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METHODOLOGICAL PROBLEMS IN THE MODELING
AND ANALYSIS OF ECOLOGICAL SYSTEMS

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First Day Overview Presentation

C.J. Walters & William C. Clark:

Methodological Problems in the Modeling and
Analysis of Ecological Systems

(Presented by Dr. Walters)

I would like to give you an overview of basic ecological modeling and analysis problems by discussing three things. First, I will try to explain the general attitude of systems-oriented ecologists towards their subject matter. This is a different perspective from that of many here, and we will almost certainly fail to understand each other if you imagine us to be, say, economists with an interest in animals. Second, I will review those structural characteristics of ecological systems which have made their analysis particularly difficult. We like to think that it is at least in part these difficulties which have kept us rather behind the rest of you in a number of methods-related areas. Finally, I'll give a brief picture of the kinds of dynamic and stability behavior which we encounter in real and model ecological systems, using as examples cases presently under investigation at IIASA and available for study at this workshop.

I. An Ecological Perspective

As you look out over a forest or field or lake or whatever, you will see a system of interacting plants and animals. In its broadest sense ecology is a science attempting to understand how these interactions are structured, how spatial and temporal patterns of species distribution are influenced by these interactions, why some creatures persist while others

die out, and so on. The interactions and resulting dynamics which concern us are highly complicated and subtle, but tend to exhibit a fairly strong hierarchical structuring. At the level of most immediate reference to this workshop, the hierarchy can be viewed as one of the "eaters" and the "eaten" (i.e. of predators and prey). Further, the hierarchy is given a directional component by the fact that energy enters the system only at the lowest level of the hierarchy (plants), and flows through it (dynamically) from level to level in a manner determined by the inter-animal interactions I referred to earlier (Figure 1).⁽¹⁾

Some interesting and essential work has been done on dynamics and stability properties related to the structure of the hierarchy⁽²⁾. Most of the interesting analysis of ecological stability properties, however, has concerned itself with the structure and behavioral properties of the prey-predator and competitor-competitor interactions per se, largely extracted from their larger hierarchical settings. Of course, this isn't to say that the larger picture is unimportant, but rather to observe that brute force attempts to tackle the hierarchy en masse have been largely confusing, unproductive and crippling in terms of our analytical capabilities. With this in mind, I'll turn now to a description of the general structural properties underlying the interactions of the hierarchy, couching my presentation largely in terms of the prey-predator interactions⁽³⁾.

II. Structural Characteristics of Ecological Interactions

Without pretending to a comprehension or detailed analysis, I'd like to note several fundamental properties of ecological systems which have caused us problems in their modeling and analysis.

(A) Nonlinearity: Ecological processes are essentially nonlinear in nature. At a fundamental level this is often due to the existence of saturation phenomena--an animal's rate of feeding will increase with available food concentration only until the animal is spending all his time feeding; higher survival rates of a parental generation will increase production of young only until all breeding sites are taken; and so on. Additionally, many biological processes--not only ecological ones--function "optimally" only under a narrow range of conditions of temperature, water availability, etc., with process rates dropping off in nonlinear ways on either side of the optimum. Although local linearization sometimes constitutes a useful approximation of system behavior over a specified range of conditions, it cannot be justified in general⁽⁴⁾.

(B) Thresholds: Ecological interactions are largely threshold phenomena. They switch on and off in an essentially discontinuous manner, with dramatic effects on system behavior. Hibernation is the most obvious example. Minimum food densities necessary to stimulate feeding response are another.

(C) Stochastic effects: Many ecological interactions are essentially stochastic. Colonization, low density breeding, predation search success, and such pertain here. From another

perspective, the parameters of population interactions are distributed, even if those of individual interactions are assumed to be unique values. We know from experience that it is the tails of these parameter distributions which largely determine the long term success of populations, and one is invariably led into stochastic modeling in an effort to deal with them effectively. Finally, the environment within which ecological interactions occur provides important random inputs of such factors as weather, food supply, and so on. How far we can get through deterministic modeling of these essentially stochastic processes remains to be seen.

(D) Discrete time: The threshold problem alluded to earlier appears under a slightly different guise in the discrete time nature of ecological processes. Biological organisms are generally not continuous systems. They come in integral units of organisms, exhibit periods of feeding, of reproduction, of quiescence, of dispersal which are discrete and not interchangeable. Some progress has been made through use of continuous system (differential equation) approximations which treat populations as pools of biomass or energy, but these approaches are approximations and their results must be interpreted with this in mind. Several of the stability analysis properties related to this discrete time nature of ecological processes will be shown in Dr. Jones' talk later on (5).

(E) Spatial heterogeneity: The ecological world is full of situations in which an interaction occurring at a given place and time affects interaction at other places only as a non-trivial function of time and location. In a sense, this is very much like the spatial problem discussed by Dr. Charney

in the climatological context. In ecology, however, the problem is complicated by the existence of a variety of poorly understood dispersal (or "diffusion") mechanisms, many of which exhibit the stochastic, discontinuous, nonlinear properties referred to above. Some work in biological oceanography has applied differential equation models of diffusion and turbulence, drawn from the fluid dynamics literature, to spatial dispersal problems in simple ecosystems⁽⁶⁾. In more complex cases governed by biological rather than physical diffusion rules, the only workable approach has been to perform numerical simulations on a model with explicit physical grid structure. I will describe one such study later on, but the obvious disadvantage is the lack of generality inherent in the brute force approach. Nonetheless, there is no conceivable ecological problem in which the spatial component is not an essential one in the determination of stability properties and dynamic behavior.

(F) Evolving parameter structure: The ultimate problem for ecological modeling and analysis is that the so called parameters of our systems are, for the most part, actually dynamic ("control") variables which the process of natural selection is inexorably pushing towards local system "optima". I won't go any further into this for the moment, except to call your attention to the fact that even where we can identify dynamic and/or stability properties of an ecological system (or model), these must be viewed as in some sense transients. The subsequent inquiry into the parametric and even structural sensitivity of the solutions is carried out not merely to see

what would happen if we got the measures wrong, but more importantly to see what we expect the system to be doing next.

III. Dynamics and Stability Behavior of some Ecological Systems

Let me now say a few words about the behavior of prey-predator systems. If we examine the state space representation of such a system, the most common case for simple experiments and models is that of Figure 2a. Here, from all starting points including some predators, the predator eats all the prey and then itself starves to death. Two trivial equilibria, unstable to positive perturbations, exist for the zero predator and zero predator-prey cases, respectively. Under different values of model parameters, and in imperfectly mixed experimental systems we get the globally stable limit cycles of Figure 2b. An additional range of parameter values yields Figure 2c's globally stable equilibrium, a situation which I may add, seems to be extremely rare in natural ecological systems. Finally, it is possible in slightly more complicated models to get multiple equilibria of the sort shown in Figure 2d. (Of course, a variety of cases are possible; one of the most interesting in an ecological sense is shown). These multiple equilibria cases arise as a result of a variety of ecological phenomena such as compensatory mortality, predator learning, or even simple minimum densities below which one or both of the species fail to reproduce. This last situation is shown for the discrete generation case in Figure 3. Note that the very small X_{\min} zone is 'reflected' in a much larger portion of state space, points in which have the property of describing

trajectories which enter the X_{\min} region. Note also that the discrete nature of the prey-predator interactions allows "trajectories" to jump over the central stability region. You will find such systems described in more detail in the working paper distributed by Dixon Jones (7).

As a last example, I'd like to talk about a real system we've studied in which the spatial heterogeneities referred to earlier play an important role.

The system consists of the conifer forests of eastern North America and an insect--the spruce budworm--which periodically undergoes tremendous epidemic outbreaks and defoliates the forest. In a small area--say a couple of acres of trees--the time behavior of the budworm is as shown in Figure 4. This is analogous to the prey-predator system I discussed earlier: the budworm goes along for a time at very low densities, suddenly increases its density over 5 orders of magnitude, eats all the trees, and then almost disappears as a result of starvation. It takes 35 years or so until the forest has recovered enough to support an additional outbreak.

If we look over the whole of eastern North America, however, the system is much less "peaky", looking more like Figure 5. Somewhere in this region, there is almost always a local outbreak in progress, with the result that the average density of budworm is much more constant. What is really happening appears neither in Figures 4 nor 5, but rather in a physical map of eastern North America in which we trace the temporal spread of outbreaks. These turn out to be a wave or "ripple" phenomena, akin to that produced by dropping a stone in a lake. The wave

of the outbreak pass outward from its point of origin (Figure 6) giving local effects such as those shown in Figure 4 and the global ones shown in Figure 5. Restart of the cycle may occur by insects dispersing from the $y=40$ wave front back to the area devastated in $y=0$, and now recovered sufficiently to support a new outbreak. The process is, therefore, one which in any small (local) interaction can be described by a stable limit cycle of high amplitude in foliage-budworm space. These small areas are connected by dispersal of insects which leads to the large scale almost constant ("equilibrium"?) behavior of Figure 5. The very concept of "stability" seems a spatial one ... But our management interest here is precisely one of controlling or influencing the local "peakiness" of the system, trying to spread the inevitable budworm damage over longer periods so that the acute free mortality caused by the outbreaks is reduced. We are trying to find a way to break up the waves of Figure 6, perhaps by reducing the amplitude of the cycle in Figure 4b. We would be very interested to know, for instance, whether there exists (even in a mathematical sense) a nontrivial stable equilibrium to the system at both the local and regional spatial level. At present, the very high dimensionality of the spatial system makes grid search techniques for such stable points hopelessly inefficient. We wonder if any of the computational methods known to you people can help us. And we're equally interested in getting some comments from the other applied people here on what seem to be useful conceptualizations of such concepts as "stability", "equilibrium", "periodicity", in such cases

as this. We just don't have a useful way of even talking about these problems at present. And with that rather forelorn plea, I guess I'll stop⁽⁸⁾⁽⁹⁾.

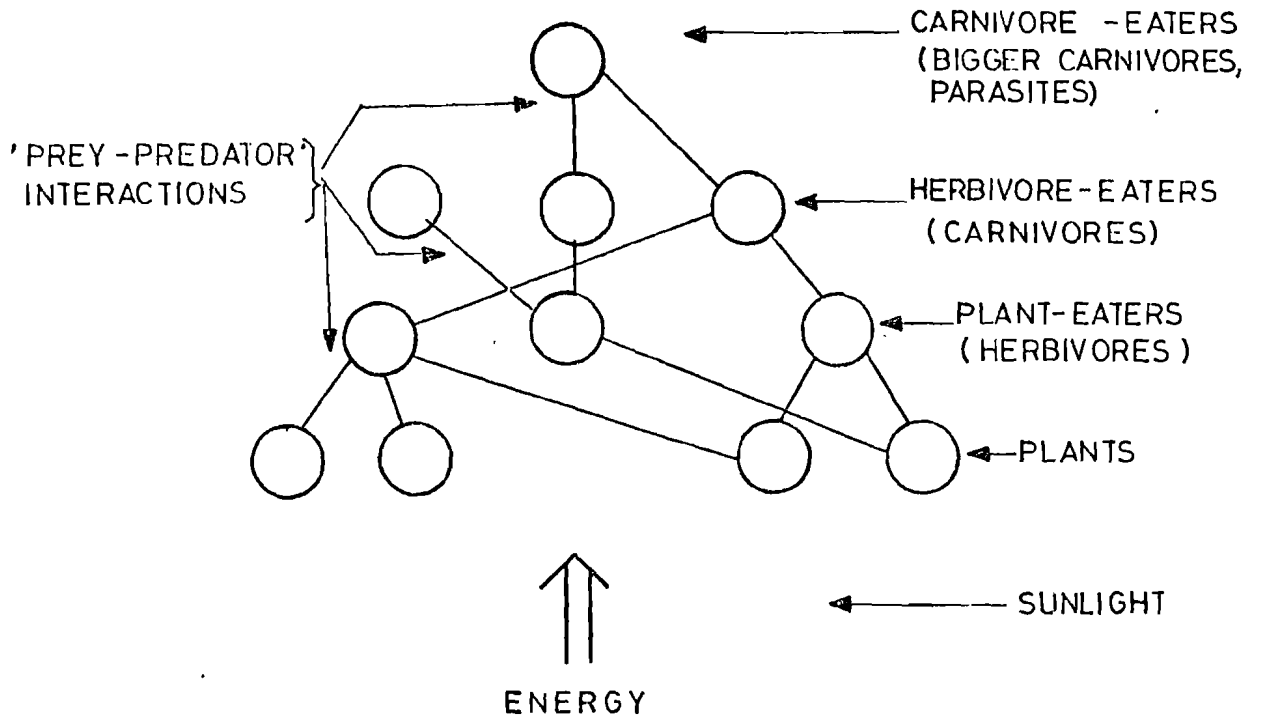


Figure 1: Hierarchical nature of ecological systems.

Note that the figure is highly oversimplified in that among other things, real systems are less strictly hierarchical, are not fixed in their interaction patterns, and include recycling (or decomposer) links from all levels back into the bottom one or two. Note also that important competitor interactions within hierarchy levels are not shown⁽¹⁾.

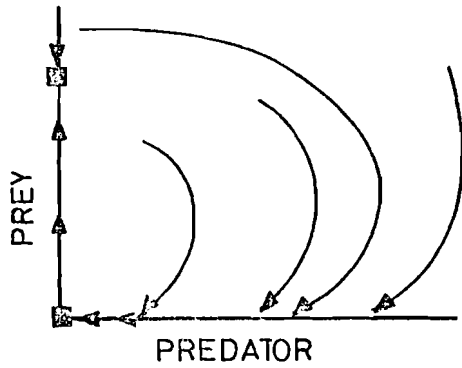


Figure 2a: Unstable.

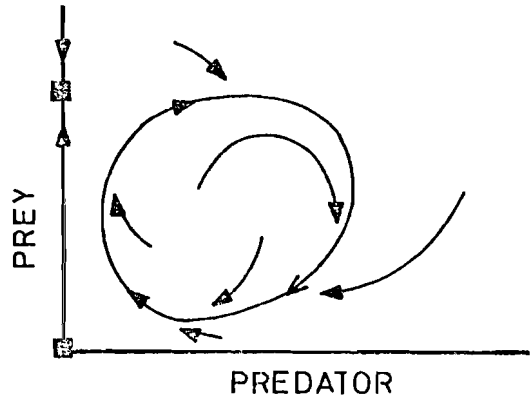


Figure 2b: Stable limit cycle.

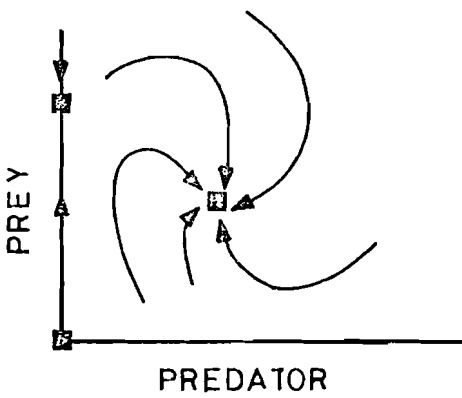


Figure 2c: Stable equilibrium.

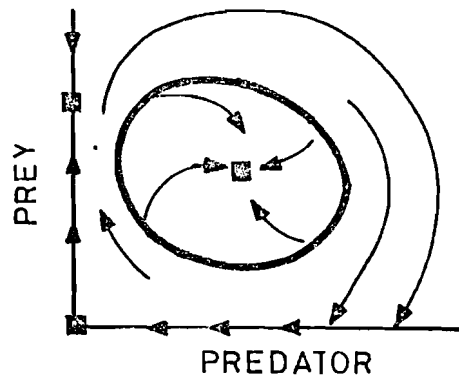


Figure 2d: Multiple equilibria with separatrix.

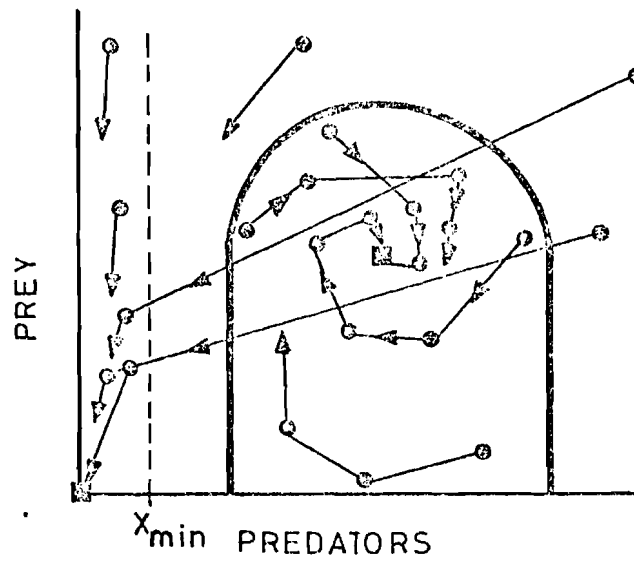


Figure 3: Multiple equilibria, caused by minimum density x_{min} below which predators fail to reproduce.

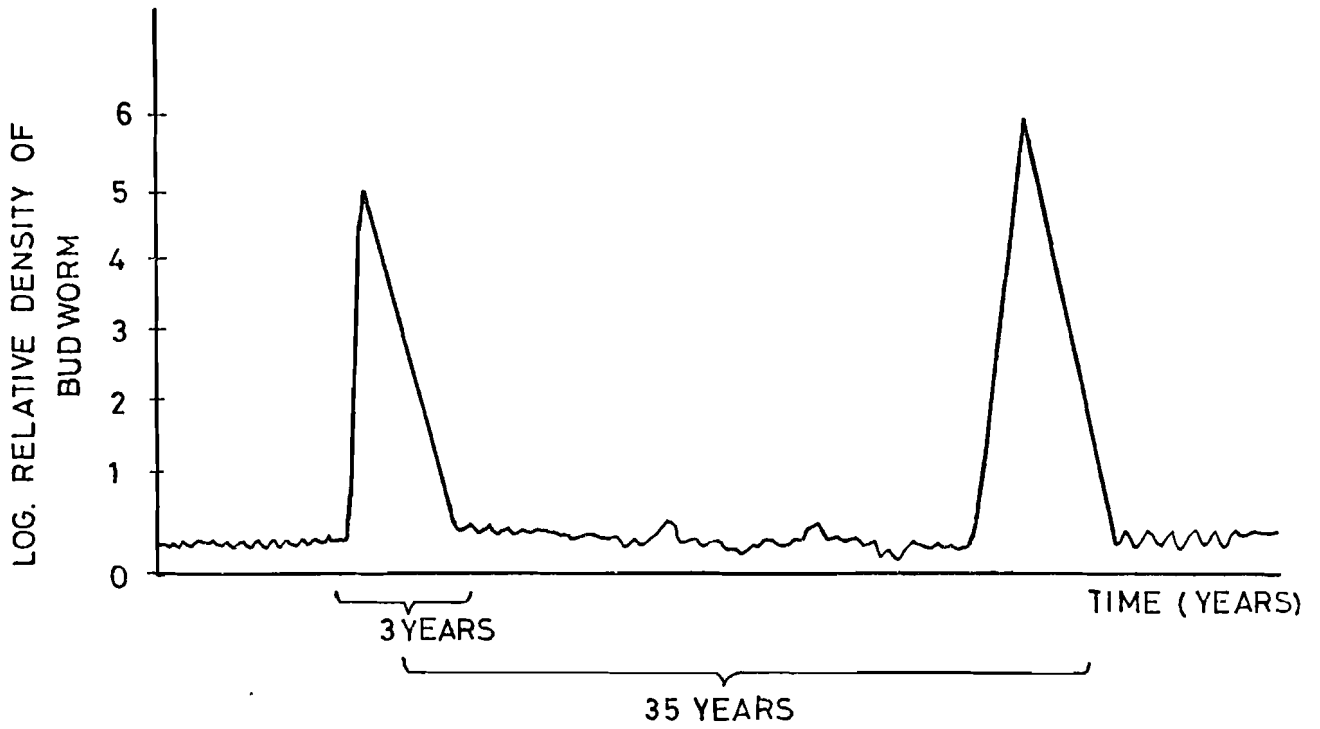


Figure 4a: Local time pattern of budworm densities.

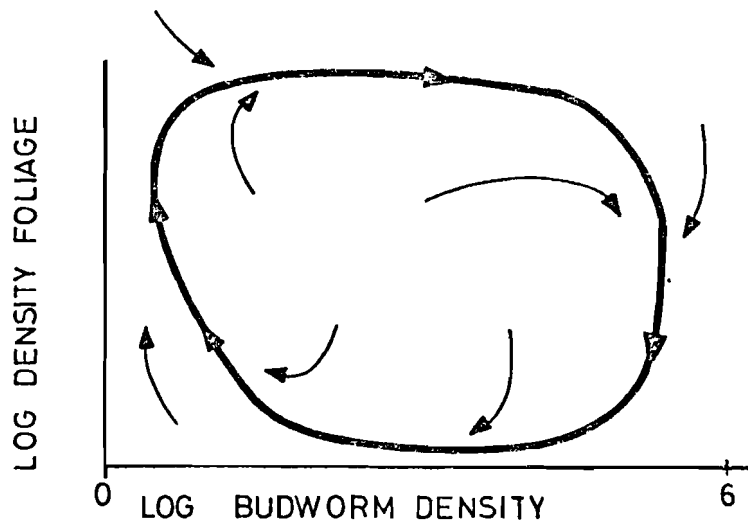


Figure 4b: State space pattern of local budworm-free interactions.

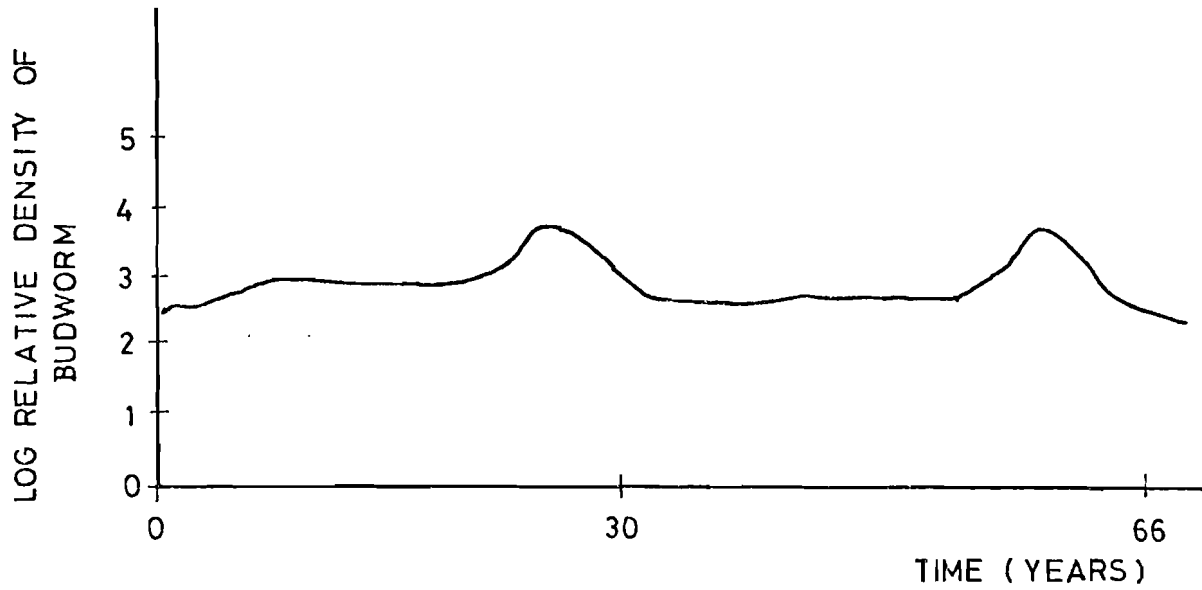


Figure 5a: Large scale time pattern of budworm densities.

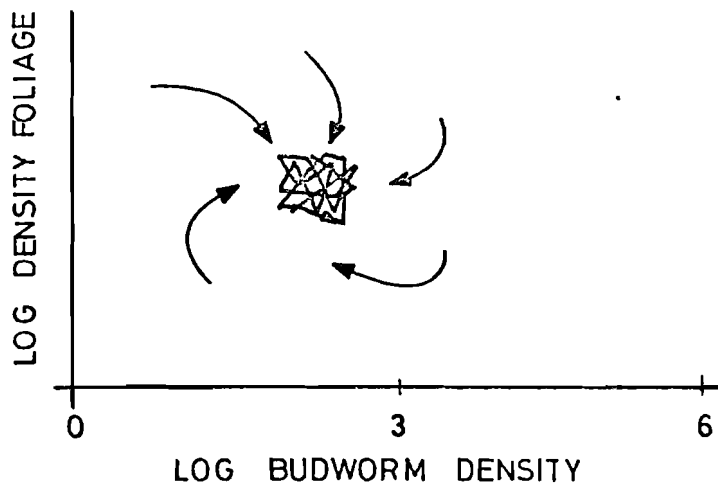


Figure 5b: State space pattern of large-scale average interactions (an apparently smaller stable limit cycle).

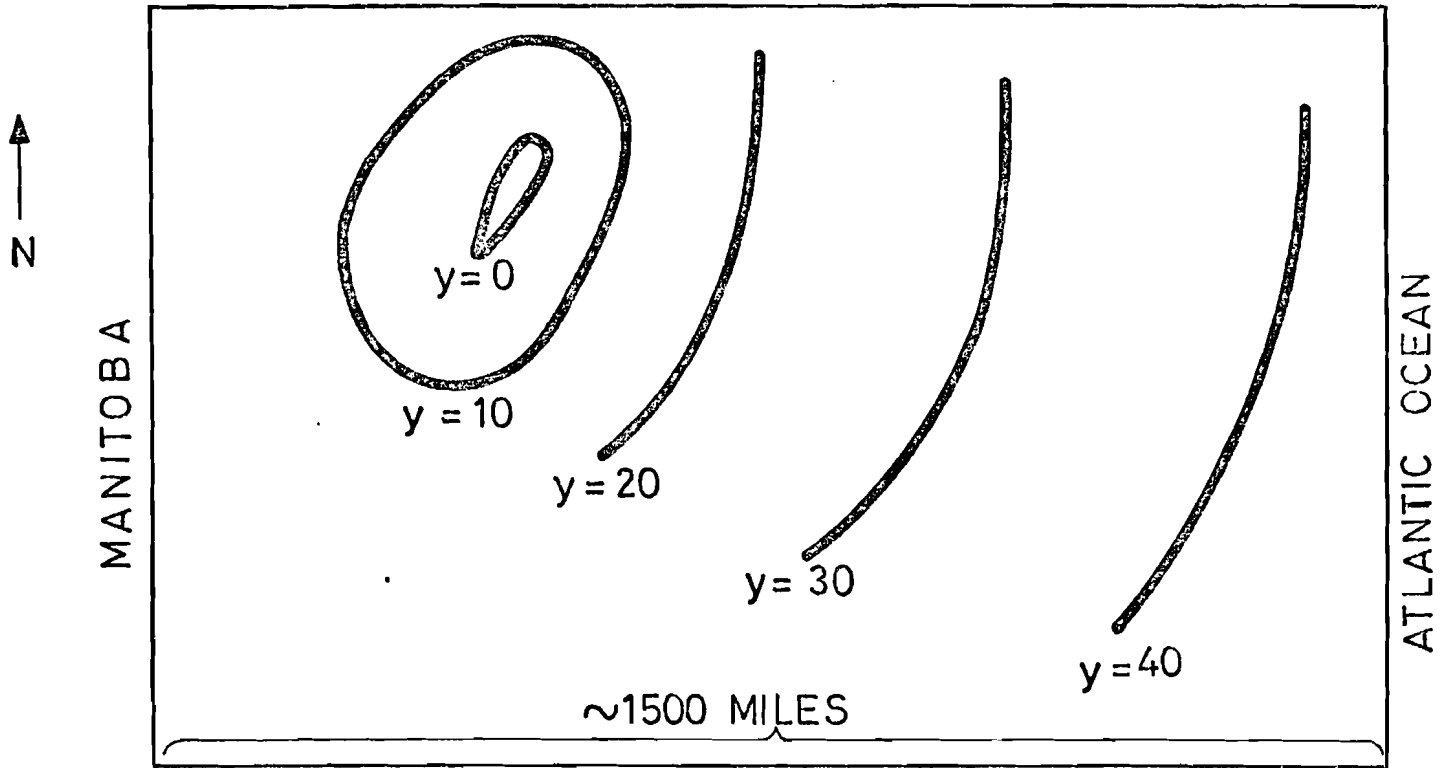


Figure 6: Physical location of budworm outbreak in Eastern North America, by year.

Notes and Selected Bibliography

- (1) See, for example, Odum, E.P., 1972, Ecology 3rd ed., Saunders, Philadelphia for a development of the hierarchy concept.
- (2) See the following for discussion of the relation between a hierarchy's structure and its stability properties.

May, R.M., 1973, Stability and Complexity in Model Ecosystems, Princeton University Press.

Gardner, M.R., and W.R. Ashby, 1970, "Connectance of Large Dynamical Systems: Critical Values for Stability," Nature, 228:784.
- (3) The competitor interactions are at one level structurally identical to the prey-predator ones, requiring only a change in sign of the equations. But competition studies, even at the theoretical level, have taken an approach which might be characterized as comparative statics as opposed to the comparative dynamics of most prey-predator work. See MacArthur, R.M., 1972, Geographical Ecology, Harper and Row, for the mathematical treatment of simple competition models, and May, R.M., op cit. for that of simple prey-predator ones. See also (9) below.
- (4) See Dr. Bazykin's presentations later in this volume on the relevance and implications of the Michaelis-Menton model to saturation processes.
- (5) See Maynard-Smith, J., 1974, Models in Ecology, Oxford, for a discussion of the difference in stability properties of difference and differential equation models in ecology; see also May, R.M., op cit.
- (6) See Steele, J.H., 1974, "Stability of Plankton Ecosystems," (in) M.B. Usher (ed.), Ecological Stability, Chapman and Hall, for a treatment of spatial effects.
- (7) See Jones, D.D., 1974, "Analysis of a Compact Prey-Predator Model." IIASA WP-74-34 for a further development of the prey-predator model.
- (8) For a further treatment of the budworm system see:

Morris, R.F., 1963, "The Dynamics of Epidemic Spruce Budworm Populations," Mem. Ent. Soc. Canada, 31.

Jones, D.D., 1975, "The Application of Catastrophe Theory to Ecological Systems," (in) G.S. Innis (ed.), Simulation in Systems Ecology, Simulation Council Procs. (in press). Also, IIASA RR-75-15.

Holling, C.S., et al., 1975, "A Case Study of Forest Ecosystem Pest Management," (in) Proc. Int. Can. Conf. on Applied Systems Analysis, 1975 (in press). Also, IIASA WP-75-60.

- (9) Note added in proof: There is a large quantity of competition model literature concerned with determining how many different species can coexist (i.e. exhibit positive densities) in an ecological system at equilibrium. Much of the argument is essentially tautological, concluding only that at most there can be as many species as there are "different" resources. But in its "limiting similarity" form, the issue remains an interesting one (see MacArthur, op cit.). It would seem that this "how-many-coexisting-species-problem" is the one best suited to solution by existing fixed-point techniques.