka-Volterra model in the space of dynamic systems, which may be reached through arbitrarily small perturbations in the right direction. Although qualitatively quite different, these S.S. systems will be quantitatively similar to the Lotka-Volterra system - though the similarity will diminish as the perturbation away from this model increases.

It now starts to become clear how this might strengthen our conjecture at the start of this section. It may be convenient to picture a real-world predator-prey system as having a representative model in our space of dynamic systems. As random environmental fluctuations alter the system, so too does the representative model wander erratically in the dynamical system space. Its closeness to the Lotka-Volterra model would depend largely on how strong any of the effects from factors in category B would be That is, the closer to the Lotka-Volterra model it is, the more strongly it will resemble a classical predator-prey interaction.

There is one further implication arising from this kind of overview. If the representative model lies close to the Lotka-Volterra model, stochastic fluctuations may cause this model to undergo a series of bifurcations in a relatively short space of time, so that the observed dynamics over this period of time may be difficult to pin down.

Establishing the potential versatility of the model is one thing, but determining exactly what its neighbouring systems look like is another. Unfortunately, very little work has been done on conservative systems, so it is difficult to supply an answer.

More specifically, we recall Walker's suggestion that several limit cycles surrounding the interior equilibrium point may be a more realistic representation in some cases. Can an arbitrarily small perturbation of the Lotka-Volterra system lead to this type of behaviour? The answer is yes, and in fact a much stronger theorem, holding for all two-dimensional systems with a centre, is proven in the next section.

Freedman and Waltman (1975 a,b) actually considered general perturbations of this system along similar lines to Freedman's approach to the Kolmogorov model [see §3.2].

$$\begin{aligned} \frac{dx}{dt} &= x(\alpha-\beta y) - \varepsilon f_1 (x,y) \\ \frac{dy}{dt} &- y(-\gamma+\delta y) + \varepsilon f_2 (x,y) \end{aligned} \qquad \ldots (6.2.1)$$

The authors provided criteria for the existence of a limit cycle for this sytem, including a detailed exposition for the special case when the equilibrium point in E^o remains unperturbed for $\varepsilon > 0$.

Lin and Kahn (1976) found that a class of predator-prey models which included general prey growth and a general functional response still involved basic dynamics resembling weakly perturbed Hamiltonian systems (special cases of conservative systems).

An interesting paper from Gatto and Rinaldi (1977) discovered that Volterra's ecological energy constant H (given by the closed paths of the Lotka-Volterra model), was found to be a Lyapunov funcation for a wide range of predator-prey models.

All this is really little more than circumstantial evidence. It is hoped that when more is understood about both the real-world and the mathematical systems involved, the viewpoint that has been outlined may even prove useful. For example, in a discussion following Dubois (1979), an attempt was made to actually maximise the amount of energy 'flow' in a representative model. Using a Volterra-Gause-Witt model, the energy flow was maximised with respect to the carrying capacity K. The maximum was achieved when $K = \infty$, with the system reducing to the Lotka-Volterra model. Moreover, the total average biomass increases as K increases. It would be worth exploring in the near future, exactly to what extent the Lotka-Volterra system can be considered the most 'productive' stage of a predator-prey system.

Andronov et al. have defined a norm on the space of dynamic systems which would provide a measure to establish just how close systems are to the Lotka-Volterra model. A more practical measure may be needed, however. For example, nonlinear correction techniques given in the last section could be used to provide estimates of the expected period of a stable oscillation, to be compared with the actual period observed. A measure could then be defined, based on these comparisons.

Ultimately, it is hoped that a clearer idea of the structure of the dynamic space near the Lotka-Volterra 'point' can be developed, so that combined with the measure outlined above, predictions of the qualitative (and hence quantitative?) behaviour of the system can be made. These predictions could be based on probability distributions placed on the environmental parameters.

§ 6.3 On The Number Of Limit Cycles From A Perturbed System With A Centre

Let (S_0) be a two-dimensional dynamic system with a centre, which without loss of generality may be supposed to be at the origin. Let the Jacobian of (S_0), evaluated at (0,0), be given by

$$\Delta_{S_0}(0,0) = \begin{bmatrix} A & B \\ C & D \end{bmatrix}$$

so that the eigenvalues of the linearized system are

$$\lambda = \tfrac{1}{2}\left[(A+D) \pm \{(A+D)^2 - 4(AD-BC)\}^{\frac{1}{2}}\right]$$

The necessary conditions for (0,0) to be a centre are

$$\begin{cases} A + D = 0 \\ (A+D)^2 - 4(AD - BC) < 0 \end{cases}$$

$$\Leftrightarrow \quad \begin{cases} D = -A \\ BC < -A^2 \end{cases} \qquad \ldots(6.3.1)$$

Further, we assume that $\qquad B < 0,\ C > 0 \qquad \ldots(6.3.2)$

This ensures that the closed paths near the origin run counterclockwise with increasing time.

Let G be a deleted open neighbourhood of the origin such that all trajectories lying in G are closed paths completely contained in G, nested and surrounding (0,0).

Suppose now the system (S_0) is perturbed by rotating the vector field by a small angle $\alpha > 0$, with the perturbed system (S_α) given by

$$\begin{aligned} \frac{dx}{dt} &= \cos\alpha . P(x,y) - \sin\alpha . Q(x,y) = \overline{P}(x,y,\alpha) \\ \frac{dy}{dt} &= \cos\alpha . Q(x,y) + \sin\alpha . Q(x,y) = \overline{Q}(x,y,\alpha) \end{aligned} \qquad \ldots(6.3.3)$$

Note that $\overline{P}(0,0,\alpha) = 0 = \overline{Q}(0,0,\alpha)$, so that the equilibrium point remains unperturbed. Hence the Jacobian of S_α evaluated at (0,0) is

$$\Delta_{S_\alpha}(0,0) = \begin{bmatrix} A\cos\alpha - C\sin\alpha & B\cos\alpha + A\sin\alpha \\ C\cos\alpha + A\sin\alpha & -A\cos\alpha + B\sin\alpha \end{bmatrix}$$

so that the eigenvalues of the linearized system becomes

$$\lambda = \tfrac{1}{2}\left[(B-C)\sin\alpha \pm \left\{(B-C)^2\sin^2\alpha + 4(A^2 + BC)\right\}^{\frac{1}{2}}\right] \qquad \ldots(6.3.4)$$

Clearly $(B-C) < 0$ from (6.3.2), and for α sufficiently small, the term $4(A^2 + BC)$ will be dominant in the square root above. Using the second condition in (6.3.1), we conclude that the equilibrium point (0,0) is a focus in (S_α).

Let M be any point in G. For the system (S_0), there will be a unique close path L_0, passing through M, with direction vector $\underset{\sim}{m}$ at M, say.

Lemma 6.3.1 The field vector $\underset{\sim}{m}_{\alpha}$ at M in the perturbed system (S_{α}) is directed into the interior of the closed path L_0.

Proof Let F(Q,P) be the direction of the vector field at any particular point on the closed path L_0 in the system (S_0), and let $\overline{F}(Q,P,\alpha)$ be the direction of the vector field at the same point for the perturbed system (S_{α}). Then

$$F(Q,P) = Q/P$$

and
$$\overline{F}(Q,P,\alpha) = (Q\cos\alpha + P\sin\alpha)/(P\cos\alpha - Q\sin\alpha)$$

Define the change of slope due to the rotation of the vector field as

$$W(Q,P,\alpha) = \overline{F}(Q,P,\alpha) - F(Q,P) = (P^2 + Q^2)\sin\alpha / P(P\cos\alpha - Q\sin\alpha)$$

Now the closed path L_0 can be partitioned into six parts, and M must lie in one of them:

$Z_1 = \{$ points in L_0: $P=0$ $\}$
$Z_2 = \{$ points in L_0: $P < 0,\ Q > 0$ $\}$
$Z_3 = \{$ points in L_0: $P < 0,\ Q < 0$ $\}$
$Z_4 = \{$ points in L_0: $P > 0,\ Q < 0$ $\}$
$Z_5 = \{$ points in L_0: $P > 0,\ Q > 0$ $\}$
$Z_6 = \{$ points in L_0: $Q=0$ $\}$

The partition is illustrated in figure (6.3.1), though it should be stressed that L_0 need not be convex.

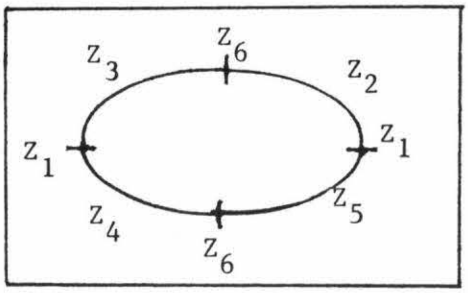

Figure 6.3.1

The following table determines the fate of the direction vector for each member of the partition by comparing signs [either positive (+), negative (-), zero (0), or undefined (und)]. There are four cases omitted from the table as they cannot arise for small values of α.

Part	Q	P	$P\cos\alpha - Q\sin\alpha$	$Q\cos\alpha - P\sin\alpha$	F	$\overline{F}$	W
Z_1	−,+	0	+,−	−,+	und	−	und
Z_2	+	−	−	+	−	−	+
Z_3	−	−	−	−	+	+	+
Z_4	−	+	+	−	−	−	+
Z_5	+	+	+	+	+	+	+
Z_6	0	−,+	−,+	−,+	0	+	+

In every case, it is clear that $\underset{\sim}{m}_0$ is rotated into the interior of L_0.

Lemma 6.3.2 Let L_α be the unique trajectory passing through M in (S_α). Then L_α intersects L_0 exactly once, at M.

Proof Let Γ represent the interior of L_0. Clearly L_α and L_0 intersect at least once at M, say at $t=t_0$ in (S_α). Now suppose L_α intersects L_0 again at some point N (which may or may not coincide with M), say at $t=t_1>t_0$ in (S_α). Without loss of generality, we can assume that time t_1 is the first time L_α intersects L_0 after time t_0. Hence L_α must approach N from within Γ, applying lemma 6.3.1 to M.

Now L_α will pass through N either transversally with respect to L_0 or with an identical direction vector to that of L_0 at N. Since L_α approaches N from within Γ , the direction vector of L_α at N must either be directed to the exterior of L_0 in the former case, or lie tangent to L_0 in the latter case. Either way, lemma 6.3.1 applied to N is directly contradicted. Hence such a point N does not exist.

Using the lemma above, the following result is easily proven.

Theorem 6.3.1 The perturbed system (S_α) has no closed paths in G.

Proof Suppose L^* is a closed path contained in G for (S_α). Let M be any point on L^*. Hence there exists a closed path of (S_0), which passes through M. Since L^* is a closed path, it must pass through M more than once, directly contradicting lemma 6.3.2. Thus no such L^* exists.

We now wish to modify the perturbation in such a way as to actually fix one of the closed paths of (S_0) in G, so that one closed path exists in G for (S_α)

Consider the system (S_0) in terms of polar co-ordinates (r,θ), where the centre lies at $r=0$. Let L be a closed path of (S_0) in G, described by the equations

$$\begin{aligned} r &= \rho(t) \\ \theta &= \chi(t) \end{aligned} \qquad \ldots(6.3.5)$$

Define

$$\begin{aligned} r_2 &= \min\{\rho(t) : t \in \mathbb{R}\} \\ r_3 &= \max\{\rho(t) : t \in \mathbb{R}\} \end{aligned}$$

Then one further restriction can be made. Let L be such that the circle $r=r_3$ is completely contained in G. Then let H be the closed annulus enclosed by the two circles $r=r_2$ and $r=r_3$. Clearly L is the only closed path of (S_0) which is completely enclosed in H.

Let $k > 0$ be an arbitrarily small constant.
Define

$$\begin{aligned} r_1 &= r_2 - (k/2)^{\frac{1}{2}} \\ r_0 &= r_1 - (k/2)^{\frac{1}{2}} \\ r_4 &= r_3 + (k/2)^{\frac{1}{2}} \\ r_5 &= r_4 + (k/2)^{\frac{1}{2}} \end{aligned}$$

Then we can define the rotation of the vector field of (S_0) by the angle $\alpha(r)$ as follows:

$$\alpha(r) = \begin{cases} k & \text{, for } 0 < r < r_0 \\ k - (r - r_0)^2 & \text{, for } r_0 \le r < r_1 \\ (r_2 - r)^2 & \text{, for } r_1 \le r < r_2 \\ 0 & \text{, for } r_2 \le r \le r_3 \\ (r - r_3)^2 & \text{, for } r_3 < r \le r_4 \\ k - (r_5 - r)^2 & \text{, for } r_4 < r \le r_5 \\ k & \text{, for } \quad r > r_5 \end{cases}$$

Basically $\alpha(r)$ can be viewed as a constant (=k) except for values of r approaching the closed path L. At this stage $\alpha(r)$ is scaled down in magnitude in a smooth fashion ($\alpha'(r)$ is continuous in G) so that the system (S_0) remains unperturbed in the annulus H. This can be better viewed in the graph of figure 6.3.2.

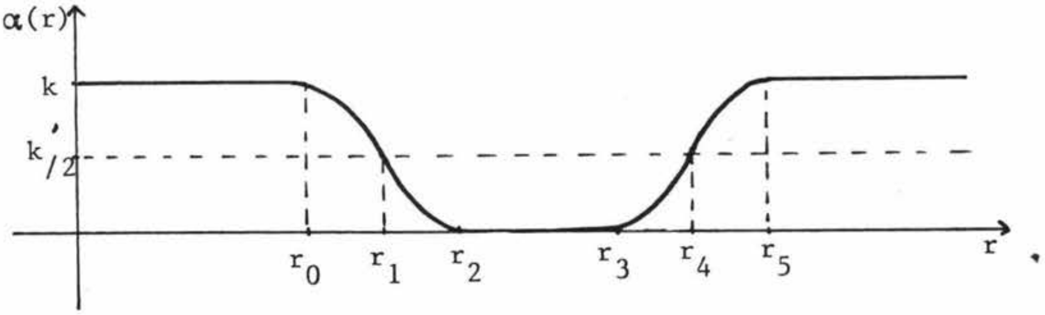

Figure 6.3.2

Theorem 6.3.2 The perturbed system $(S_{\alpha(r)})$ has exactly one closed path in G. This closed path is a semi-stable limit cycle (stable from the outside, unstable from the inside).

Proof Since the entire annulus H remains unperturbed, L will be a closed path for the system $(S_{\alpha(r)})$. Now suppose L^* is a different closed path in the interior of L for $(S_{\alpha(r)})$.

Hence there exists a point M in L^* not in H. Now since $\alpha(r) \geq 0$ for every point in L^*, then lemmas 6.3.1 and 6.3.2 can be applied to each point (where the value of r is fixed), and an argument analogous to the proof of theorem 6.3.1 can be used to show that no such closed path L^* exists and that all trajectories wind into the origin.

A similar argument demonstrates that all trajectories in G outside L will wind into L. Hence the result.

Note that if a stable limit cycle was desired, the same procedure can be used except that $\alpha(r)$ can be set to -k initially. This would result in the same effect except that the origin would be an unstable focus, as indicated by equation (6.3.4). So the modified perturbation angle would be given by

$$\alpha_1(r) = \begin{cases} -k & ,\text{for } 0 < r < r_0 \\ -k + (r - r_0)^2 & ,\text{for } r_0 \leq r < r_1 \\ -(r - r_0)^2 & ,\text{for } r_1 \leq r < r_2 \\ \alpha(r) & ,\text{for } r \geq r_2 \end{cases}$$

Finally, we note that another close path of (S_0) can be chosen such that its furthest departure from the origin is less than r_2. Then the perturbation function could be modified to fix this closed path into $(S_{\alpha(r)})$ as well. This leads to the final, and most important result.

Theorem 6.3.3 There exists a continuous, differentiable perturbation function $\alpha_{n(r)}$ which will rotate the vector field of (S_0) in such a way as to fix n closed paths in G for system $(S_{\alpha_{n(r)}})$, where n is any positive integer. Furthermore, each closed path is a limit cycle which can be set to be stable, unstable or semi-stable.

Proof The first part of the theorem is proven straightforwardly by expanding the argument outlined above, so as to fix n closed paths.

The second part depends simply on the sign of $\alpha(r)$ outside and inside the fixed annulus of the particular closed path.

Returning to the Lotka-Volterra model then, this result clearly has important implications as far as Walker's suggestion goes, particularly as the open set G is the entire first quadrant of the phase-plane.

It should be stressed that such an artificial perturbation as $\alpha(r)$ is used only to prove the possibility of such behaviour, not to suggest that this specific perturbation could arise in natural circumstances.

7 APPLICATIONS

§7.1 Harvesting

A natural application of the theory developed so far in resource management would be the harvesting of a species in a predator-prey system. When it is the predator that is desirable, the need for prey in the system is obvious. Yet if it is the prey that is harvested , it is not immediately clear why the predator should be allowed to remain. Talbot (1978) discusses the role of predator in such systems, pointing out that their existence does more than just keep the average prey yield down.

Destroying any part of a food chain is dangerous, and the consequences of such an action should be well thought out beforehand. More specifically, predators play a selective role, weeding out the weaker prey, and so improving their overall fitness. Furthermore, predation stabilizes the prey populations in the sense that the magnitudes of the oscillations of the prey population are restricted to practically stable regions.

Until recent times, practical studies on harvesting situations were generally applied only to the single species in question. In a resource management system with only one species, whose food intake can be controlled with some degree of accuracy, a single-species model is all that is really necessary. However, situations where species interactions are prevalent and, even worse, the dynamics of which are unknown, indicate the need for a more comprehensive approach.

This need was outlined in some detail by May et al (1979), where the concept of maximum sustainable yield (MSY) as applied to a single species of fish was found to be insufficient for the purposes of safe-guarding the stock available. A suggestion was made that these safe-guards may be better based on multi-species considerations, and by using two and three species models representing krill, baleen whales and seals in the Southern ocean, the following points were made.

For the populations at the top trophic level of an ecosystem (the highest level predator), single species considerations such as MSY remain useful. For other species however, stocks must be kept at such a level as to ensure that no significant reductions of other populations dependent on it occur. An appropriate criterion for this 'significant reduction' would be difficult to obtain, though one possibility would be to set proportion levels on the other populations which would represent lower bounds. It was noted that time scales vary amongst the different species, and that the slowest time scale (often set by the highest level predator) should be used when monitering an ecosystem from the management viewpoint. Finally, it was stressed that economic and political factors cannot, and should not, be ignored (and could even be incorporated into the models).

Given the above guidelines, can we utilize the theory given in §3.8 more specifically? We are essentially interested in the yield, and this is usually derived as some function of effort. This effort is applied in such a way as to maximize the yield, provided the ecosystem does not suffer either in the short-term (practical stability) or in the long-term (asymptotic stability). Since the effort is frequently measured in terms of several system parameters, the discussions on the potential dangers of parameter variation are clearly relevant.

Legović et al (1979) investigated two particular predator-prey models with optimum harvesting in mind. Using proportional harvesting of predators, it was discovered that optimal harvesting rates did exist. Interesting was the fact that even when the unharvested model was practically stable, it was capable of losing this stability when harvested at the MSY level, regardless of the asymptotic stability of the system. As one might expect, enrichment tended to increase the MSY of the predators. However, the MSY tended to decrease in average value when random environmental fluctuations were introduced. This suggests that the true MSY may actually be smaller than the deterministically calculated value. Furthermore, the variations in the observed MSY would probably fluctuate with a greater amplitude.

The concept of controlling effort to maximize yield can be generalized, coming under the heading of control theory. The potential applications are much wider, and are discussed in the next section.

§7.2 Control Theory

The concept behind control theory is a simple one. Given a system and a desired result as a target, the system is modelled, the parameters which can be controlled are identified , and the model is treated as an optimization problem - the optimum with respect to the control parameters representing the target solution.

It seemed only natural that once models used in the physical world were transferred and adapted to the ecological world, control theory would not be far behind. Of course the major obstacle to such applications is the lack of accurate mathematical models of the dynamics of an ecosystem. Nevertheless, several attempts to investigate the use of control methods have been made.

Goh et al (1974) used the Lotka-Volterra model to initiate preliminary studies on pest control, using a variety of approaches. Four different methods involving pesticides and predation were investigated, and it is worth briefly discussing them in turn:

(i) Control by an ideal pesticide

By ideal, it is meant that the pesticide (chemical or biological) kills only the prey (pests), leaves no residue, and destroys the pests in a density-dependent manner. Let the control variable u(t) represent the rate of application of the pesticide at time t. Then this can be applied to the Lotka-Volterra model to give

$$\begin{aligned} \frac{dx}{dt} &= x(\alpha - \beta y) - b_1 ux \quad (b_1 > 0) \\ \frac{dy}{dt} &= y(-\gamma + \delta x) \end{aligned} \qquad \ldots (7.2.1)$$

Since the equlibrium point $P^* = (\gamma/\delta, \alpha/\beta)$ of the original Lotka-Volterra system was found to be desirable in the sense that the pest population remains constant, this was set as the target. That is, a control mechanism was set up numerically so as to drive the trajectories to P^* in the most efficient manner (in this case a cost function was minimized based on the cost of the pesticide and losses through crop damage by the pests).

(ii) Control by insecticides which kill only predators

Although an unusual notion, the rationale behind the use of such an insecticide is based on the qualitative behaviour of the system. That is, the insecticide could be used to reduce the predator population at a particular stage in the cycle so as to prevent a subsequent collapse of the predators, and hence an outbreak of the pests.

The target, the cost functions and the control variable are the same as in (i) except that the system is now written as

$$\frac{dx}{dt} = x(\alpha - \beta y)$$
$$\frac{dy}{dt} = y(-\gamma + \delta x) - b_2 uy \qquad (b_2 > 0) \qquad \ldots (7.2.2)$$

(iii) Control by insecticides which kill both predators and prey

Assuming no residue is left behind (otherwise a third differential equation would be necessary), the following system can be discussed.

$$\frac{dx}{dt} = x(\alpha - \beta y) - b_1 ux$$
$$\frac{dy}{dt} = y(-\gamma + \delta x) - b_2 uy \qquad \ldots (7.2.3)$$

(iv) Control by releasing predators and prey into the system

It is stressed that up till now, the threat to health by use of pesticides have been ignored in the cost function. This is why an alternative approach such as this should also be considered. The authors note at the time of writing about 300 cases of successful biological control had been reported, all involving the release of predators only.

It was felt that the release of pests at the right time may actually lower the overall population of the pests in the future, using the argument that such a measure may prevent a collapse of the predator population.

Thus using u(t) and v(t) as the control variables representing the rates of release of prey and predators respectively, the following system was considered.

$$\frac{dx}{dt} = x(\alpha - \beta y) + u$$
$$\frac{dy}{dt} = y(-\gamma + \delta x) + v \qquad \ldots (7.2.4)$$

The Lotka-Volterra model was found to be suitable, in the sence that all the results obtained were plausible from a biological viewpoint. Each method appeared most efficient in differing circumstances, suggesting the control of pest populations by using a rational combination of all possible procedures available.

In conclusion,the authors stated the following possible guidelines. Given that the system is not already resting at a steady state, and that P^* is a desirable target, then

(a) If both the predator and the prey population are low, then method (iv) should be used with v(t)=0 and u(t) set to the maximum allowable level.

(b) If the predator population is low, but the prey population is increasing, then method (iv) is best with u(t)=0 and v(t) at its maximum level.

(c) If both populations are high, then the use of a pesticide is probably best.

Walsh (1978) also used the Lotka-Volterra model as a basis for controlling pests with the simultaneous use of both chemical (to inhibit prey growth) and biological (to increase predator growth) agents. However little was added to the results already established by Goh et al above (he did not seem to be aware of their work).

For more specific applications, clearly an improvement in the choice of models is necessary. Wollkind and Logan (1978) studied the possibility of biological control of a spider mite pest feeding on apple tree foliage, by introducing a predacious mite.

A model which included a general type II response was devised, and the predicted qualitative behaviour was found to agree satisfactorily with a simulated model based on extensive field data. Adjustments were made to improve the quantitative accuracy, while still preserving the qualitative behaviour.

The control parameters, having been estimated using the data available, were then varied in a somewhat hit-or-miss style until desirable phase-plane plots were obtained, with the idea that growers could plan control strategies which best suited them.

While the importance placed on the qualitative dynamics of the system is to be applauded, clearly the trial-and-error method used should be improved upon - particularly as the qualitative behaviour had to be rechecked at each new trial. A knowledge of the structure of the system and its bifurcation points would be far more helpful, and would also point out the danger areas where random environmental fluctuations could alter the dynamics in a fashion undesirable for the grower. This general approach is outlined in the next section.

§7.3 A General Approach

Ideally, given a management system which utilizes the features of both simulation and knowledge of the dynamics, one should be able to find a practical optimal policy. An outline of the systems analysis approach was given in §1.2, so some sort of guideline on the use of theoretical models is required. If the model involves the use of differential equations, then the following approach could be used.

(a) Model - This can either be done totally on a conceptual basis, or previously collected data could be used as an aid. Certainly the data would be used for parameter estimation.

Once the qualitative behaviour of the model seems to match that of what is observed, small adjustments can be made so as to improve the quantitative accuracy, ensuring that the structure of the model does not change in the process.

(b) Identify transitions - By this, it is meant that all the structurally unstable configurations given by the bifurcation values of specific parameters should be identified. If the system has only one or two dimensions, then phase-plane diagrams of these transitions could be provided.

Noting where the transitions occur, the resource manager could then select the structurally stable configuration which seems most appropriate. The criteria for this selection will clearly depend on the system and on the facilities available. If the selection proves to be impractical (for example, if the control parameters cannot be varied to obtain this configuration, or if it is uneconomical), then the next best configuration can be chosen.

(c) Optimize - Using the techniques provided by modern control theory, an optimal policy can be determined. Note that the constraints will also include the requirement that once the qualitative behaviour desired is obtained, it stays there! Hence probability distributions have to be attached to the parameters to ensure that this is likely to be the case. Further constraints will be included to allow for practical stability as well.

(d) Compare results - If the optimal policies given by this do not differ to any great extent from those given by systems analysis, then these policies can be used with some grater degree of confidence. If the difference is marked, however, then a certain degree of caution will be necessary before employing the systems analysis. Obviously the situation would improve if the exact reason as to why they differ could be pinpointed and discussed.

§7.4 Applications In Related Disciplines

Since predator-prey ecology has at its core the theme of 'one population exploiting another', it is not surprising that the established theory is being put to use in other areas. Bell (1973), for example, initiated the first mathematical treatment of the 'immune response' of a body to an infection. His model was developed by establishing the patient's body as the environment, and arguing that once the antigen (bacterial, viral or some other type of infection) has invaded, it begins to fall 'prey' to the antibodies, which are produced in the body as a response to the invasion.

For simplicity, it is assumed that each antibody has only a single site for binding a unit of antigen, and similarly each unit of antigen can be bound by only one antibody.

Let x and y be the concentrations of antigen and the antibodies respectively. Then Bell's model is given by

$$\begin{aligned} \frac{dx}{dt} &= x \left[\frac{\lambda_1 + k\,\lambda_1 x - k(\alpha_1 - \lambda_1)y}{1 + k(x+y)} \right] \\ \frac{dy}{dt} &= y \left[\frac{-\lambda_2 + k(\alpha_2 - \lambda_2)x - k\lambda_2 y - (k\alpha_2/\theta)xy}{1 + k(x+y)} \right] \end{aligned} \qquad \ldots(7.4.1)$$

where θ is the maximum antibody concentration level (carrying capacity).

λ_1 is the growth rate of antigen in the absence of antibodies.

α_1 is the rate at which antigen are bound (hence eliminated by antibodies).

λ_2 is the rate of decay of antibody concentration, given no antigen.

α_2 is the antibody production rate, stimulated by antigen.

k is an association constant, assuming some kind of equilibrium is possible.

It was stressed that this model was only intended to explore some of the underlying mechanisms of such a system. Realistic applications are difficult as estimation of the parameters would involve complex procedures. Furthermore, the model omits two important phenomena - a time lag between antigen infection and antibody production, and the fact that antibody concentrations would be unevenly distributed throughout the body.

Bell primarily considered the local behaviour of the model near the equilibrium point in E^o, using standard linearization techniques. Even so, there was a wide range of behaviour, and the following was concluded.

Once the antibody production was triggered by the appearance of antigen, there were two possibilities. Either the antigen concentration was driven directly to extinction (through random fluctuations), or it was driven sufficiently low that further antibody production was halted. The latter case resulted in typical predator-prey oscillations, the nature of which depended on the difference between the rates α_1 and α_2.

When $\alpha_1 > \alpha_2$, the oscillations increased in amplitude, thus endangering the patient as well as the antigen! For $\alpha_1 < \alpha_2$, the oscillations were damped.

Pimbley (1974a,b) explored the qualitative aspects of Bell's model in tremendous detail, making frequent use of bifurcation theory. A special parameter β was defined as a function of the other five parameters. Most of the seemingly endless variety of configurations possible centred around one critical value of β. At this bifurcation value, the equlibrium value E^o is a multiple focus for $\theta < \infty$; and a centre for $\theta = \infty$.

As α_1 was increased, a critical value was reached, so that for higher values of α_1, the system is destabilized. Similarly as α_2 increased the system stabilized past its critical value. Looking into further secondary bifurcations of the system. Pimbley found that parameter adjustments beyond a certain critical points lead to transitions from asymptotically stable equilibria to limit cycles, which could be interpreted as a sudden worsening in the patients' condition. In some cases, where $\theta < \infty$, multiple limit cycles were found which 'forked' into a finite number of stable cycles, which were thought to represent changes and complications in the course of the disease of the patient. Pimbley (1974c) also investigated a three-dimensional model which included the cells that produce the antibodies within the patient.

Others to use predator-prey models include Allen (1975), who used a stochasticized Lotka-Volterra model to explore the mechanisms of genetic drift in an ecosystem by observing the spread of localized mutations of prey, under diffusion. Noy-Meir (1975) used graphical analysis extensively to investigate modified predator-prey models representing grazing systems (herbivore-plant).

Finally, with increasing concern over the state of the environment becoming apparent, more attention is being devoted to ecological education -

particularly in the schools. While even the simplest predator-prey model requires certain mathematical skills, the mechanism behind the oscillations predicted by the Lotka-Volterra model is straightforward. For this reason, a game developed by Thompson (1979) based on this model, has great potential for allowing school pupils to discover the concepts themselves.

Simple to construct, the game equipment consists of a modified chessboard [as in figure 7.4.1] and a set of counters; black ones representing foxes and white ones representing rabbits.

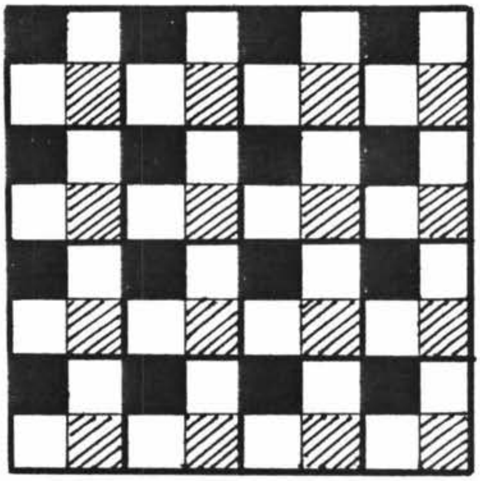

Figure 7.4.1

Starting with 20 of each colour, the counters are thrown at the board (to ensure random dispersalof the counters, they must be thrown quite vigorously, so that raised edges on the side of the board will be necessary). Then the following processes take place in order:

(1) Any fox falling on a black square is deemed to have died, and the counter is removed.

(2) Any rabbit falling on a white square has reproduced so that, the counter is replaced by two white counters.

(3) Finally, pairings of rabbits with foxes are made within the confines of each large square (consisting of four small squares) bordered by thick lines. The rabbit in each pair is considered eaten, and is replaced by a fox.

This particular game is based on the finite difference form of the Lotka-Volterra model given by

$$\begin{aligned} \Delta X &= \frac{1}{2} X - \frac{1}{40} XY \\ \Delta Y &= \frac{1}{40} XY - \frac{1}{4} Y \end{aligned} \qquad \ldots(7.4.2)$$

After each throw (representing a time unit), the resultant populations can be graphed (fox population versus rabbit population, as with a phase-plane plot). Concepts such as oscillations, extinction, population explosions, randomness, choice of initial starting points and equilibria are all well illustrated. The author points out that foxes rarely become extinct using (7.4.2), but that there is no reason why the parameters cannot be varied, or the dynamics increased in complexity by modifying the board.

APPENDIX

Let S be the separatrix from the saddlepoint at (K,0) in E^0, having a positive curvature for all $t > 0$. Furthermore, let L be the line of zero curvature in E^0 for this system. Suppose an arc segment of L from the point P_1 to (K,0) coincided with S.

Let P_2 be any point in the interior of this arc segment, with T as its tangent to S, as in Figure A.1 .

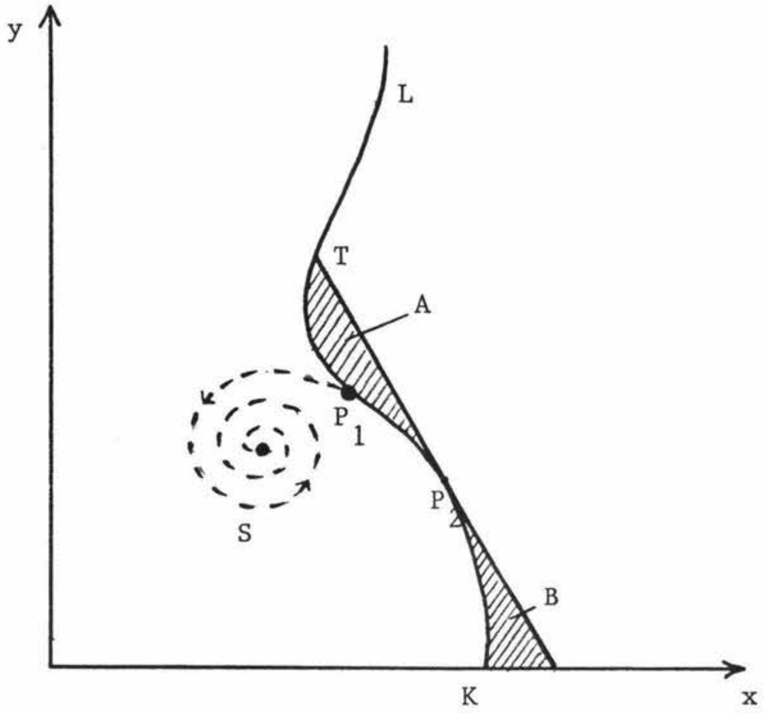

Figure A.1

Let regions A and B be defined as in Figure A.1 . Clearly any trajectory entering B from the right must leave this area and cross L at some point above P_2. This trajectory must have a gradient greater in magnitude than that of T if it is to escape from region B. The steepness of the slope cannot decrease until it crosses L, since it must inflect to do so. Thus any trajectory crossing into area B will not enter area A, as shown in Figure A.2 .

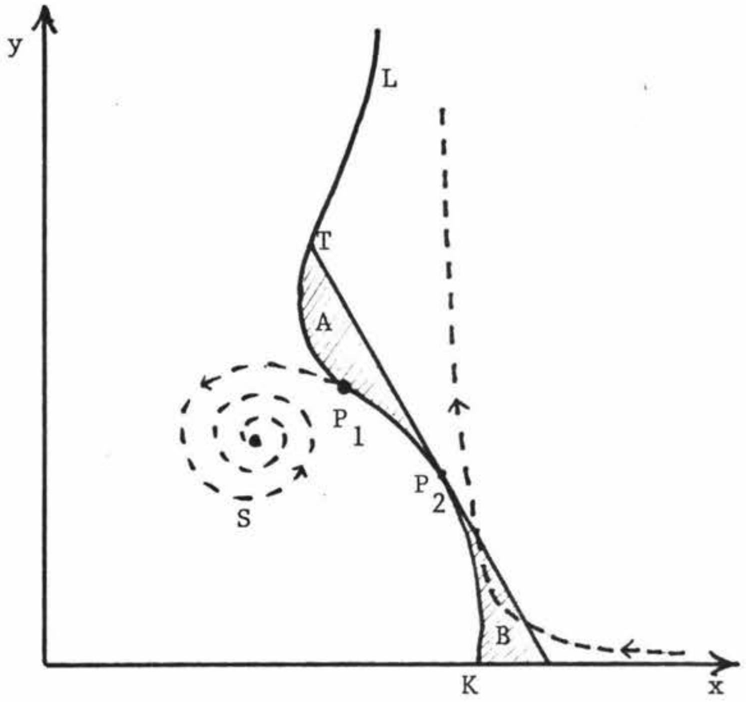

Figure A.2

Hence A becomes a set of points for which no solutions to the system exist ... a contradiction. So the arc segment of L from the point P_1 to (K,0) does not coincide with S.

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