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PREDATOR-PREY DYNAMICS:
A REVIEW

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David Gordon Johnstone
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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.*

*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 bibliography, 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 heterogeneity.

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 representation 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) expresses 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 tractable, 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 equilibrium, the corresponding stochastic model would predict long-term survival, whereas if the deterministic model shows no equilibrium, 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:

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

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 equilibrium 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

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

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.