THE USE OF PARAMETER SPACE IN RESOURCE MANAGEMENT OR LETS STOP THINKING IN TERMS OF EQUILIBRIUM-ORIENTED METHODS

Ray Hilborn

November 1974

WP-74-65

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INTRODUCTION

Environmental management has developed a long tradition of equilibrium oriented methods. The system manager states his goals in terms of a certain desired equilibrium and then manages the system to be as close to that equilibrium as possible. The actual method of management usually involves direct manipulation of system variables so as to push them towards the desired equilibrium.

Most environmental management involves predator-prey systems, largely because many of man's exploitive activities involve the process of predation or harvesting.

Two examples of resource systems in which management has attempted to maintain the system at an equilibrium are the spruce budworm in Eastern Canada, and the Pacific salmon stocks in the U.S. and Canada. The spruce budworm is known to have undergone periodic outbreaks that caused large-scale destruction of economically valuable spruce forests. Over the last 30 years, a great deal of effort has been spent trying to reduce the level of these outbreaks by spraying with pesticides. The managers have attempted to maintain the desired equilibrium, low budworm numbers and high forest condition, by reducing budworm numbers.

In the Pacific salmon stocks, the management strategy has been to maintain the maximum sustained yield of the fish stocks by reducing the number of boats in the fishery and limiting their effectiveness. This approach is basically manipulating the number of boats so as to maintain the fish stocks at some hypothetical, fixed optimum level for producing yield.

In both these examples, the management strategy involves manipulation of state variables to push the system towards a desired point or acceptable region of the phase plane. The theory of the phase surfaces in predator-prey systems has been well examined (Lotka, Volterra, Rosenzweig, and Macarthur), and the concept of stability and resilience was recently reviewed by Holling (1973). Fiering and Holling (1974) have recently described and formalized this approach to environmental management. They describe a formal approach for system management based on cost and values of manipulation of the system to the desired region in the phase plane by manipulation of the state variables. The approach implicit in their treatment is movement of the system over the phase surface, assuming stability of the phase surface over time. An alternative approach is to manipulate the structure of the phase surface itself to let the system move naturally to the desired equilibrium due to the new shape of the surface. This approach involves manipulating parameters of the system instead of state variables. Jones (1973) has considered this problem and used the concept of parameter space instead of state space. He also presents parameter space plots for several systems. This is clearly the logical next step beyond the state variable manipulation approach. We have found in simulation models and real systems that the shape of the phase surface can frequently be altered by a slight manipulation of system parameters.

We shall desribe a simple simulation of a predation system; then produce a parameter surface plotting one parameter on one axis and another parameter on the other. On that surface we define several regions that have similar system properties, for example, predator goes extinct, prey goes extinct, stable equilibrium,stable oscillation, etc. We will show how small changes in parameter values can produce major changes in system dynamics and we suggest that environmental managers consider parameter manipulation as a major tool in management. We believe that this approach will suggest new and hopefully very useful ways of designing environmental management policies.

SYSTEM DESCRIPTION

The simulated predator-prey system we used in this work was modelled after the laboratory predation system involving a mite species which feeds on oranges and another mite species which preys on these herbivorous mites. Huffaker (1958 and later papers) has described the dynamics of this predation system in great detail, and has experimentally manipulated the structure of the environment to examine the stability properties of this system. We believe that our simulation incorporates many of the ecological properties of a hide-and-seek predation system, in which the predatory species must maintain a high rate of dispersal in seeking out new populations of prey. In Huffaker's system the herbivorous mites would disperse from one orange to others and build up large populations on these oranges until a dispersing predator found the population and the predators began to build up and eventually destroyed all the herbivorous mites on that orange. Our model has similar properties. The prey species can exist on 50 food supplies (oranges) and disperse between them. Once an orange is colonized by the prey species, they build up to a carrying capacity (K) and will remain at that level indefinitely unless discovered by dispersing predators. The predators will begin to destroy the prey population on a food supply until all prey individuals have been eaten, at which time the prey population and then the predator population will go extinct on that food supply. The rules of change used in this model for change in numbers of prey on a food supply are:

$\text{Prey}_{t+1} = \text{prey}_t + \text{birth} + \text{immigrants} - \text{deaths} - \text{emigrants}$

$\text{Births} = \text{prey} * \text{prey birth rate } ((K-\text{prey})/K)$

$\text{Deaths} = \text{number of predators} * A,$

where A is the number of prey eaten by each predator per unit time. The number of deaths cannot be greater than the number of prey.

Emigrants = prey * emigration rate of prey

Immigrants = (ND * SDY)/NCELL

where

ND = number of prey dispersing from all cells at this time period,

SDY = the probability that a dispersing prey will reach a new cell,

NCELL = number of cells to which individuals may disperse; in this case 50. When the total number of dispersing individuals is small, then the individuals are randomly assigned to the cells.

The rules of change for the predator species are as follows:

$$\text{Predators}_{t+1} = \text{predators}_t + \text{births} + \text{immigrants} - \text{deaths} - \text{emigrants}$$

Births = NF * birth rate

where NF is the number of predators which find food. Which is number of prey/A or number of predators, whichever is less.

Deaths = number of predators - NF

Emigrants = predators * predator emigration rate

Immigrants = (NDD * SDD)/NCELL,

where

NDD = number of predators dispersing from all cells at this time period,

SDD = the probability that a dispersing individual will survive.

These are the rules of change for each cell. Dispersal between cells may be viewed as a fixed proportion of individuals taken off in a random flight. A proportion of these (SDY for prey and SDD for predators) survive and actually reach a new cell. When a prey individual reaches an empty cell, it immediately begins to reproduce and multiply according to the above rules. (The implicit assumption is made that all individuals are capable of asexual reproduction.) Predator individuals will die if they land on a cell with no prey species or they will immediately begin to multiply and wipe out the prey if the cell has been previously colonized. Other implicit assumptions in this model are

(1) there is no density dependent dispersal. It would probably be more realistic to assume that once a predator population has eliminated the prey on a cell all the predators on that cell would disperse instead of dying;

(2) prey species do not wipe out their food supply, rather it is a constant quantity with a fixed carrying capacity;

(3) dispersal is random. There is no effect of distance between individual cells; and

(4) the predators will always eliminate every prey in a cell. There are no refuges for prey except dispersal between cells.

Although this is a very simple model and is clearly not a complete representation of even Huffaker's laboratory system, it does represent many of the ecological properties of many predator-prey systems in nature.

TYPES OF OUTCOME

There are three general categories of outcomes from this model. (1) Long-term oscillation; (2) relatively stable conditions, and (3) either predator or prey is eliminated. Figure 1 illustrates a relatively long-term fluctuation which is very similar to the classic predator-prey cycles generated by the Lotka-Volterra equations for predator-prey systems, although there does seem to be a general damping trend in this simulation run. This type of system behavior falls roughly into the category of limit cycles, which are schematically outlined as a phase plot in Figure 2. Figure 3 shows the results of a simulation in which both the predator and the prey are relatively stable, which corresponds most closely to a classic equilibrium (see Figure 4 for phase space representation). Figure 5 shows a run in which the predators went extinct. The prey then increased up to their carrying capacity in all cells which is an unstable system schematically represented by Figure 6. These three system behaviors are determined solely by the success of dispersal of predators and prey (SDD and SDY), all other parameters were held constant. Although these examples were chosen from a wider range of values, we will show later how differences in system behavior similar to those shown in Figures 1 to 6 can be produced by very slight changes in parameters.

PARAMETER SPACE REPRESENTATION

Figure 7 presents the parameter space for predator success at dispersal and prey success at dispersal. Both successes are plotted logarithmically and were run from .001 to 1.0. 50 runs were sampled on the surface by setting the predator and prey success at dispersal equal to various values and running the model with those values. From these runs, the regions as outlined in Figure 7 were readily identifiable. The region of predator crashing was very well defined in the sense that the predator crashed at all points within that region. The region of system survival was also quite well defined. There does exist a region of variable results which is the area I have labelled prey crashes. Within this region there were many points where in fact the predator crashes, but at most of the points it was the prey who disappeared and I have classified this generally as the prey crash region.

Within the region of system survival there was a wide range of outcomes, from highly oscillatory to very stable. Figure 8 plots in three dimensions the coefficient of variation of prey numbers. The x and y axis represent the success of dispersal of predator and prey as per Figure 7; and the height represents the prey coefficient of variation. The predator and prey crash regions are not shown. A low height on Figure 8 represents a region of relative stability, while a high height represents one where there is much fluctuation.

Thus, the regions of low variation correspond to the type of system behavior shown in Figure 3, and the regions of high variability correspond to those in Figure 1. A manager of such a predator-prey system might be interested in maintaining a low prey density, for instance if he is working with biological control of an insect pest and thus would be most interested in a plot of average prey density as shown in Figure 9. This figure is similar to Figure 8 except that the high is now the average prey density. If the manager were interested in maintaining a low density of prey, as opposed to complete eradication, he would try to manage the system to get it toward the lowest region on Figure 9, which would be by maintaining a relatively high predator success at dispersal and a low prey success at dispersal. Huffaker manipulated the predator success of dispersal by putting up artificial barriers to their movement between oranges. He increased the prey success at dispersal by setting up pedestals for them to jump off. In a realistic management situation, one might manipulate the relative successes by spacing of crops, aligning rows of crops with wind patterns, etc.

We see two primary problems with this sort of analysis of system behavior, the first is that the results of running a model at any point on the phase space may be a function of the starting conditions of the state variables, in which case you would have to present the parameter space as a series of probabilities instead of discrete outcomes. The second major problem is that the actual shape of the parameter space for any two parameters may be, and probably is, a function of the values of the other parameters in the system.

We can see no good solution to the first problem, if the results are dependent on starting conditions; you will just have to try many starting conditions at each point and do some sort of probability distribution. However, the realities of real ecological management are such that the system is at a certain state when management is to begin, and you might be justified in always using the starting conditions as they are at the current time in the management program. The problem of parameter interaction is probably not as serious as it might appear. In any management system there are likely to be only a few parameters that are both important in the system behavior and realistically possibilities for manipulation due to economic or ecological reasons. Although we have little experience in such techniques, it may be that in most cases the manager will be able to identify two or three variables that can be manipulated, and this is a reasonable number to manage by running several parameter space plots.

We see two major lines of development for this concept. A specific case study of a management problem should be examined to identify which parameters in the system can be manipulated to move the system both into a desirable region of general behavior, and which to move the equilibrium. These parameters can be identified from simple analytic models, the results of which can be tested on large scale simulation models, and finally, any suggestions can be applied to actual management.

Within the context of a case study, the parameters which can be manipulated would have to be identified, the models used to test what sort of effects these would have, and then some estimation of the costs, both social and economic, would have to be made of the parameter manipulation technique as opposed to the state variable technique as analyzed in detail by Fiering and Holling (1974).

A second major line of development should center on identifying, for general classes of ecological systems, which parameters are most useful for changing system behavior and equilibria. Such general classes of models would include, but not be exclusively confined to, predator-prey systems, single species, several species, and other models of such processes as competition, succession, etc. We would hope to see a set of fairly general rules emerge which would suggest that if the ecological system is of type x, for instance predator-prey, then certain parameters will be very useful to manipulate, for instance harvest rate, and other parameters will be of little use, e.g., growth rate of the prey species.

A third possible line of work would be to analyze the parameter space approach in a fashion similar to that done by Fiering and Holling for phase space. Our purpose here has been to point out the potential of parameter manipulation, not to analyze in a rigorous fashion its application. However, there is certainly a great deal of work to be done in analysis of parameter space configurations, and how to relate these to costs of environmental management and to environmental standards. We hope that readers of this will be more aware of the variety of methods available for environmental management and be willing to explore the use of these methods in actual situations.

R.W. Hilborn
October 1974

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Figure 1

Long term oscillation in predator and prey numbers

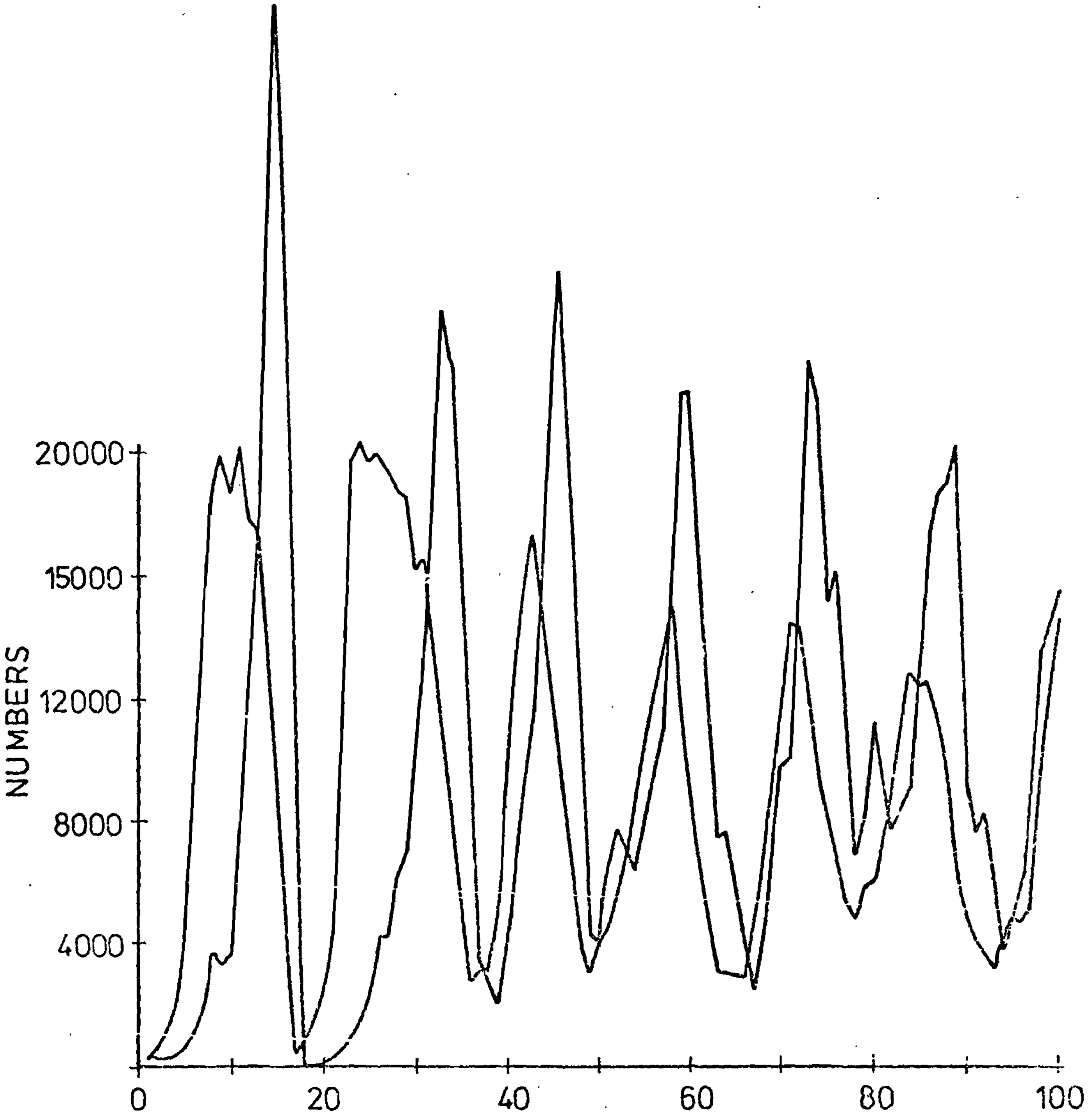


Figure 2

B Stable limit cycle

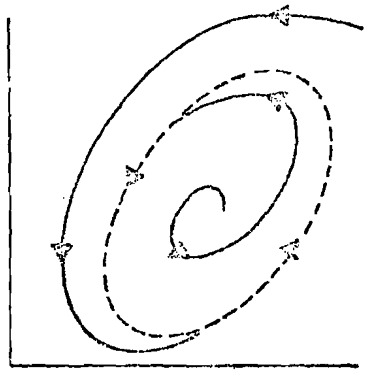


Figure 3

Relativly stable "equilibrium" between predator and prey

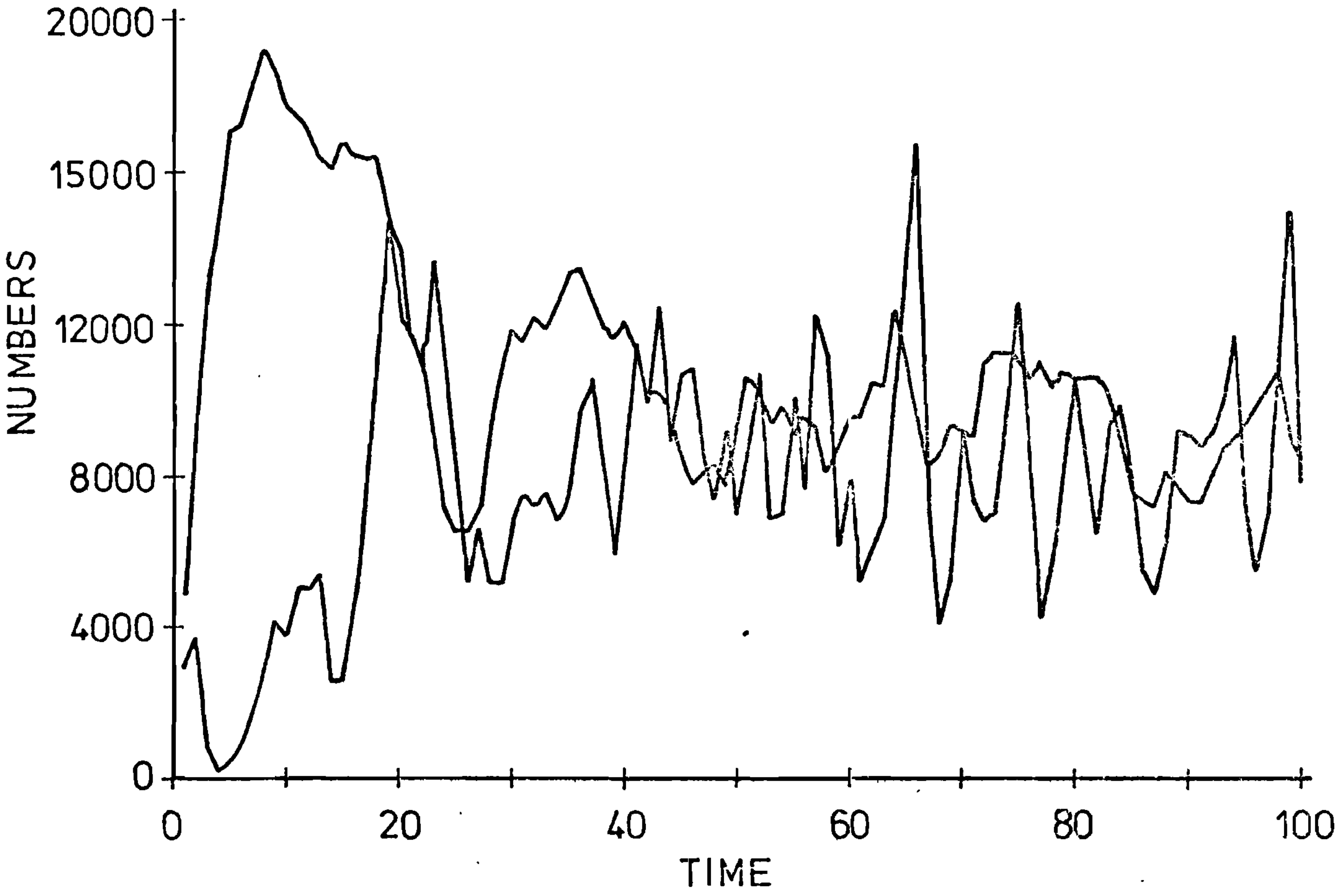


Figure 4

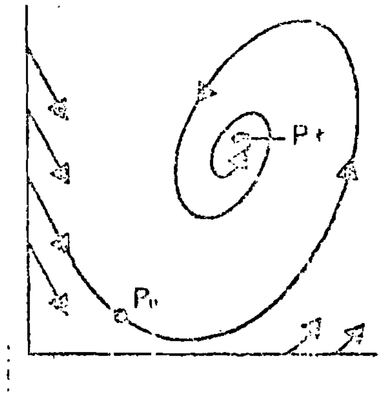

A Stable equilibrium

Figure 5

Scenario in which predator goes extinct.

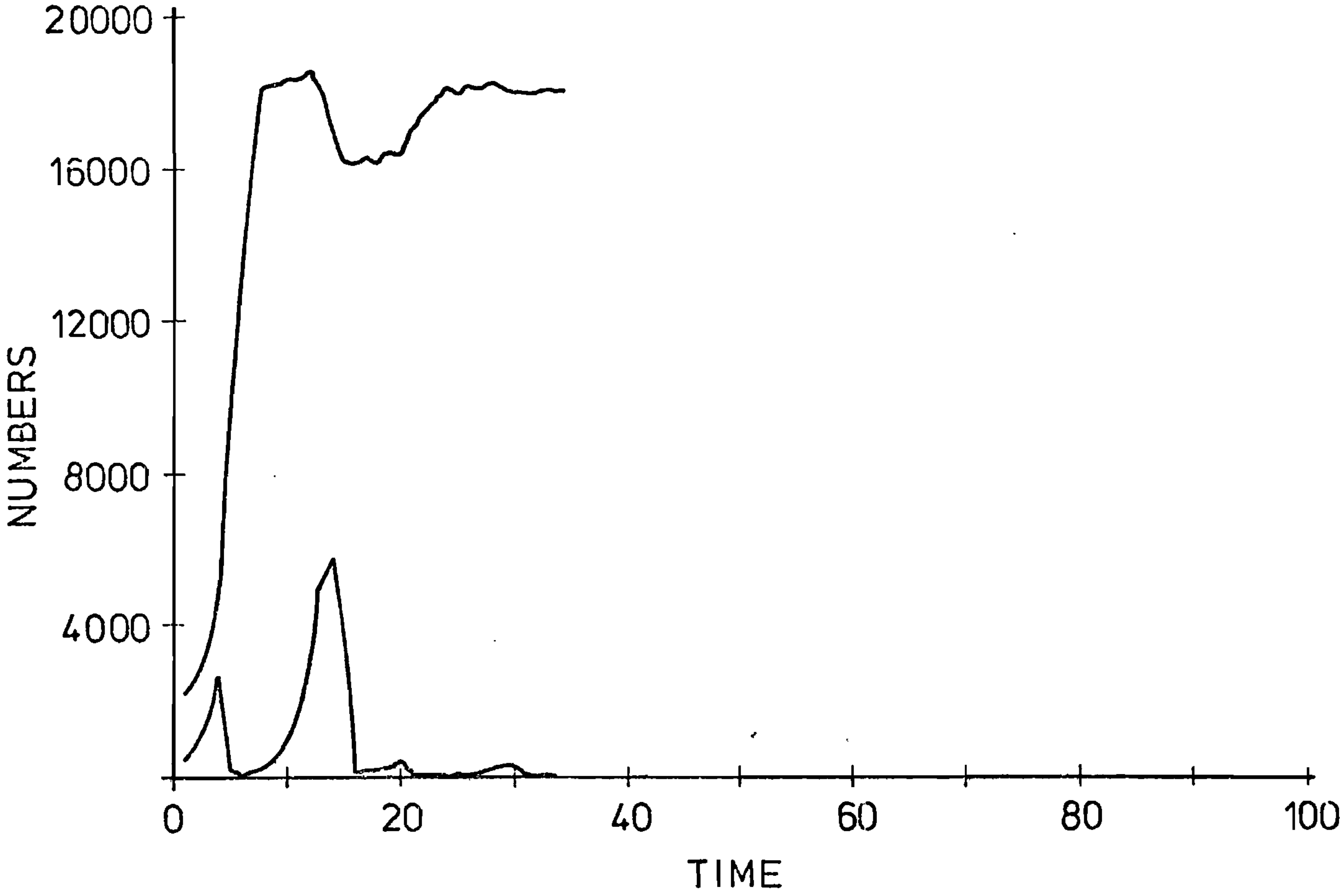
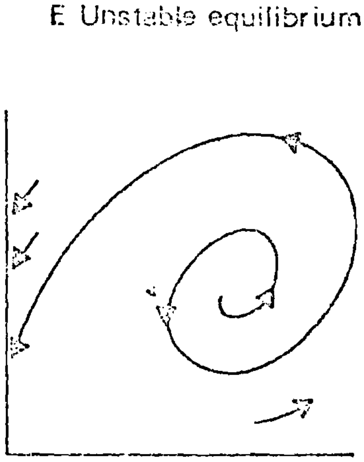


Figure 6



E Unstable equilibrium

Figure 7

Parameter space plot for success at dispersal of predator and success at dispersal of prey.

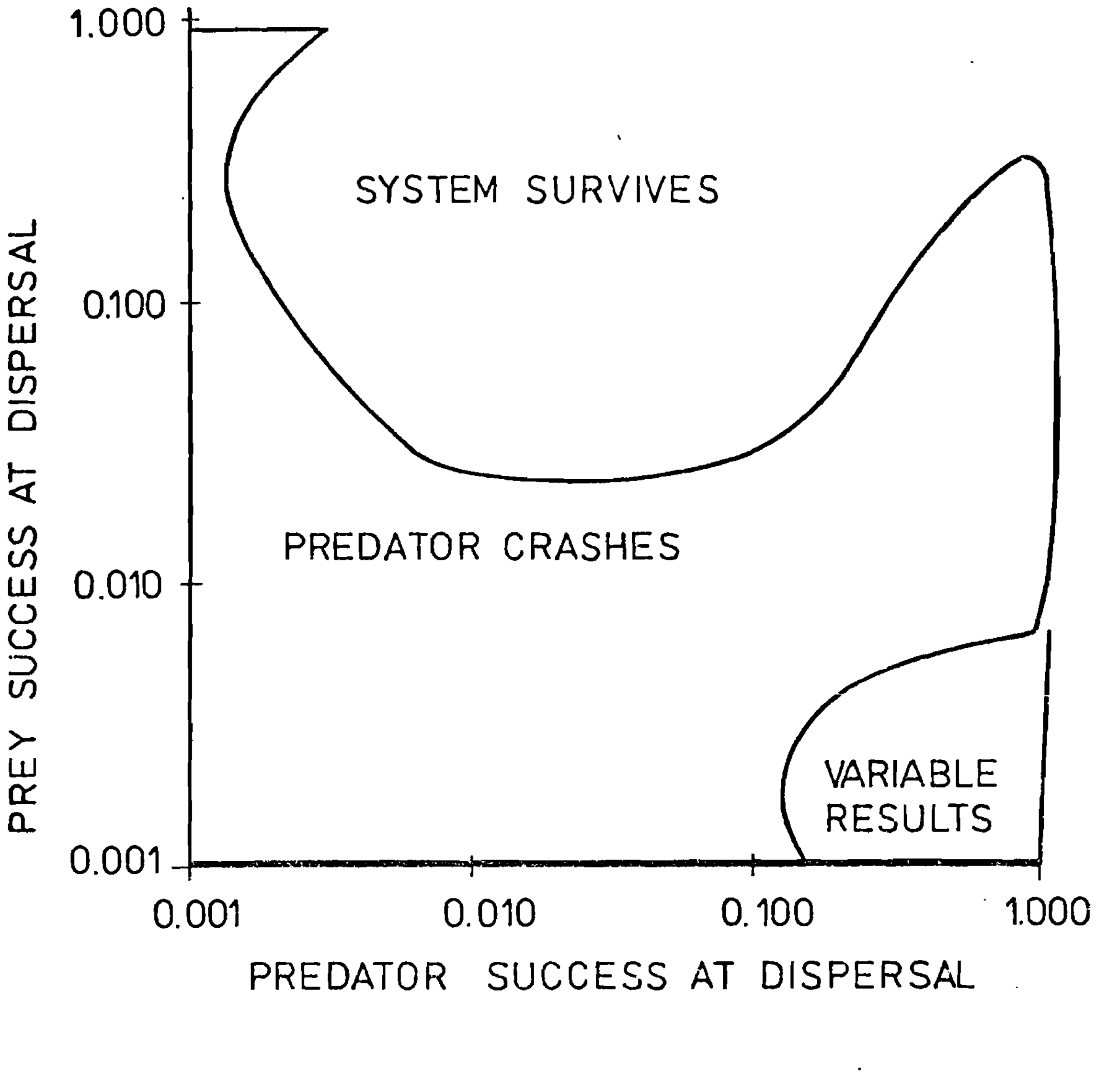


Figure 8

Parameter space where the height represents the coefficient of variation of prey numbers

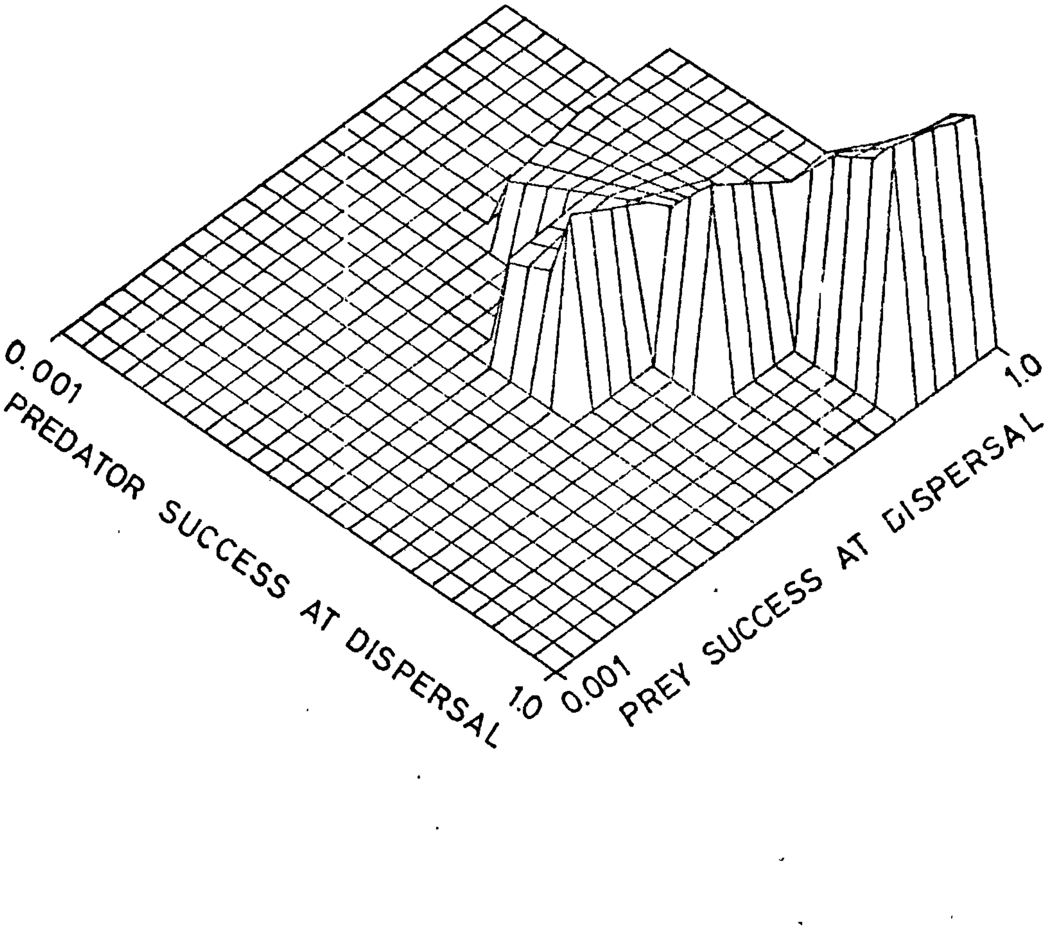


Figure 9

Parameter space plot where height represents the average prey density.