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MULTI-MODEL MULTI-FORMALISM
MODELLING:
AN ECOSYSTEM EXAMPLE

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Modelling:

An Ecosystem Example

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1. Introduction

Ecosystems, as examples of large scale multifaceted systems, require that a multiplicity of models be developed since a single all encompassing model, however desirable as a conceptual goal, is not a practical object. By decomposing questions and modelling objectives into an ordered structure of elements called experimental frames (Zeigler, 1976a), useful partial models may be constructed, validated and employed, each one attuned to a particular experimental frame. Concomitant with the pluralism of such partial models is the recognition that models are expressible in different formalisms, each offering conceptual and computational advantages within its domain of application (Zeigler and Barto, 1977). But now, in addition to the familiar activities involving construction and validation of individual models, there is required a host of organizational activities aimed at integrating the collection of models into a synergistic whole. Our belief is that the computer can be programmed to aid in executing these activities to a much greater degree than it is doing today.

We have recently sketched a theoretical basis for structuring the organization of partial models (Zeigler, 1977a). In this paper, we illustrate our approach by considering an ecosystem example in some detail. After briefly reviewing this approach, we discuss its application to the patch structured universes employed by Huffaker (1958, 1963) to study predator-prey coexistence. We show how the approach facilitates the development of mutually supportive detailed and abstract models that in conjunction, provide both accurate ecological realism at one extreme and general insight into the essential mechanisms at work, at the other.

2. The Ecosystem: Questions of Interest and Models

The problem of predator-prey coexistence in patchy environments has received much theoretical attention of late (Levin 1976, Hassel and May, 1974, Maynard Smith, 1974). Most of this work has employed the conventional differential and difference equation formalism but following on suggestions stressing the importance of discrete processes (Maynard Smith, 1974), we have shown (Zeigler, 1977b) that the discrete event formalism and associated simulation languages can provide effective comprehensible explanations predator-prey co-existence. Also, there have been very few attempts to fit the theoretical models to laboratory or field data. In contrast, our general approach is illustrated in this case by our development of four related models, expressed in either the differential equation or discrete event formalism, and constructed at different levels of abstraction, ranging from the most detailed level where close comparison of model behavior with experimental data is possible, to the most abstract where overall properties are discernable in a relatively simple manner.

The real system to which the modelling is directly addressed is that of the controlled universes constructed by Huffaker (1958, 1962). Basically, these consist of spatial arrays of oranges (patches) of controllable nutritional value, inhabitable by prey and predator mites, and interconnected by migration pathways of controllable difficulty. Many other discrete food unit environments fit this general form.

Our most detailed model, the base model, is of the stochastic differential equation type. In it, the local state (situation on each patch) is determined by a Lotka-Volterra type differential equation governing the joint food, prey

and predator dynamics; the impetus for emigration and the effect of immigration are logically determined from the local state (food, prey, predator); and the migration process is of the stochastic random walk variety. This model enables us to identify the parameters of the local Lotka-Volterra dynamics from data for single patches. It is not feasible for computer simulation however, and this motivates the construction of a second model which is both simulateable and amenable to validation against data collected from universes in which the effect of migration is at issue.

This (second) model is of the stochastic discrete event type and is simulated in SIMSCRIPT, a well known discrete event language. The model keeps track of the same state variables as its predecessor but updates them only at "event times". The tables required for scheduling events and executing the updates were derived by appropriately partitioning the local state space and summarizing the Lotka-Volterra trajectories between partition boundaries. (This required a once-and-for-all simulation of the Lotka-Volterra equations.) This technique for representing differential equation models in summary form as discrete event models is quite general (Zeigler, 1977c).

Our third model in the hierarchy is also of the discrete event type. It is an abstraction of its predecessor, in which the local situation is represented by a small number of discrete states [empty, some prey, etc.] and the migration processes are also suitably simplified. Since actual population counts have been discarded, this model cannot make quantitative global population predictions. The model lends itself however to convenient parameter study of persistence and the development of patterned interaction.

Our last lumped model is of the deterministic different equation type. It describes the global behavior of its predecessor operating under the so called "random phase-random space" mode (Zeigler, 1977b). The model yields simple algebraic expressions for the equilibrium distribution of patch states and thus explains the form of the dependence of persistence on migration parameters.

3. Organization of Questions and Models

The integration and organization of the above models is achieved within the formal system suggested by Zeigler (1976a, 1977b). The following is an informal review of the concepts involved.

We distinguish the following elements:

\mathcal{E} -- a collection of experimental frames. A frame $E \in \mathcal{E}$ represents a restricted set of questions by specifying the restrictions on experimental access to the real system sufficient to answer them. Such a frame E determines a collection of data sets $\mathcal{D}(E)$, such that each $D \in \mathcal{D}(E)$ is an a priori possible result of complete data acquisition within frame E .

\mathcal{R} -- the real system, is comprised of the specific data that has been, or would be, collected by experimenting with the system. Thus \mathcal{R} associates with each experimental frame E a unique data set $\mathcal{R}(E) \in \mathcal{D}(E)$.

\mathcal{M} -- The domain of possible models. These are assumed to be transition systems which are specifiable at various levels of structure and behavior and within various short-hand conventions such as the sequential machines, discrete event and differential equation formalisms.

A full description of these basic elements and the concepts they embody may be found in Zeigler, 1976, Chapters 2 and 11. In a moment, we shall formulate these elements in the context of patch structured universes and the experiments of Huffaker (1958, 1962) in particular. Roughly, the "experimental frames" will encode the various choices of observables (species counts in patches) and conditions (initial stocking of species, structure of universe) under which experiments were run. The "real system" is the data collectable by making the implied observations under the given conditions. Finally the "models" are the various distributed and lumped models which can be postulated to account for the observed data and to predict the results of future experiments.

We can imagine an ideal state of affairs in which for each frame $E \in \mathcal{E}$ there is a known model $M \in \mathcal{M}$ which "best" answers the questions possible in E . By "best" we mean that the model can reproduce without error the data set $\mathcal{R}(E)$ in a manner which requires the least consumption of computer resources. Realistically, this ideal is not realizable after a necessarily finite span of data acquisition. The dynamics of modelling concern successive approximations to the ideal.

We formulate the problem as follows: At any time t , the data already acquired in frame E will be some subset $\mathcal{R}^t(E) \subseteq \mathcal{R}(E)$. Many, perhaps most frames, will not even have been considered. Those that have, form the subset $\mathcal{E}^t = \{E | \mathcal{R}^t(E) \neq \emptyset\}$. Similarly, only a small subset \mathcal{M}^t of the possible models \mathcal{M} will have been constructed as potential model candidates. Thus the state of affairs at any time t is reflected in the triple $\mathcal{E}^t, \mathcal{R}^t, \mathcal{M}^t$.

4. Experimental Frames

Let us examine the elements of the triple at time $t =$ June 1961, the date of the last observation recorded by Huffaker (1962).

There are four main types of experimental frames. As displayed in Table 1, these types are distinguished by the descriptors "global", "local", "total", and "occupancy". The "global" descriptor refers to the fact that all cells (locations where an orange or a substitute rubber ball may be placed) in the universe are being observed. In contrast, in the "local" condition, only some subset of the cells are of interest. The "total" descriptor refers to the fact the quantities of interest in a frame have been totalled to produce aggregate quantities, so that only those aggregates are observable in the frame. Finally, the "occupancy" descriptor refers to the fact that a

frame permits only the observation of discrete occupancy states, such as whether or not a cell is empty, whether or not a prey colony has been established on the cell, and whether there are no, few, or many predators present.

Table 1 also summarizes the kinds of questions associated with each frame. The "occupancy" frames are the most restricted. Nonetheless they permit consideration of persistence of predator-prey relations since to determine whether there are any prey or predators requires only a binary categorization (present/not present) for each cell. At the other extreme, the "global" frames permit observation of detailed spatial distribution of species. The "total" frames correspond to classical populations in which spatial structure has been averaged out. It is evident that certain frames are potentially more informative than others. In a moment, we shall formally characterize this fact in terms of the "derivability" relation (Zeigler, 1977a).

The experimental frames \mathcal{E} are defined in Table 2. Each frame names a set of variables of interest, called the compare variables, and a set of variables determining the conditions under which experiments are to be performed, called the control variables. The most inclusive frame, $\mathcal{E}_{\text{global}}^{\text{food,prey,pred}}$ specifies as compare variables: food amount, prey, and predator population counts in each cell. This constitutes a total of $3N$ variables where N is the number of cells in the universe. There are no control variables for this frame. An example

Table 1

Experimental Frames and Their Possible Questions

<u>Plane of Frame</u> (representative frames) <u>given</u>	<u>Description</u>	<u>Possible Questions Concern:</u>
E_{global}	Food amount and population variables for each cell	Spatial characteristics of predator-prey, prey-food interaction
E_{local}	Food amount and population variables for a subset of cells keeping all others zero	Predator-prey, prey-food, interaction in local patch
$E_{global, total}$	Food amount and population variables totalled over all cells	Space averaged population sizes in predator-prey, balance of prey-food, interaction (classical lumped populations)
$E_{occupancy, global}$	Discrete food and population states for each cell (empty, some prey, many prey, some predators, etc.)	Persistence of predator-prey, balance of prey-food, interactions; effect of cell geometry
$E_{occupancy, global, total}$	Totals of cells in the various states as given in $E_{occupancy, global}$	Persistence of predator-prey, balance of prey-food, interactions under random phase-random space conditions.
(degree of abstraction = 2)		

Table 2

Experimental Frames and Relevant Data Sets in Huffaker Universe

<u>Frame, E</u>	<u>Description</u>	<u>Associated Data Set, R^t (E) (Table 3)</u>
E_{Global} Food, prey, pred	Food, prey, predator variables for each cell	missing
E_{Global} Food, prey/pred	Food, prey variables for each cell in absence of predator	missing
E_{Global} Food/prey, pred	Food variable for each cell in absence of prey and predator	missing (but partial descriptions of the orange replenishment schedules used are given)
$E_{\text{Global, total}}$ Food, prey, pred	Totals of food, prey and predator over all cells	58, II(A-I), Figs. 9-18 63, II(3,4), Figs. 3,4 63 I-(4,5,6), Fig. 5
$E_{\text{Global, total}}$ Food, prey/pred	Totals of food, prey over all cells in absence of predator	58, I(A,B,C) Figs. 6, 7, 8 63, E-2, Fig. 2
$E_{\text{Global, total}}$ Food/prey, pred	Total of food over all cells in the absence of prey and predator	missing

Table 2 (continued)

<u>Frame</u>	<u>Description</u>	<u>Associated Data Sets $R^T(E)$ (Table 3)</u>
E_{local} $E_{\text{Food,prey,pred}}$	Food,prey,predator variables for a subset of cells keeping all others zero	missing
E_{local} $E_{\text{Food,prey/pred}}$	Food, prey variables for a subset of cells in absence of predator	missing
E_{local} $E_{\text{Food/prey,pred}}$	Food variable for a subset of cells in absence of prey and predator	missing (some very incomplete description of orange quality and spoilage rates given)
$E_{\text{local,total}}$ $E_{\text{Food,prey,pred}}$	Totals of food, prey, predator variables for a subset of cells keeping all others zero	58, II A, Fig. 9 58, II B, Fig. 10 58, II C, Fig. 11
$E_{\text{local,total}}$ $E_{\text{Food,prey/pred}}$	Totals of food, prey variables for a subset of cells in absence of predator, keeping all others zero	58, IA, Fig. 6; Initial Parts of: 58, IB, Fig. 7 58, IC, Fig. 8 63, E2, Fig. 2
$E_{\text{occupancy,global}}$ $E_{\text{prey,pred}}$	Occupancy states of prey and predator for each cell	58, II I, Fig. 18 63, II-(3,4), Figs. 3,4
$E_{\text{occupancy,global,total}}$ $E_{\text{prey,pred}}$	Totals of cells in prey and predator occupancy states	computable from: 58, II I, Fig. 18 63, II-(3,4), Figs. 3,4

Table 3

Data Elements For Huffaker Universes $\mathcal{R}(t = 1961)$

<u>Data Element Key*</u>	<u>Description (as given by Huffaker)</u>
58, IA, Fig. 6	Predators Absent, Simplest Universe, Four Large Areas of Food, Grouped at Adjacent, Joined Positions
58, IB, Fig. 7	Predators Absent, Four Large Areas of Food Widely Dispersed
58, IC, Fig. 8	Predators Absent, 20 Small Areas of Food Alternating With 20 Positions With No Food
58, IIA, Fig. 9	Predators Present, Simplest Universe, Four Large Areas of Food, Grouped at Adjacent Joined Positions
58, IIB, Fig. 10	Predators Present, Eight Large Areas of Food, Grouped at Adjacent Joined Positions
58, IIC, Fig. 11	Predators Present, Six Whole Oranges as Food, Grouped at Adjacent Joined Positions
58, IID, Fig. 12	Predators Present, Four Large Areas of Food Widely Dispersed
58, IIE, Fig. 13	Predators Present, Eight Large Areas of Food Widely Dispersed
58, IIF, Figs. 14, 15	Predators Present, 20 Small Areas of Food Alternating with 20 Foodless Positions
58, IIG, Fig. 16	Predators Present, 40 Small Areas of Food Occupying All Positions
58, IIH, Fig. 17	Predators Present, 120 Small Areas of Food Occupying All 120 Positions (Barriers to Migration Added)
58, II I, Fig. 18	Predator-Prey Oscillations, 120 Small Areas of Food Occupying all 120 Positions (Barriers to Migration Added)
63, E-2, Fig. 2	Predators Absent, Complex 3-Shelf Universe, 210 Small Areas of Food
63, II-(3,4), Figs. 3,4	Predators Present, 3-Shelf Universe, 252 Small Areas of Food
63, I-(4,5,6), Fig. 5	Predators Present, Complex 3-Shelf Universe, 252 Larger Areas of Food

* (58, IA, Fig. 6) denotes that the data set is presented in Fig. 6 and discussed in Section IA of Huffaker (1958).

of a frame which has a non empty set of control variables is $E_{\text{food,prey/pred}}^{\text{global}}$ whose compare variables are all $2N$ food and prey variables and whose control variables are all N predator variables.

In a frame with no control variables, compare variables readings are recorded against time for the duration of any particular experiment (See Fig. 1). This yields a time function (also called a segment, or trajectory) which we refer to as a data element belonging to the frame. The set of all such data elements observable in a particular Huffaker Universe is the data set $\mathcal{R}(E)$ assigned by such a real system to frame E . The set of all such possible data sets assignable by the possible Huffaker Universe is $\mathcal{D}(E)$.

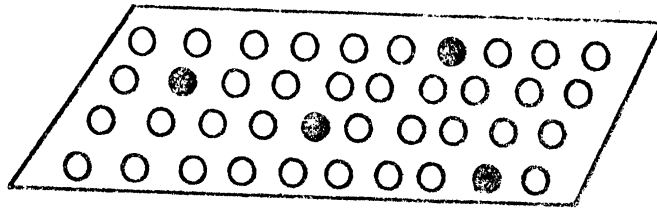
In Table 3, we have listed the data elements recorded by Huffaker (1958, 1962). The collection of these data elements constitutes \mathcal{R}^t the real system data till time $t = \text{June } 1961$. In Table 2, we distribute these data elements among the experimental frames. The data elements associated with a frame E in Table 2 constitute the subset $\mathcal{R}^t(E)$ of $\mathcal{R}(E)$, namely, the data acquired until time t in frame E .

Table 2 displays some frames as having "missing" data sets. A frame such as $E_{\text{food,prey,pred}}^{\text{global}}$ for which this is true is conceivable, i.e., it is an element of \mathcal{E} , but up to time $t = 1961$, no data has been collected for it i.e., it is not an element of $\mathcal{E}^{(t = 1961)}$. $E_{\text{food,prey,pred}}^{\text{global}}$ is marked as "missing" because the food amount at each individual orange is not recorded in the Huffaker experiments, even though certain aggregate utilizations are.

Although many of the conceivable frames were actually realized in the Huffaker experiments, in the current modelling effort we found that the missing frames often contained information which could have been extremely helpful. One of the benefits of representation of experimentation in the

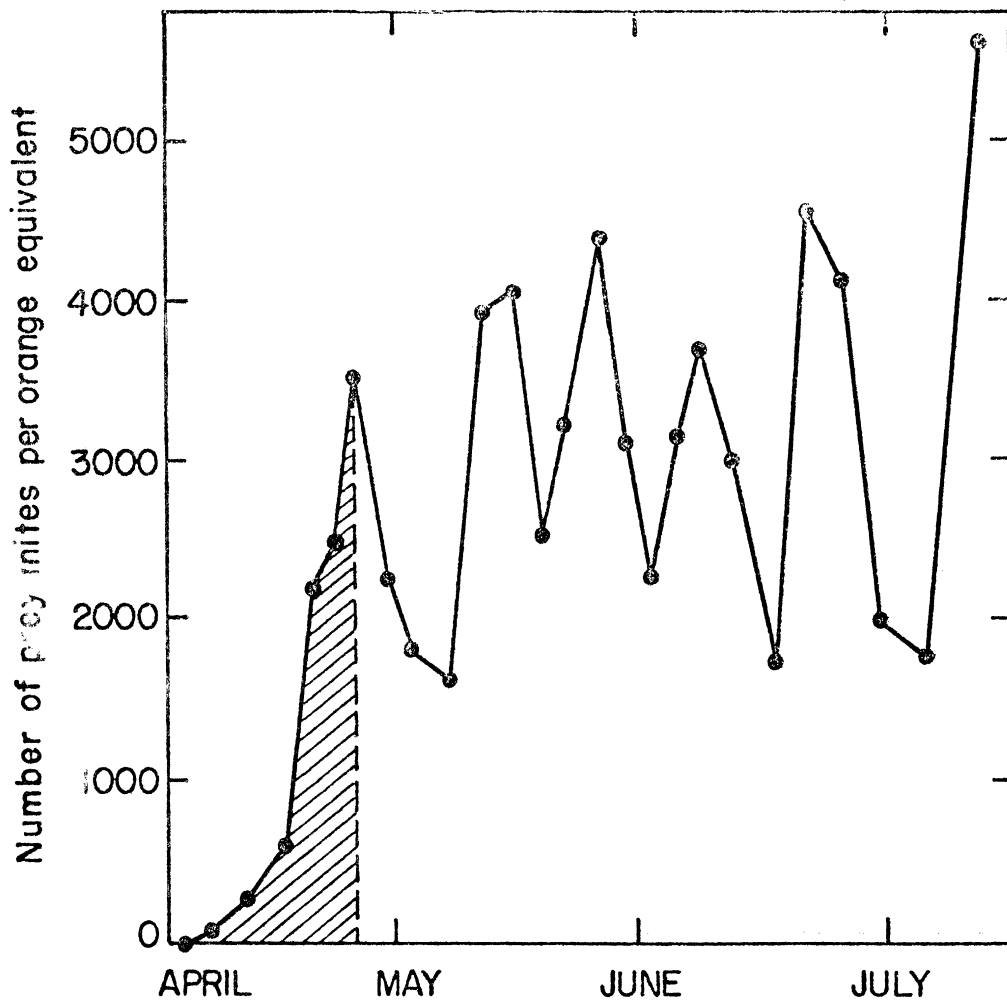
experimental frame formalism is that certain experiments may be suggested by the logical structure of frame organization which may turn out to be crucial in later modelling. These might not have been thought of in an unstructured experimental approach.

In a frame with control variables specified, the above concepts hold except that the compare variable readings are recorded only so long as the control variables remain zero. Thus for example in the class of frames denoted by $E_{\text{food,prey,pred}}^{\text{local}}$, each frame specifies a subset of cells S such that the food amount, prey, and predator counts of cells in S are the compare variables, and all other prey and predator densities are control variables. Data is collectable within such a frame so long as no prey or predators establish themselves on oranges other than those in S . When S consists of a single orange, such data give a picture of the local interaction of food, prey and predators uncontaminated by colony establishment on other oranges,



a)

(Captions to be found at end of paper)



b)

Figure 1

or subsequent remigration from these colonies. While Huffaker did no experiments with single oranges, the same principle holds when S is taken as the subset of initially seeded oranges, given Huffaker's observation that migration occurs only due to food depletion or overpopulation (indeed, this is the basis of our discrete event models). For example, see Fig. 1 .

We note that "keeping control variables zero" is a special case of the "range of validity" specification given by Zeigler (1976, Chap. 11).

4.1. Organization of Frames

The frames in \mathcal{E} are partially ordered by a relation "is derivable from" or in short " \leq ". $E' \leq E$ means that the restrictions on data acquisition imposed in frame E' are over and above those in frame E . As a consequence, data collectable in E' can also be deduced from data collectable in E and questions posable in E' are posable in E as well.

Formalizing one step further, we require an onto mapping from $\mathcal{D}(E)$ to $\mathcal{D}(E')$ where mapping D to D' has the interpretation that data set D' is derivable from data set D (we write $D' \leq D$) by employing the unique set of operating specified by the pair (E', E) . Such operations will in general be information destroying in nature, so that, questions answerable given D cannot be answered given D' .

Figure 2 displays the "is derivable from" relation in our current example. Three types of operations are employed in this case to reduce data sets, one to another. This is apparent in the following definition given first for frames having no control variables:

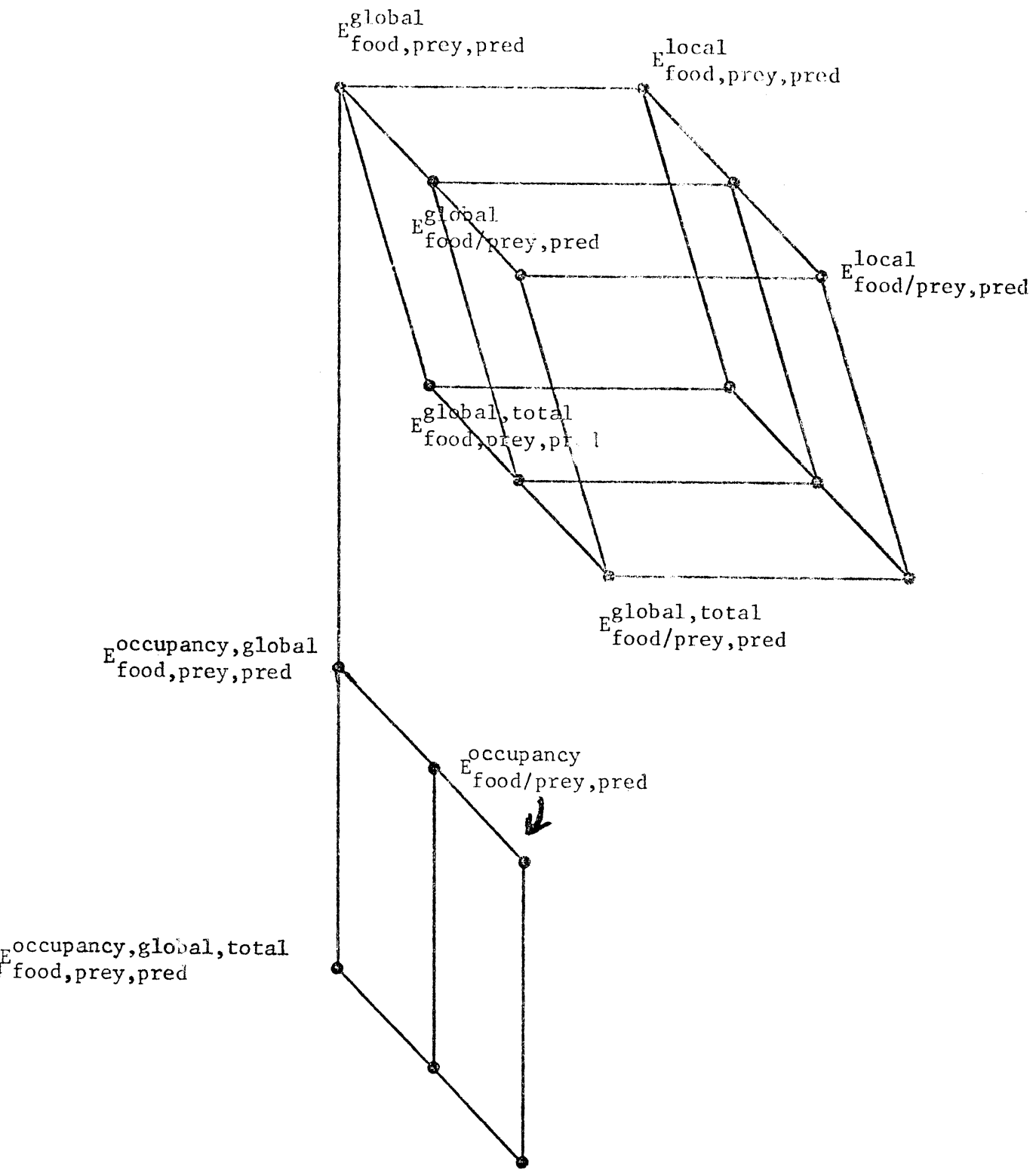


Figure 2

$E \leq E'$ if:

1. the compare variables of E are a subset of compare variables of E'

or

2. the compare variables of E are simple sums of the compare variables of E' ,

or

3. the compare variables of E are obtainable by discretizing the compare variables of E' (for example, the variable with range {empty, some prey, maximum prey} is obtainable from the variable "prey count",

or

4. any composition of the above .

The operation types associated with 1., 2., 3. above are selection, aggregation, and coarsening, respectively.

For frames having control variables the definition is

$E \leq E'$ if:

- a) the compare variables of E may be computed from the compare variables of E' employing selection, aggregation or coarsening, in any composition (as above).
- b) the control variables of E include those of E' , and if there are any additional control variables in E , they may be computed from the compare variables of E' employing selection, aggregation and coarsening, in any composition.

In Figure 2 and Table 2, the frames are further organized into planes. Frames in the same plane are relatable using only the selection operation.

If $E \leq E'$, then we place E on a lower plane than E' if at least one aggregation or coarsening operation must be used to derive the variables of E from those of E' . In fact, the minimal number of such operations necessary to make this derivation is a measure of the distance between planes. In particular, the distance from the base, or most inclusive, plane to a given plane is a measure of the degree of abstraction embodied by the latter plane.

Note however that the \leq relation is a partial order so that there may be more than one distinct plane with the same degree of abstraction.

Table 1 shows the naturalness of the plane notion in the ecosystem context by relating the plane of a frame to the kind of question possible with in it. As expected, the higher the degree of abstraction, the more restricted the questions possible. But note that the global/local distinction does not involve a change in degree of abstraction.

5. Constructed Models

Table 4 provides summary descriptions of the models constructed to date, $N_t = 1977$. The conceptual basis for the Occupancy and Random-Phase-Space models has been fully described by Zeigler (1977b). We proceed to describe our base model and the discrete event lumped model derived from it.

5.1. Base Model

The base model postulates food, prey, predator interaction on an orange in isolation to be specified by the differential equation:

$$\frac{dr}{dt} = -ux \text{ pos}(r) \quad \dots 1a)$$

$$\frac{dx}{dt} = (b \text{ pos}(r) - d)x - cxy \quad \dots 1b)$$

$$\frac{dy}{dt} = -d'y + c'xy \quad \dots 1c)$$

where r is the food amount (measured in fraction of unused orange surface), x , y are prey and predator population sizes, and $\text{pos}(r)$ is 1 if r is positive and 0 otherwise. The meaning attached to the 6 parameters involved is given Table 5. The underlying time unit is one day.

Table 4

Models and Brief Description

<u>Model</u> (Formalism)	<u>Description</u>
<u>Base</u> (Combined differential equation-discrete event; Combined stochastic-deterministic)	Local state (situation on each orange) determined by Lotka-Volterra type differential equation governing joint food, prey, and predator dynamics; impetus for emigration and the effect of immigration are logically determined from local state (food, prey, predator); migration process is of stochastic random walk variety; orange replacement schedule simulates that employed by Huffaker.
<u>Lumped</u> (Discrete Event; Combined Stochastic-deterministic)	Keeps track of same state variables as base model but updates them only at "event" times. The tables required for scheduling events and executing the updates were derived from base model local interaction as discussed in text.
<u>Occupancy</u> (Discrete Event; Combined Stochastic-Deterministic)	The local situation is represented by a small number of discrete states (empty, some prey, etc.) and the migration processes are simplified to the Bernouli trial type.
<u>Random Phase-Space</u> (Differential Equation; Deterministic)	Derived from Occupancy Model under random phase-random space hypothesis. Describes the dynamics the occupancy probabilities of the discrete states when occupancy model is operating in random phase-random space mode.

Table 5

Use of Experimental Frames in Identifying Model Parameters

<u>Model Component</u>	<u>Parameter</u>	<u>Description</u>	<u>Identified in Experimental Frame:</u>
Local Interaction (large population model)	b	prey birth rate	E ^{local, total} food, prey/pred
	d	prey death rate	"
	u	prey food utilization	"
	d'	predator death rate	E ^{local, total} food, prey, prey
	c	predation rate	"
	c'	predation efficiency	"
Food Replenishment	threshold	threshold on prey population below which orange is replaced	E ^{local, total} food, prey/pred
Prey migration	pyrem	prey fraction remaining after emigration	E ^{global, total} food, prey/pred
	pysurvive	probability of migrating prey finding a cell	"
	meanpysearch	mean search time for prey finding a cell	"
	pydif ₁ , pydif ₂	prey diffusivities in horizontal and vertical directions	"
Pred Migration	pdrem	analogous	E ^{global, total} food, prey, pred
	pdsurvive	to	"
	meanpdsearch	prey	"
	pddif ₁ , pddif ₂		"
Local Interaction (small population model)	d''	predator death probability at low prey size	E ^{global, total} food, prey, pred
	c''	minimum prey required to initiate predator reproduction	E ^{global, total} food, prey, pred
	\bar{c}	fraction of prey used to create 1 predator	E ^{global, total} food, prey, pred

Equation 1a asserts that food utilization is proportional to prey density (recipient limited interaction) so long as food remains. Eqs. 1a and 1b are Lotka-Volterra relations without self-limitation.

We assume, following Huffaker's observations, that prey migrate only when food is exhausted (r first becomes 0). The migration is effected as follows:

1. When (and if) food is exhausted, a fraction \underline{pyrem} of the current prey remain on the orange (and are subject to the dynamics of Eq. 1).
- 2) Of the migrating prey [(1- \underline{pyrem}) times current population)], a fraction, $\underline{pysurvive}$, are assumed to actually reach a cell (the rest are lost to the system)
3. For each of the migrating individuals, a search time T_s is sampled from an exponential distribution with mean $\underline{meanpysearch}$.
4. The cell assigned to the individual is computed by quantizing spatial coordinates derived from normal distributions (independent for each dimension) with mean, the current cell location and standard deviation $\underline{pydif}_1 \cdot \sqrt{T_s}$ (in case of horizontal dimensions) or $\underline{pydif}_2 \cdot \sqrt{T_s}$ (in case of the vertical dimension).
5. After time T_s has elapsed, the individual is added to the population of his assigned cell if food remains there; otherwise, with probability $\underline{pysurvive}$, he is sent to step 3) for further migration (with probability, 1- $\underline{pysurvive}$, he dies).

The migration thus implemented is a random walk with constant probability of stopping. We postulate our mites to search blindly and "bump into" orange locations. It is important to note that emigration is not continuous but occurs only at certain points in the local cycle. We have shown (Zeigler, 1977b) that continuous migration is unlikely to stabilize a locally unstable system such as Huffaker's.

Predator migration is carried out exactly as prey migration with respective parameters \underline{pdrem} , $\underline{pdsurvive}$, \underline{pddif}_1 , \underline{pddif}_2 with the following exceptions:

- 1') Predator migration is initiated when a local maximum in predator density is reached
- 5') After time T_s has elapsed, the individual is added to the population of his assigned cell unless the prey population is below \underline{eqprey} , the equilibrium prey level computed from Eqs. 1b) and 1c).

If the prey population is below \underline{eqprey} , a small-population stochastic model takes effect. With probability \underline{pdrem}' , the invading predator remains, otherwise it is migrated as in step 3). A predator that remains dies with probability d'' . If the predator lives, it creates another predator if there are at least c'' prey and $\bar{c}\chi$ are used up as a result (where χ is the current prey population size).

The foregoing decision sequence is instantaneously computed and with $T_s = 1$, the predator(s) are returned to step 5').

Note that although the small-population submodel is a stochastic version of the deterministic Lotka-Volterra model used for large numbers, it may be a crude summary of the local interaction in these circumstances, thus optimal settings of the primed parameters may bear little relation to their deterministic counterparts.

Indeed, our methodology suggests that a second level spatial characterization of each orange could be built. Such a model would be tuned to more finely structured local observations and a simplified version would replace (or perhaps turn out to be identical with) our current base submodel. In our general terminology, no such experimental frame currently belongs to Σ^t , though one might be forced to create such a frame, if the current models (in which the small-population submodel participates) prove unable to match the data gathered within existing frames. (See Appendix.)

5.2. Discrete Event Lumped Model

Our first lumped model (illustrated in Figure 3) is a discrete event version of our base model. The migration is unchanged but the local interaction is described in summary transition function form obviating the necessity for step-by-step simulation of the differential equations.

For example, consider the food-prey submodel, Eqs 1a) and 1b) with $y = 0$. For positive $r(0)$, it is possible to solve analytically to find

$$r(t) = r(0) - \frac{u}{a} (x(t) - x(0)) \quad \dots 2a)$$

$$x(t) = x(0) e^{at} \quad \dots 2b)$$

where $a = b - d$ (net prey growth rate).

The time for r to reach 0 is given from Eq. 2 by

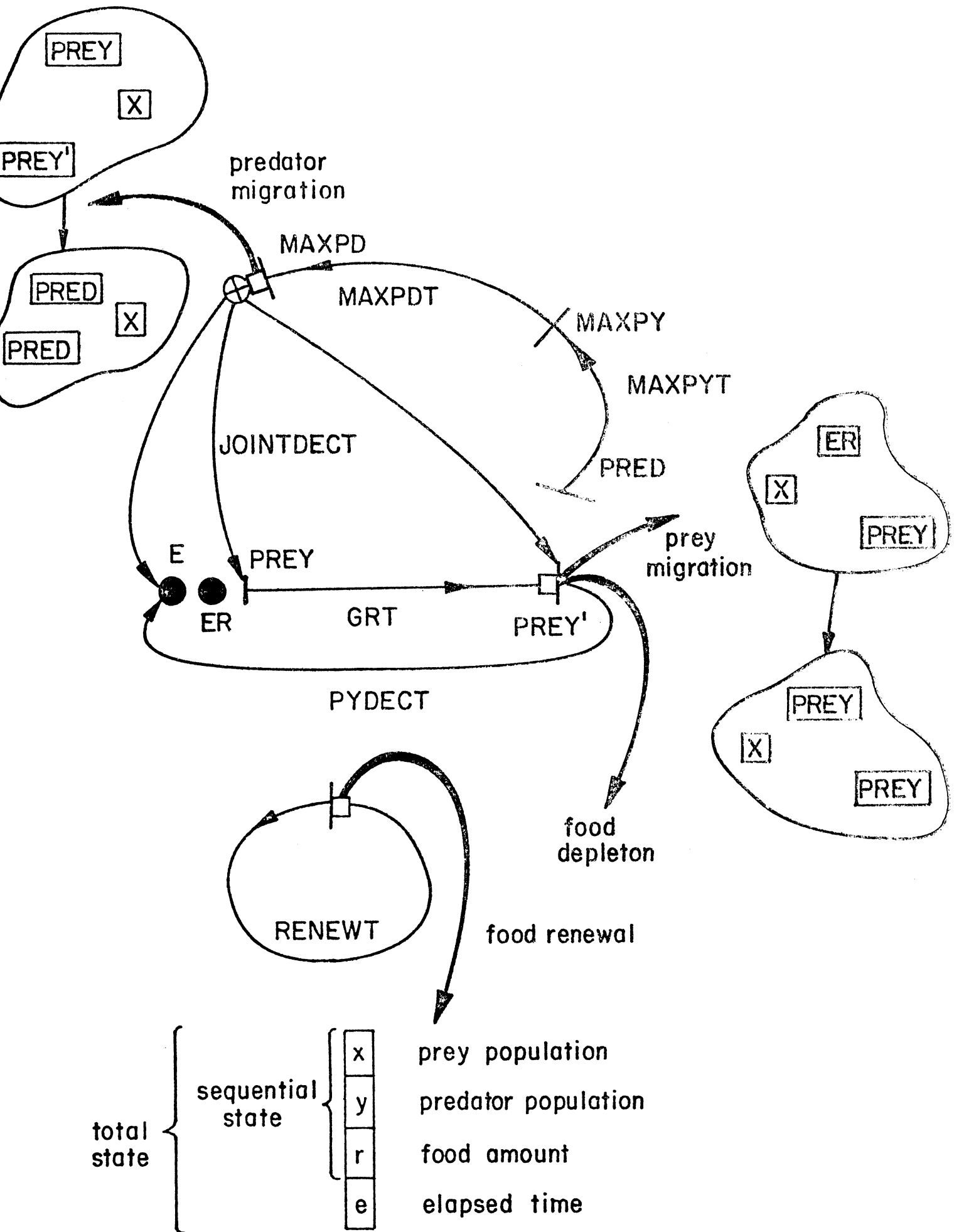


Figure 3

$$\tau = \frac{1}{2} \ln \left[\frac{ar(0)}{ux(0)} + 1 \right] \quad \dots 3a)$$

and the prey population at that time is:

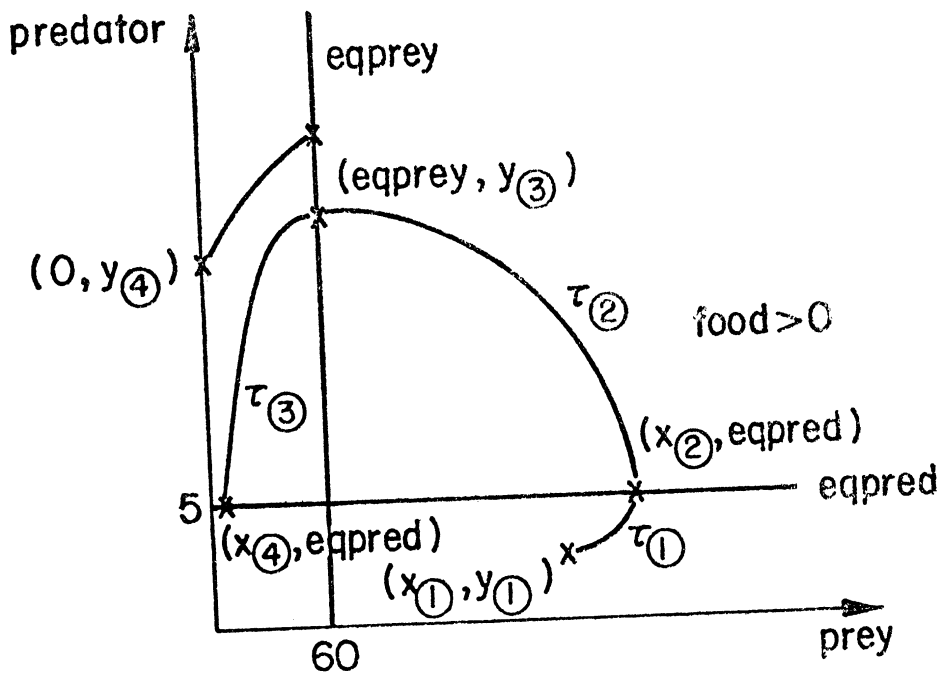
$$x(\tau) = \frac{ar(0)}{u} + x(0) \quad \dots 3b)$$

The discrete event model keeps track of the values r, x , and y for each cell. If at some time t , a prey individual migrates to an empty cell with food amount Eq. 3a), with $x(0) = 1$ and $r(0) = r$ is used to schedule the subsequent emigration occur at $t + \tau$). When the emigration event occurs, Eq. 3b) is used to update the prey population, and of course, the food amount is set to zero. The consequent prey die-out is scheduled to occur in elapsed time $(1/d) \ln[x(0) \cdot p$

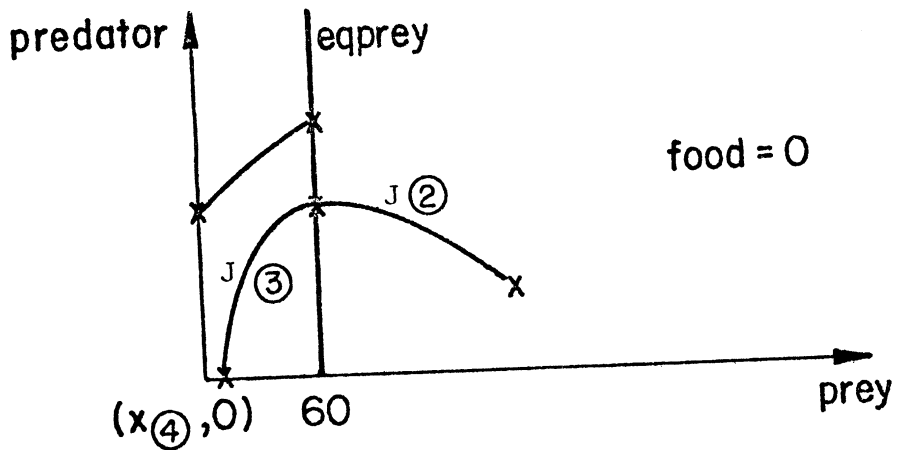
At every subsequent immigration the cell state is updated. Suppose that a time e has elapsed since the last immigration. Then using Eq. 2 with $t = e$, and $r(0), x(0)$ being the values at the last update, the correct state pertaining just before the immigration is computed. To the prey number so computed we add 1 to account for the immigrating individual and then use Eq. 3a) to reschedule the emigration event.

It can be shown that this discrete event algorithm exactly reproduces the behavior of the base model prey-food interaction. The addition of the predator is handled in principle in the same way, except that the scheduling and update functions cannot be obtained analytically but can be approximated with a once-and-for-all sampling of the trajectories generated by Eq. 1 (Zeigler, 1977c). We shall provide a brief description of this process.

Consider the case where prey have colonized an orange but have not yet exhausted the food. Then Eqs 1b) and 1c) reduce to the Lotka-Volterra dynamics and one easily obtains the equilibrium prey and predator isoclines, namely



a



b

Figure 4

$$x^* = eqprey = d'/c'$$

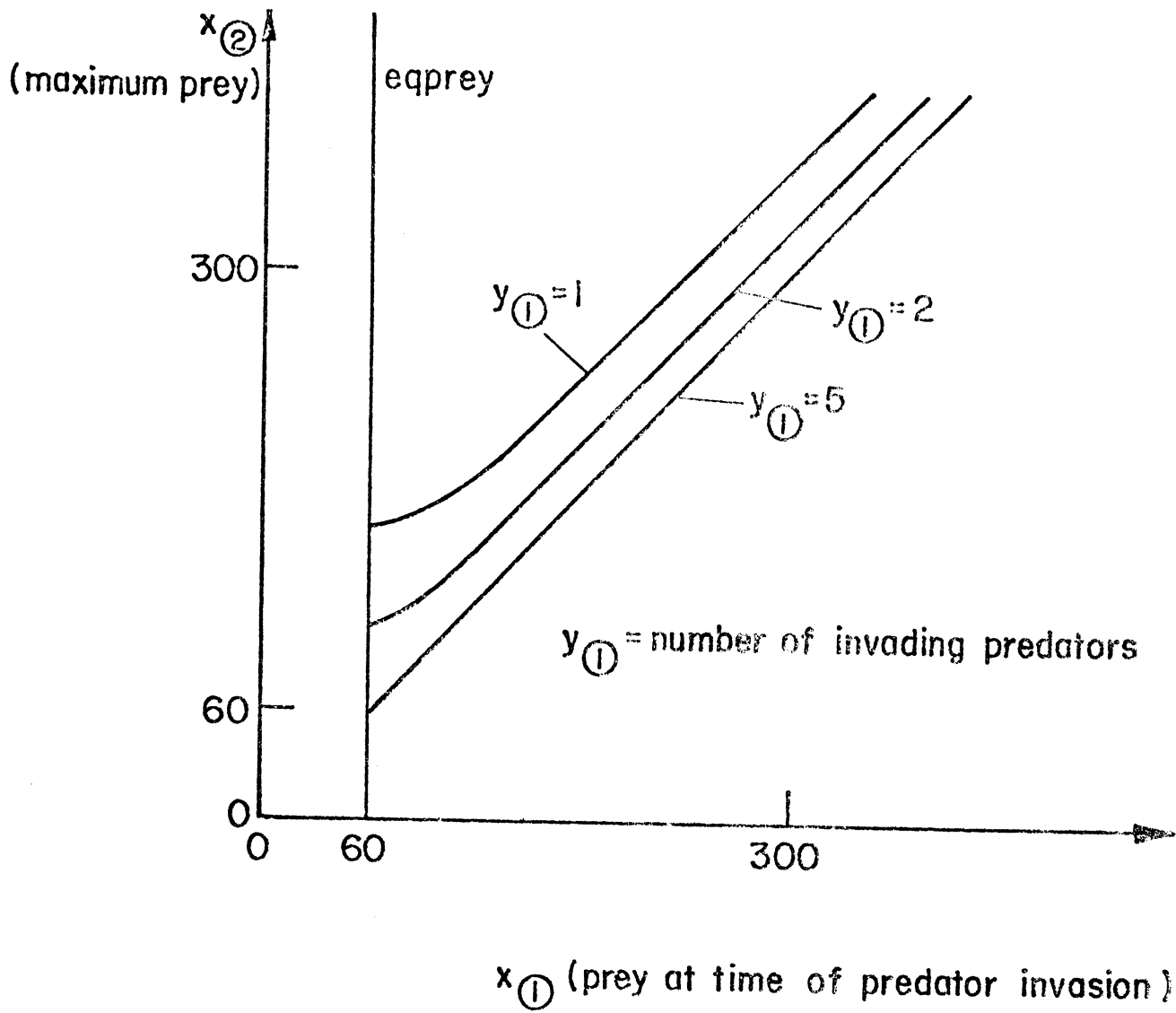
$$y^* = eqpred = c/a$$

These isoclines divide the plane into four regions as shown in Figure 4a). A typical trajectory initiated by a predator immigration is segmented into an initial joint growth phase $\tau_{(1)}$, a predator growth phase $\tau_{(2)}$ and a joint decline phase $\tau_{(3)}$. Generalizing Huffaker's observation to predators, we postulate that predators emigrate at maximum predator population at the end of the $\tau_{(2)}$ phase on the eqprey isocline and at the end of the $\tau_{(3)}$ phase when the prey minimum is reached (either a crash occurs if predators are numerous enough or the eqpred isocline is reached). Any prey left are assumed to remain on orange and subsequently take part in the standard food-prey interaction.

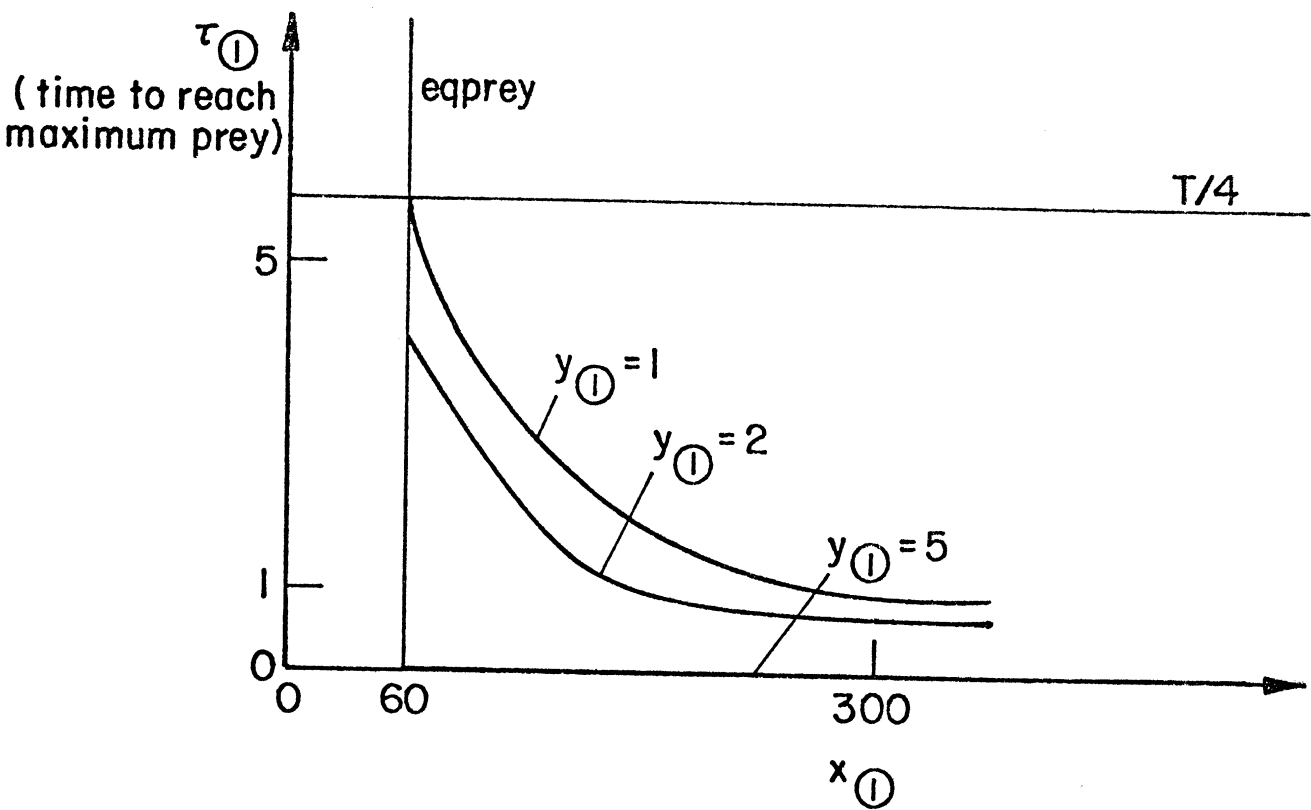
Scheduling and updating for each of these boundary crossings was done by use of tables generated from a CSMP simulation of Eq. 1 and shown in Figure 5. These tables are interesting in themselves; to our knowledge, they represent the first such global study of Lotka Volterra dynamics. The parameter T shown is the period of the cycle obtained by linearization around the equilibrium point, $T = 2\pi/\sqrt{ad}$. The time to cross from one boundary to the next is approximately $T/4$ near the equilibrium but declines rapidly as initial populations increase.

A disadvantage of the generating tables by simulation is that it must be done potentially anew for each set of parameters. This makes it important to be able to identify the local interaction parameters before all others (Section 7.1).

The theoretical basis for discrete event representation of systems is given by Zeigler (1977c).



a



b

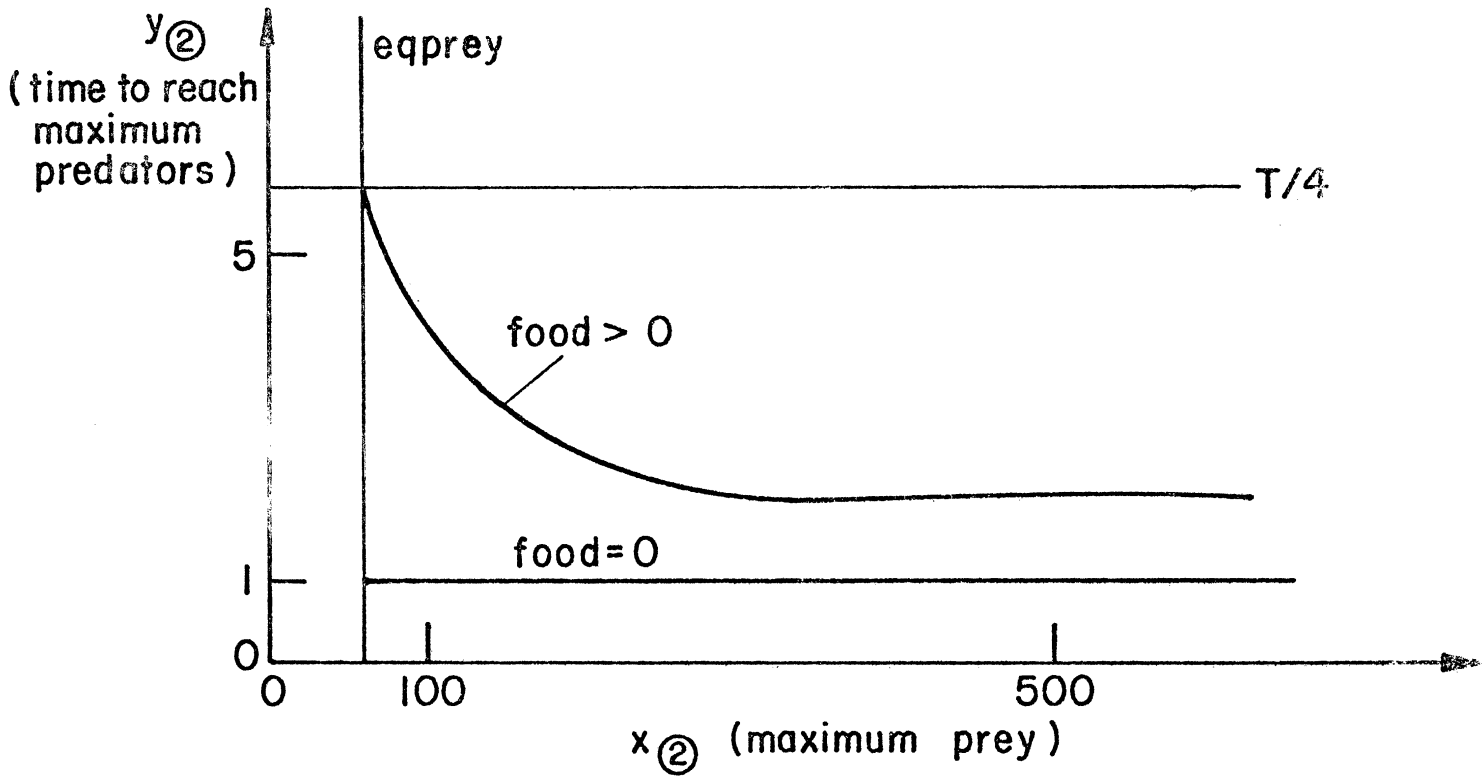
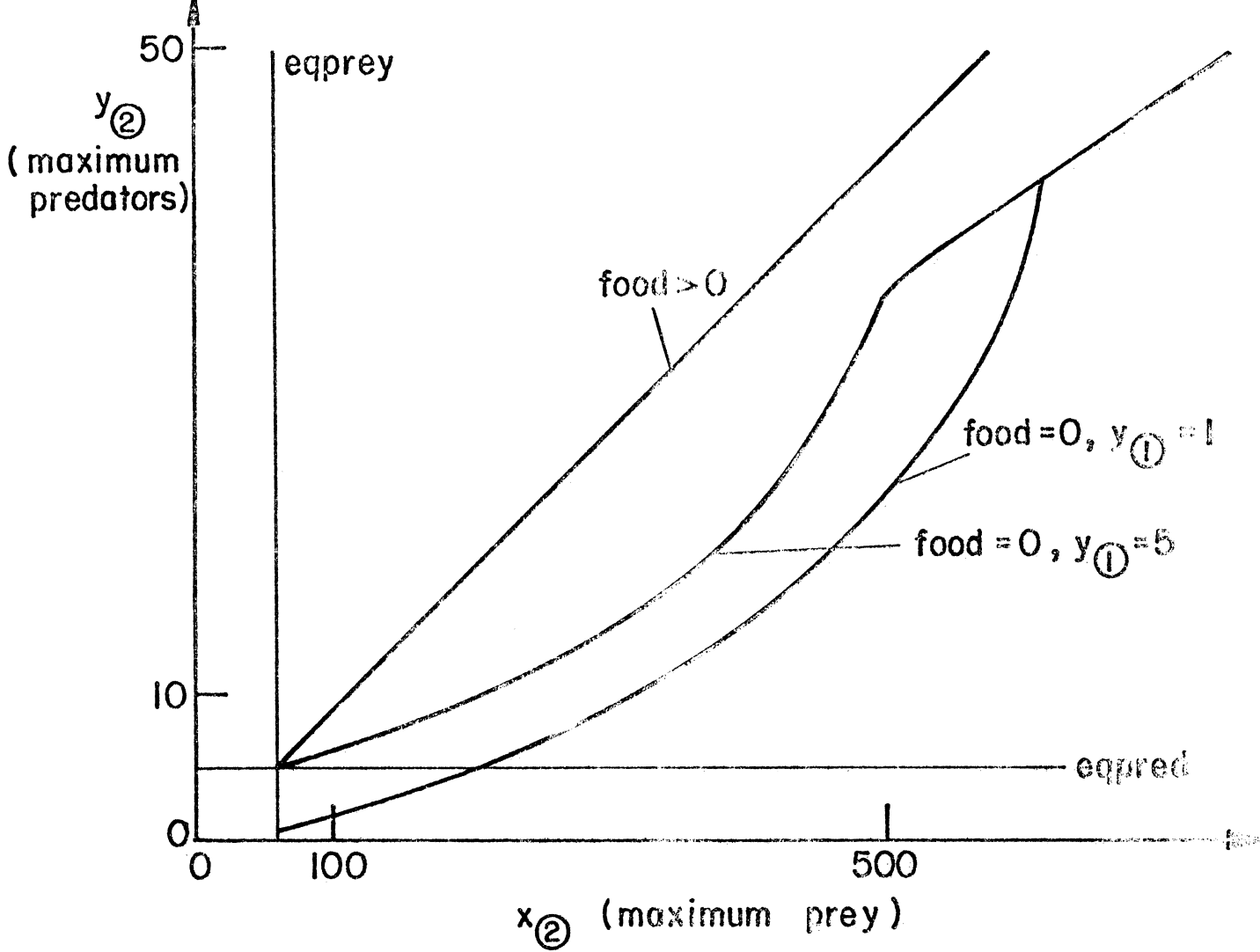


Figure 5

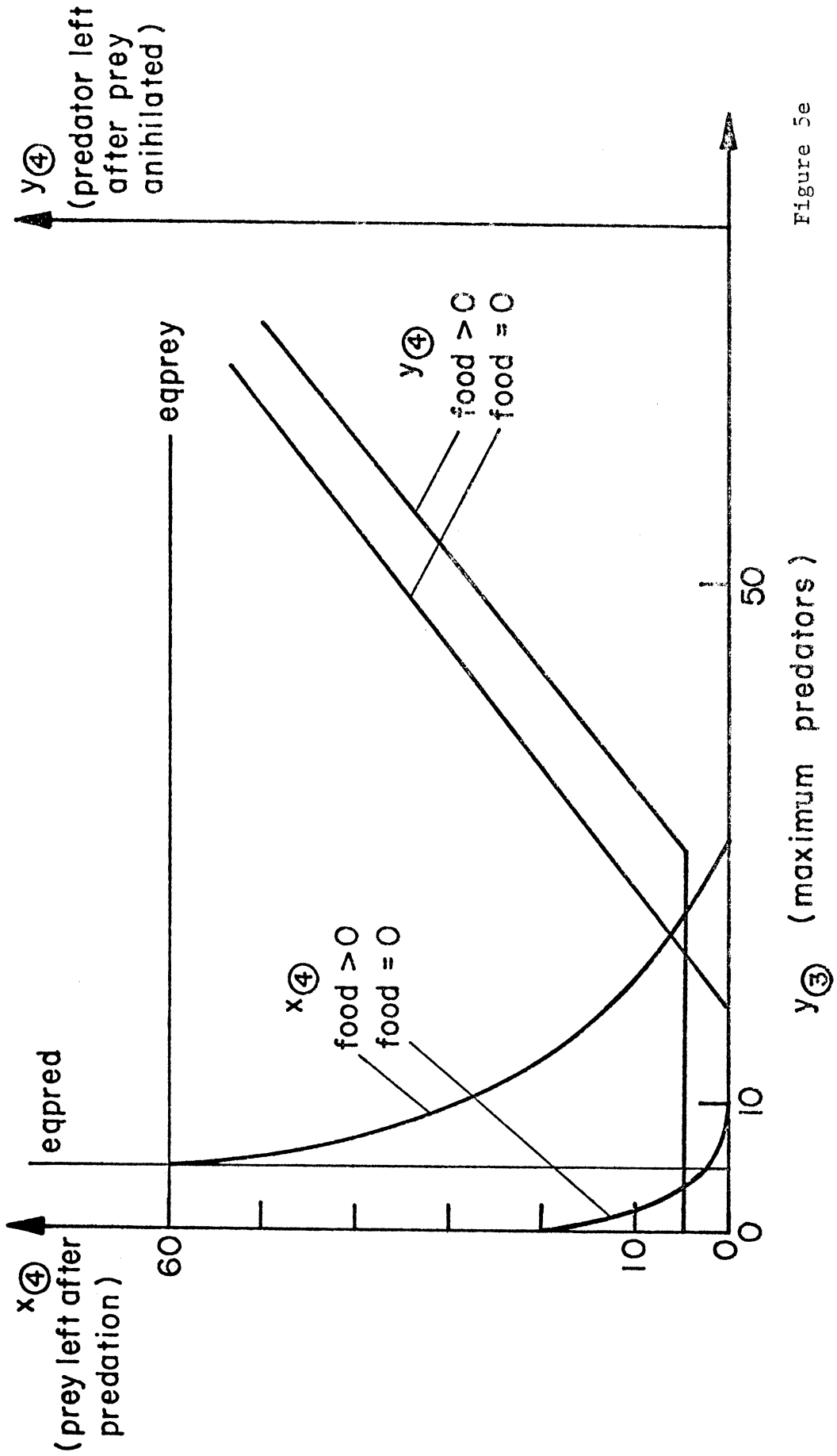


Figure 5e

y_3 (maximum predators)

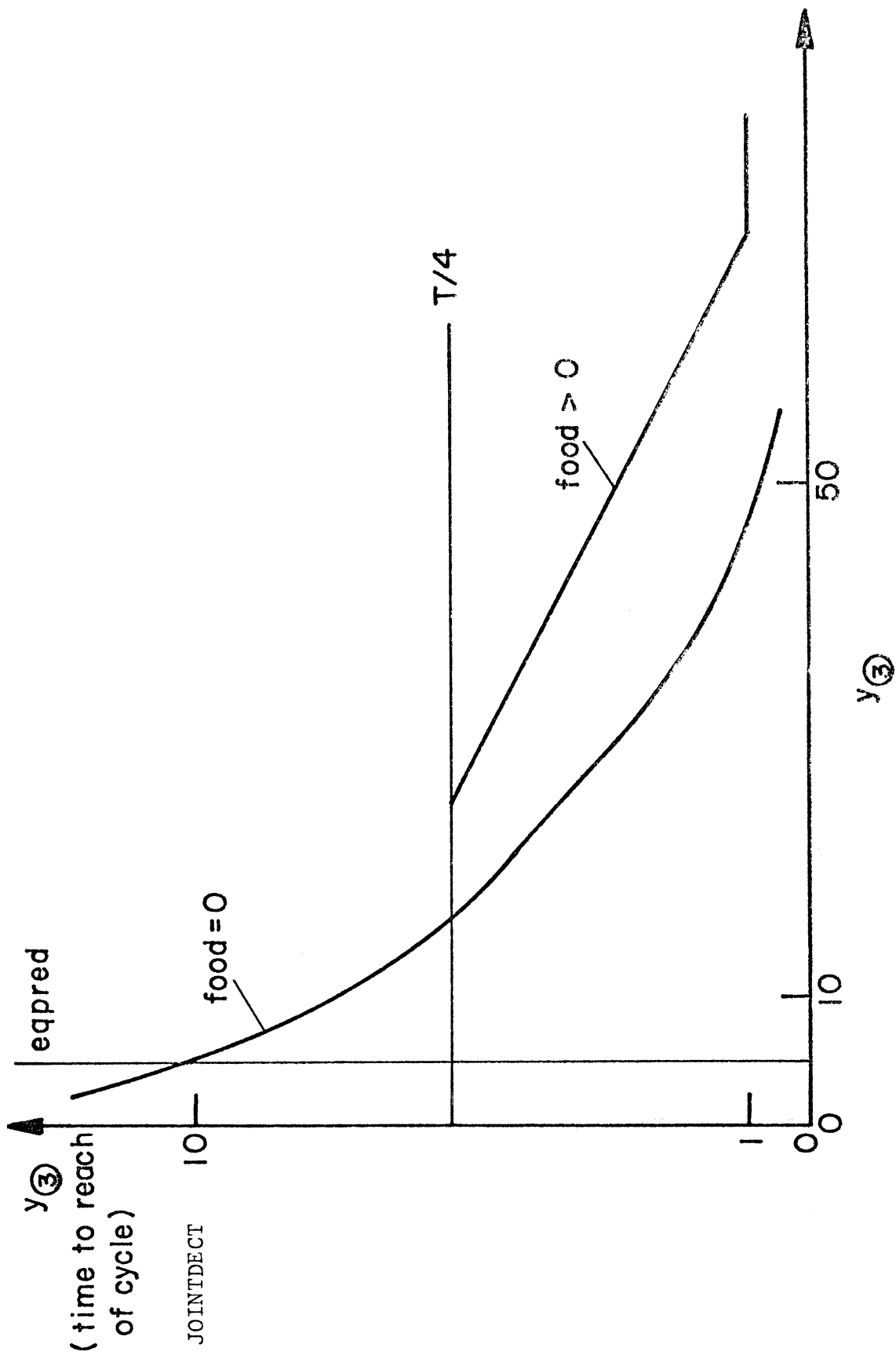


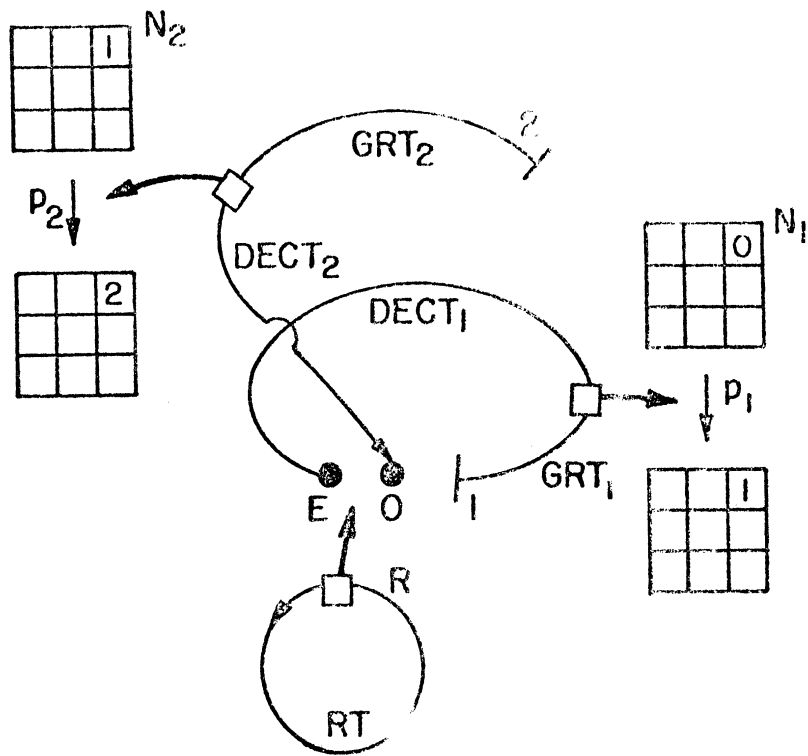
Figure 5f

5.3. Occupancy Models

The overall occupancy model is described in Figure 6. As can be seen, the local description is reduced to a small number of states (empty, patch occupied by prey only, etc.) and the local dynamics are reduced to timed transitions from state to state. The migration component is also simplified by specifying neighborhoods for each species (for each cell) and migration is effected by means of independent Bernouli trials governed by specified probabilities and conditions at the cells in the neighborhood of a migration-active cell. (See Zeigler, 1977b for a full explanation.) Cell spaces up to quite large sizes (we have commonly investigated 30×30 arrays [900 cells]) can readily be simulated in discrete event languages such as SIMSCRIPT. We are able to study by this means the spatial patterns which are associated with persistence and extinction as they are governed by the geometry of the space, the characteristics of the neighborhoods, and the settings of the other parameters.

5.4. Random Phase-Space (RPS) Models

The RPS hypothesis assumes that the cells in a given state are uniformly distributed in both space and phase (elapsed time in the state) at all times. On the basis of this hypothesis we may derive the differential equation system shown in Table 6. These equations are simple enough to be solved for equilibrium isoclines and thus give qualitative information about how persistence is governed by the various parameters. Here persistence is judged relative to prespecified extinction levels such that if the prey and predator occupied cell fractions fall below these levels the system is



cell

E. Wait

O. Wait

1. Hold (GRT₁)

\forall cell' in $N_1(\text{cell})$,
 cell' in 0 \rightarrow cell' in 1
 P_1

Hold (DECT₁) go to E

2. Hold (GRT₂)

\forall cell' in $N_2(\text{cell})$,
 cell' in 1 \rightarrow cell' in 2
 P_2

Hold (DECT₂) go to O

R. Hold (RT)

cell in E \rightarrow cell in O

go to R

Figure 6

Table 6

Random Phase - Space Model

Let x = fraction of cells in state 1 (some prey)
 y = fraction of cells in state 2 (some prey, some predator)
 z = fraction of cells in state 0 (empty, some food)
 u = fraction of cells in state \bar{E} (empty, no food)

Then

$$\frac{dx}{dt} = -\frac{x}{T_1} + zx \frac{p_1 N_1}{T_1} - yx \frac{p_2 N_2}{T_2}$$

$$\frac{dy}{dt} = -\frac{y}{T_2} + yx \frac{p_2 N_2}{T_2} \quad u = 1 - (x + y + z)$$

$$\frac{dz}{dt} = \frac{u}{RT} - zx \frac{p_1 N_1}{T_1} + \frac{y}{T_2}$$

where

$$T_1 = GRT_1 + DECT_1, \quad T_2 = GRT_2 + DECT_2$$

Equilibrium Relations

<u>Equilibrium fraction</u>	<u>no predator (food, prey/pred)</u>	<u>some predator (food, prey, pred)</u>
x^* (avg. prey cell)	$1 - (p_1 N_1)^{-1} / 1 + RT \cdot T_1^{-1}$	$(p_2 N_2)^{-1}$
y^* (avg. pred cell)	0	$\frac{1 - (p_1 N_1)^{-1} - (p_2 N_2)^{-1} (1 + RT \cdot T_1)^{-1}}{1 + p_2 N_2 T_2^{-1} (p_1 N_1)^{-1} T_1}$
z^* (avg. food cell)	$(p_1 N_1)^{-1}$	$(p_1 N_1)^{-1} + y^* p_2 N_2 T_2^{-1} (p_1 N_1)^{-1} T_1$
u^* (avg. utilization)	$1 - (x^* + z^*)$	$1 - (x^* + y^* + z^*)$

assumed to go extinct. Moreover, the equations can be easily simulated to generate the associated dynamic behavior. The predictions thus made can be matched against the behavior of the simulated occupancy models, to the advantage of both model types (see Validation, Sec. 7).

6. Organization of Models

We display the hierarchy of models in Figure 7. Models are organized in a manner parallel to that of experimental frames. Model M is on the same plane with model M' if M is a subcomponent of M' . Models of greater degrees of abstraction (lower level planes) are derived from more refined models by simplification procedures based on aggregation, coarsening and discrete-eventization (as discussed in Section 3).

The criterion which justifies the simplification is that the mappings involved be homomorphisms. We have given extensive expositions of such model relations (Zeigler, 1976a) and their use in organizing models (Zeigler, 1977b). For an exposition and example in the compartmental ecosystem context see (Zeigler 1976b).

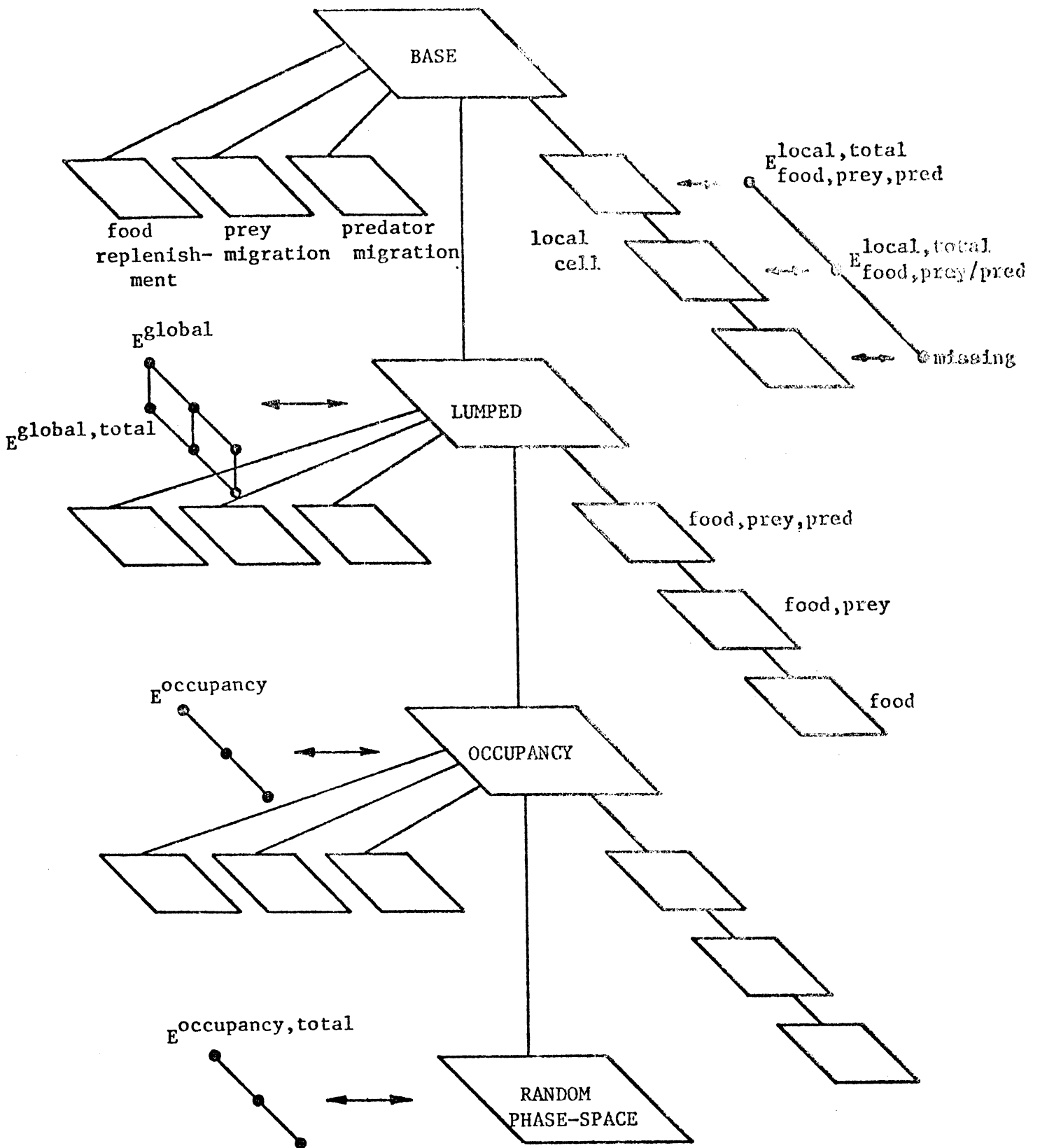


Figure 7

5.1 Relation of Parameters

Basically a homomorphism between models is a correspondence between their state spaces in which corresponding states transit to corresponding states and yield corresponding outputs. Such a relation usually implies a correspondence between parameter values as well, so that parameter settings of a lumped model may be completely determined by those of a more refined morphic preimage.

Indeed, we have given an example of such a parameter correspondence in our derivation of the discrete event lumped model (Section 5.2). The scheduling and update tables of the discrete event model are parameters — one can treat them as entities to be arbitrarily adjusted until the desired behavior is achieved. On the other hand, the morphism, which underlies the construction of the lumped model uniquely prescribes these tables for each setting of the local interaction parameters (b, d, u, d', c, c') .

The same concept of parameter correspondence is illustrated in the parameter complexes appearing in the RPS equations, as determined by the parameters of the occupancy model. (Table 6).

To complete the chain, we should indicate how the parameters of the occupancy model are related to those of the more refined discrete event lumped model. In this case, however, a morphism cannot be established to hold strictly over the complete state spaces of the two models and we must be content with estimating average parameter value settings, or at least, ranges to which they can be bounded. We now outline how this may be done.

In Table 7 we provide ranges for the patch life cycle parameters GRT_i, DCT_i $i = 1, 2$. The derivation is straightforward from Section 5.2. Although the

Table 7

Estimation of Occupancy Model Parameters

<u>Parameter</u>	Range of Values in Terms of Lumped Discrete Event Model <u>Parameter Values</u>
GRT ₁ (Growth Time of Prey Colony)	$[0, \frac{1}{a} \ln \frac{ar_0}{u}]$
DCT ₁ (Decay Time of Prey Colony)	$[0, \frac{1}{d} \ln \frac{ar_0}{u}]$
GRT ₂ (Time to Maximum Predator Population)	$[0, T/2] \quad (T = \frac{2\pi}{\sqrt{ad}})$
DCT ₂ (Time to extinction of Predator Population measured from Maximum Population Point)	$[0, T/4]$
P ₁ N ₁ (Effective Prey Colonization Neighborhood)	From Fig. 8 with number of samples $= \frac{ar_0}{u} (1 - \underline{pyrem}) \cdot \underline{pysurvive}$ and random walk parameters $\underline{meanpysearch}, \underline{pydif}_1, \underline{pydif}_2$.
P ₂ N ₂ (Effective Predator Colonization Neighborhood)	From Fig. 8 with number of samples $= \frac{c}{c'} \cdot \frac{ar_0}{u} \cdot (1 - \underline{pdrem}) \cdot \underline{pdsurvive}$ and random walk parameters $\underline{meanpdsearch}, \underline{pddif}_1, \underline{pddif}_2$.

migration mechanisms in the lumped and occupancy models are not directly comparable they can be matched through the notion of effective neighborhood. The effective neighborhood of a species is the expected number of cells colonized in a migration episode, given that all cells in the space are colonizable. In the occupancy model this is just $p_i N_i$ for species i . In the more refined model, the effective neighborhood is the expected number of distinct cells accessed in a migration episode. Figure 8 plots the number of distinct cells accessed versus the number of samples taken from the random walk distribution (with parameters typical in the case of extended coexistence). The maximum number of distinct cells accessed can be estimated by noting that the random walk distribution with mean search time and diffusivity d in one dimension appears (from simulation) to be normally distributed with standard deviation $\sigma = d\sqrt{T_s}$. Thus, the number of distinct cells rises at first in proportion to the number of samples; then it approximates the number contained within a radius 3σ of the active cell as the number of samples increases to moderate values. (Theoretically it continues to rise very slowly beyond this point.) Now the number of samples in the migration episode is just the number of migrants and can be bounded above as indicated in Table 7. Combining this number with Figure 8 yields the effective neighborhood bound.

Finally, we note that yet more refined models can be postulated which would place constraints on the parameters of the base model. Thus in our base model, the prey death rate in a patch d , the probability of survival, pysurvive, and the search time parameter, meanpysearch, are independently adjustable. If we postulate that a migrant survives only if his lifetime

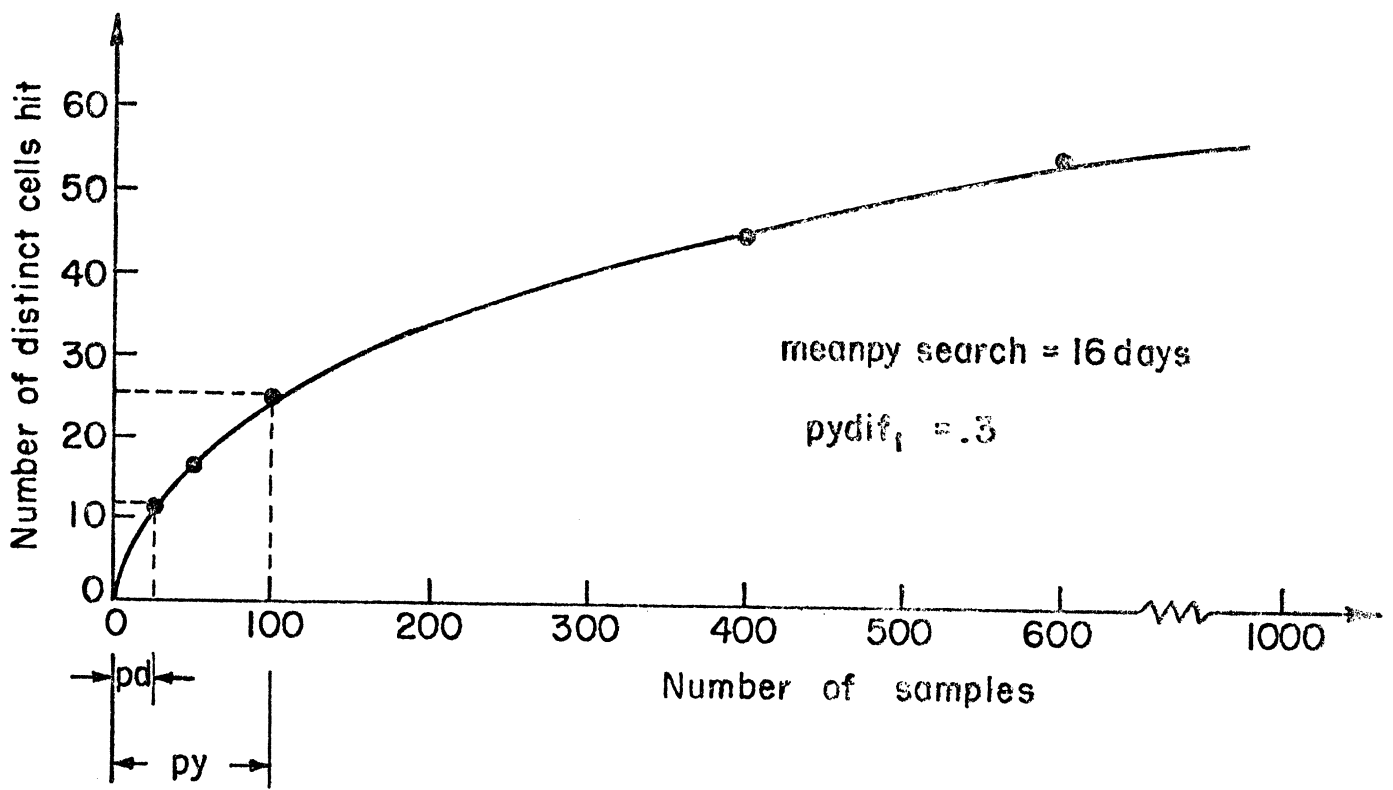


Figure 8

exceeds his search time, where these random variables are independent and exponentially distributed we derive the relation:

$$\underline{\text{pysurvive}} = \frac{1}{1 + d \cdot \underline{\text{mean pysearch}}} \quad \dots 4)$$

Parameter values obtained after adjustment can be checked against this relation. Large discrepancy might indicate dependence of the variables or give cause to reexamine the model structure and/or parameter settings.

7. Applicability of Frames to Models

A frame E is applicable to a model M if the compare variables specified by E are

1) included among the descriptive variables of M

or

2) may be obtained from the descriptive variables of M by aggregation or coarsening.

Figure 7 depicts the "core" of the applicability relation (see also Tables 1 and 5). "Core" is used here because one can infer applicability to higher plane models of frames applicable to lower plane models (Axiom 8; Zeigler, 1977b).

Roughly, if E is applicable to M , then M can potentially answer the questions of interest in E . M is valid for \mathcal{R}^t in E if M can reproduce $\mathcal{R}^t(E)$, the data collected up to time t in E . Viewed another way, E applicable to M means that the data $\mathcal{R}^t(E)$ may be employed to identify the parameters of M , i.e., the parameters may be adjusted until a best fit with the data $\mathcal{R}^t(E)$ is obtained.

7.1. Parameter Identification

As shown in Table 5 the experimental frame and model organizations made it possible to identify the parameters in a sequential manner, thus greatly reducing the search space at each stage. The parameters relating to: local food-prey interaction, local\food-prey-predator interaction, prey migration, predator migration and finally predator-prey (small-population) interaction, were adjusted in this order.

The test of such a procedure is that reasonable fits to the data are obtainable at later stages by holding fixed the parameters identified at earlier stages. When acceptable agreement at later stages cannot be obtained, this may indicate that the prerequisite independence assumed for earlier adjusted parameters does not hold. In terms of experimental frames, the control conditions of a frame may not in fact hold. Indeed, it often

is implicitly assumed by modellers that certain global interactions can be ignored in certain circumstances, and this may turn out be unjustifiable. In our case, the $E^{\text{local,total}}$ frames assume that migration effects have been nullified, the justification for which lies in Huffaker's verbal account of migration episodes accompanying the time series data.

If there is reason to doubt that the control conditions of an experimental frame are not satisfied, a readjustment of parameters may be attempted. To the extent that such a readjustment is small, the decomposition into experimental frames will have been beneficial.

In the Appendix, we report on the parameters identified in some of the key experiments and cross compare models in this regard.

8. Summary

The concepts discussed in the paper are summarized as follows:

$\mathcal{E}, \mathcal{R}, \mathcal{M}$ is the triple of conceivable experimental frames, real system data and possible models, respectively, underlying the modelling study of the Huffaker universes.

$\mathcal{E}^t = 1961$ is the subset of frames for which data had been collected until 1961. $\mathcal{R}_0^{t=1961}(E)$ denotes the data collected within frame E until 1961. $\mathcal{M}^t = 1977$ is the subset of models considered until 1977, the current time by the present modeller.

An experimental frame E in \mathcal{E} specifies a (compare, control) variable pair. A data element of a frame E is a time series of compare variable values obtained under conditions where control variables are kept at zero levels.

Frames are partially ordered by the derivability relation; $E \leq E'$ means that data elements of E are derivable from those of E' by employing selection, aggregation and coarsening operations. Each frame may be assigned a degree of abstraction equal to the minimum number of operations required to derive it from a fixed most inclusive frame.

Models may similarly be partially ordered by use of morphism relations. A homomorphism is a mapping from a refined model to a coarse one which preserves the transition structures. A homomorphism induces a mapping from the parameter assignments of the finer model to those of the coarse one.

If a frame E is applicable to a model M, this means that the behavior generated by M can be interpreted as data within frame E. One interpretation of this fact is that the real system data collected within E can be employed to identify the parameters of M.

9. Discussion

There are a number of levels at which the integrated approach to modelling illustrated here may be discussed. We briefly consider some of them.

9.1 Large Scale Multi-Faceted System Modelling

Our formalism has been constructed from a general starting point — the theory of systems and its specialization to modelling and simulation. Thus, it is aimed for application to "large scale" systems in general. We have placed the large scale in quotation marks to signify our belief that "large scaleness" is a matter of approach rather than of fact. Indeed, a real system is called large scale precisely when one recognizes that to deal with it successfully requires the consideration of many factors and aspects. There are some systems which strikingly have this characteristic — environmental systems, urban systems, etc., that are indeed large scale. But "micro scale" systems such as the biological cell are equally complex, when examined in all their facets. Thus we propose the term "multi-faceted" to connote the systems (viewpoint) we are addressing.

In this paper, we have illustrated our approach in a particular ecosystem context. But some general points clearly emerge. These are:

Simpler models can give qualitative and sometimes quantitatively accurate predictions.

The RPS model gives good estimates of average cell occupancy fractions when its underlying conditions hold. More generally it may give correct

qualitative relationships (effect of parameter settings) even when its quantitative predictions are inaccurate.

Simpler models can be employed to check more complex ones.

If the correspondence between models is known, behaviors of the models may be compared. This can be employed at:

a) the development stage; if the simpler model is known to be correctly implemented (or does not require simulation), then the logic of the more complex model can be verified by comparison of model behaviors (this is an important special case of redundancy use for program verification; Bosworth, 1976).

b) the prediction stage; the more the predictions of various models agree, the greater may be the confidence in the predictions. Where serious disagreements occur, confidence considerations may determine the choice of which to believe, or lead to the conclusion that more development is necessary.

Complex models can be employed to validate simpler ones.

Conversely, if the correspondence between models is known, a more refined model whose details are tied to a particular real system can be used to gain confidence in a more abstract but general model. Thus by validating our lumped discrete event model against Huffaker's data, and finding that our corresponding occupancy and RPS models produce matching behavior, we gain confidence in the abstractions employed to derive the simpler models, i.e., that patches, rather than individuals, are sufficient entities for analysis of persistence. Holling et al (1974) has employed a simulation model at the level of detail of our lumped discrete event model to check out the wider consequences of optimal control policies derived from a simpler analytic model.

Models may be introduced independently or derived from existing ones.

It may be sometimes advantageous to construct a model from "phenomenological considerations" rather than from "first principles". However, when a homomorphism can be established between a more refined model and such an ad hoc model, additional advantages of the kind indicated above accrue. In addition, if a base model is available on which to base construction of a lumped model, constructs may be suggested which would not have come to mind in a phenomenological approach (Whitehead, 1977).

Needed experiments may be implied by the experimental frame organization.

The logical structure of the experimental frame organization may suggest conceivable frames in \mathcal{E} that have not yet been realized to date (are not in \mathcal{E}^t), and might not be thought of in an unstructured experimental approach. For example, data on the orange spoilage and prey-food interaction suggested by frames of the form $E_{\text{food/prey,pred}}$ and $E_{\text{food,prey/pred}}$ is missing and would be helpful to model construction and validation.

Model and experimental frame organizations may be extended at all levels.

The multi-faceted system approach explicitly recognizes that model construction and validation is a never-ending process. For example, as accuracy demands in some frame increase, it may be found that the current stock of models is inadequate to meet these demands. This may spur the formulation of new experimental frames, data acquisition within them and construction and validation of models which would guide the refinement of the original models so as to meet the increased accuracy requirements. This paradigm is illustrated in our finding that small-population interaction on a patch may play a more important role in determining average population levels than was suspected originally. Development of a credible small-population sub-model could be based on a spatial model of the predator-prey interaction

on a patch developed from data acquired in an appropriately defined experimental frame. Complexity constraints would prohibit incorporating such a spatial model directly into our local interaction model and thus simplifications would be sought perhaps resulting in refinements of the classical Lotka-Volterra model along lines developed by Hassel et al. (1976).

An example of refinement at the other extreme of abstraction is given by the incorporation by Gurney and Nisbet (1977) of fluctuation terms in the RPS model which enables it to predict equilibrium fluctuation magnitudes from steady state population levels.

9.2 Ecosystem Modelling

In this paper we have illustrated our large scale multi-faceted approach in a highly restricted ecosystem context. Having dealt only with two species and 3 trophic levels, we have only scratched the surface of the possibilities and problems that would arise in dealing with a realistic ecosystem. Yet extension of the experimental frames on the same plane of abstraction to many species would simply involve the specification of frames by pairs (A,B) where A is the

subset of species to be observed (whose descriptive variables are the compare variables), and B is the subset of species where influence is to be minimized (whose descriptive variables form control variables).

A sublattice of frames represents the trophic structure of the ecosystem such that (A, B) is in the sublattice if, and only if, the A species are found at lower trophic levels than any of the B species. Competitive and cooperative structures may be similarly represented.

In the same vein, we have hinted at more than one level of patch decomposition. Indeed, the spatial structure may have a natural hierarchy, where patches isolated at one level of analysis are subordinated in larger patches at a higher level. Isolation of patches signified by frames bearing the "local" descriptor would then be possible at many levels, and the frame characterization would reflect this hierarchical structure.

Finally, ordering of frames according to plane of abstraction is clearly extendable to many degrees of abstraction, representing many possible simplification and aggregation procedures. Aggregations in time may result in successive alternate planes of differential equation and discrete event models. Aggregation over trophic levels and/or over patch hierarchy levels are possible. Compartmentalization of species according to spatial and functional criteria is yet another source of abstraction-frame construction.

Parallel to such an experimental frame structure would be the organization of models intended to answer questions within various applicable frames.

9.3 Modelling of Patch Structured Predator-Prey Universes

We have shown in particular, how the organizations of frames and models look in the highly restricted universes of Huffaker. Yet these universes are rich enough to enable non trivial multilevel, multiformalism model construction and validation. Thereby we have illustrated that there are advantages to integrated modelling, even in restricted contexts more or less amenable to conventional treatment.

Some tentative conclusions concerning predator-prey coexistence are: Predators and prey can coexist indefinitely in patchy environments where, in homogenous environments the relation would quickly go extinct. The necessary characteristics of patchy environments are:

- a) largely isolated patches — population exchange is small but non negligible,
- b) patch life cycle insensitive to emigration and to immigration except at certain key points (prey colonization, predator take-over),
- c) large number of patches.

According to our base model, in the Huffaker Universes large numbers migrate, so small population exchange can be achieved only by making migration hazardous; the effect of emigration on the native life cycle is small since emigration occurs only at certain key points; and the effect of immigration is small because of exponential prey growth after colonization and rapid extinction after predator take-over.

Gurney and Nisbet (1977), suggest a model in which a) and b) hold, but

emigration is possible throughout the cycle. Despite this discordance with Huffaker's observations, their model can be made to fit the persistence cases as viewed in the $E^{\text{occupancy, total}}$ frame (means and standard derivations of occupancy counts). Indeed, their model assumes the random phase - space mode of operation, and under these conditions, their model equations are isomorphic with our RPS equations (modulo fluctuation terms and inessential extra states). Our cross comparison of models (Appendix 4) suggests that the RPS mode can not be maintained with the number of patches employed by Huffaker, so that even though a RPS model can fit the data, it may not represent any base model which also does so. Two kinds of tests of the Gurney-Nesbit model are suggested in the spirit of the multimodel approach: a) construction and test of a base model satisfying their assumptions, b) conducting critical experiments to distinguish the alternative mechanisms.

Acknowledgements

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APPENDIX

Some Results on Estimated Parameters and Model Cross-Comparison

It is beyond the scope of this paper to describe the complete results of simulation studies of the constructed models. We shall describe, however, the results relevant to the model reproduction of predator-prey coexistence as observed in the (one) 1958 universe which manifested this phenomenon. In general, all of our models are capable of qualitatively explaining the observed persistence, and our more refined models are able to give quite close quantitative agreement as well.

We proceed to describe the results of the identification procedure outlined in Section 7.1. Refer also to Table 5.

A.1 Local Food-Prey Interaction

The parameter settings $b = 0.55 \text{ day}^{-1}$, $d = 0.33 \text{ day}^{-1}$ and $u = 1.3 \times 10^{-5}$ (fraction of orange surface per day) were estimated by employing the initial part of data element 58, IB, Fig. 7 (in frame $E_{\text{food,prey/pred}}^{\text{local,total}}$). The quantities initial prey size, initial orange surface exposed, maximum prey size, time elapsed to maximum prey were employed in Eq. 2 to estimate $a(=b-d)$ and u ; the slope of decay from maximum prey size was used to estimate d .

At the above settings, the maximum prey size on an orange is $u/a \approx 2 \times 10^4$ mites per orange equivalent (so for example a 1/10 exposed orange area can support 2000 preys at the perigee of growth).

A.2 Local Food-Predator-Prey Interaction

The parameter settings $d' = 0.30 \text{ day}^{-1}$, $c = 0.05 \text{ day}^{-1}$ and $c' = 0.006 \text{ day}^{-1}$ were estimated employing data element 58, IIA, Fig. 9 (in frame $E_{\text{food,prey,pred}}^{\text{local,total}}$). Employing a CSMP simulation of Eq. 1a,b,c) we adjusted the parameters d' , c and

c' so as to fit as closely as possible the prey and predator curves in Fig. 9 (Huffaker, 1958).

With the estimated parameters, we have the equilibrium prey and predator levels as 50 and 5 mites on a patch, respectively.

A.3 Prey Migration

The data necessary for identifying prey migration parameters in the absence of predators is available only for the hazard free universes in the Huffaker 1958 study and the complex universe of the 1963 study, but not for the 1958 universe in which prey-predator coexistence was achieved. Employing hazard free universe data sets 58, IB, Fig. 7 and 58, IC, Fig. 8 (in frame $E_{\text{food,prey/pred}}^{\text{global,total}}$) we adjusted the parameters pyrem, pysurvive, meanpysearch, and pydif₁ of our discrete event lumped model so as to have the SIMSCRIPT generated curves match the data curves as closely as possible in maximum prey produced and number of prey maxima produced in the experimental interval. Estimates obtained were pyrem = 0.9, pysurvive = 0.9, meanpysearch = 0.1 days, pydif₁ = 20. Employing the data set 63 E-2 Fig. 2 for the prey-food interaction in the complex 1963 universe, we estimated in the same manner that pyrem = 0.9, pysurvive = 0.5, meanpysearch = 13 days, pydif₁ = 0.3 and pydif₂ = 0.15. Thus as expected prey mites in the complex universe take much longer on the average (13 versus 0.1 days) to cover much less distance ($\sqrt{13} \times 0.3 \approx 1.0$ versus $\sqrt{0.1} \times 20 \approx 6.0$, see Section 7) than they do in the hazard free cases.

A.4 Predator Migration

Predator migration parameters pdrem, pdsurvive, meanpdsearch, and pddif were adjusted in the discrete event lumped model so as to fit as closely as possible the data element 58, II I, Fig. 18 representing the 1958 universe in which coexistence was established. The settings of the prey migration

parameters were those determined from the complex 1963 universe just described. (Subsequent trials with deviations from these settings did not significantly improve the results.) The predator migration parameters were initially set equal to those of the prey and a fairly broad neighborhood of parameter assignments centered on the initial settings was investigated.

It was found that coexistence is robust in this neighborhood in that most simulation runs ended with both predators and preys still around. However, it did not seem possible to achieve very close quantitative agreement. We noticed that the predator occupied cell fraction was too small and this seemed to be due to the fact that in our original model, predators invading patches of low prey density (less than eqprey) were always returned immediately for continued migration. It thus appeared that predator invasion of low density patches was a significant process and we accordingly modified our small-population submodel to its current form. With this modification we were able to bring the statistics shown in Table A.1 generated by the simulation quite close to those of the data. Although the averages agree quite well, the model overestimates the prey maximum considerably, which may point to a further needed modification. (In analogy with the predictions of a Lotka-Volterra model, the overshoot could be the sensitive result of too low an initial predator population, and thus not an intrinsic model shortcoming.) The best fit parameter settings are indicated in Table A.1.

In Table A.2, the same data is analyzed from the cell occupancy point of view (frame $E_{\text{food,prey,pred}}^{\text{occupancy,total}}$). [Note the model in question is the lumped discrete event model not the occupancy model; the occupancy states can be computed from the finer population count information.]

Table A.1

Comparison of Data and Lumped Discrete Event Behavior in
 Frame E^{global, total}_{food, prey, pred} [the Case of Predator-Prey
 Coexistence, 58 II I, Fig. 8]

<u>Density</u>	<u>Data</u>	<u>Model*</u>
maximum prey (predators absent)	missing	4600 ⁺
average prey (predators absent)	missing	2400
maximum prey	2000	3500
average prey	900	730
maximum predators	50	46
average predators	12	13

⁺all densities quoted in mites per orange equivalent (Huffaker, 1958).

*Parameter assignments are:

$b = 0.55 \text{ day}^{-1}$	$\underline{\text{pyrem}} = 0.9$	$\underline{\text{pdrem}}' = 0.3$
$d = 0.30 \text{ day}^{-1}$	$\underline{\text{pysurvive}} = 0.35$	$d'' = 0.0$
$u = 1.3 \times 10^{-5}$	$\underline{\text{meanpysearch}} = 13 \text{ days}$	$c'' = 10.0$
$d' = 0.30 \text{ day}^{-1}$	$\underline{\text{pydif}}_1 = 0.3$	$\bar{c} = 0.0$
$c = 0.05 \text{ day}^{-1}$	$\underline{\text{pdrem}} = 0.6$	
$c' = .005 \text{ day}^{-1}$	$\underline{\text{pdsurvive}} = 0.5$	
	$\underline{\text{meanpdsearch}} = 14 \text{ days}$	
	$\underline{\text{pddif}}_1 = 0.2$	

Table A.2

Comparison of Data and Lumped Discrete Event Model Behavior

in Frame $E_{\text{occupancy, total}}$
 $E_{\text{food, prey, pred}}$

<u>Cell occupancy</u>	<u>Data</u>	<u>Model</u>
average prey cell (state 1) ⁺	17	28
average pred. cell (state 2) ⁺⁺	11	15
standard deviation/prey cell [*]	16	19
standard deviation/pred. cell	11	11

⁺ a prey cell is a cell occupied by at least some prey but no predator

⁺⁺ a predator cell is a cell occupied by at least some predator

^{*} measures the amplitude of oscillation considered as a fluctuation about the average (Gurney and Nesbit, 1977)

As can be seen, the statistics from model and data are remarkably close, save for considerable overestimation in the average prey cell count. This is understandable in view of the maximum prey population overestimation.

It should be noted that the average occupancy counts are not necessarily correlated with the average population counts. As we have noted, the somewhat independent occupancy perspective was useful in diagnosing a shortcoming of the model.

A.5 Occupancy and RPS Models

Employing the parameter values of Table A.1, we can determine corresponding parameter values for the Occupancy model, using the relations of Table 7. In order to explore the behavior of the occupancy model in this space, we fixed all but the migration parameters at the extremes of their ranges and sampled the model behavior for allowable assignments of the latter parameters. Employing the equilibrium relations in Table 6, we can uniquely determine the effective neighborhoods $p_1 N_1$ and $p_2 N_2$ of the RPS model required to reproduce the occupancy averages of the data (58, II I, Fig. 8) shown in Table A.2. As shown in Table A.3, these are within but at the lower end of the ranges computed from Table 7. However, simulation of the occupancy model with these parameter settings resulted in quick elimination of the prey. Only when the effective prey neighborhood was considerably increased and the effective predator neighborhood considerably decreased was coexistence obtained in 10 x 10 cell array. (Halving the predator neighborhood was sufficient for coexistence in a 30 x 30 cell array. The 100 cell array is more representative of the 120 cell 1958 universe.) The effective neighborhoods obtained in the way are still within the ranges computed from Table 7. However, the occupancy averages obtained from the occupancy model for both predator and prey in these cases tend to exceed those of the lumped discrete

Table A.3

Cross-Comparison of Model Behavior in Frame E⁺ occupancy, total
food, prey, pred

<u>Effective Prey Neighborhood</u>	<u>Effective Predator Neighborhood</u>	<u>Occupancy⁺ Model</u>		<u>RPS⁺ Model</u>	
		avg. prey cell	avg. pred. cell	avg. prey cell	avg. pred. cell
$P_1 N_1$	$P_2 N_2$				
$\epsilon [0, 25]$	$\epsilon [0, 12]$				
4	8	10 x 10 extinct		17	17
		30 x 30 extinct			
4	4	10 x 10 extinct			
		30 x 30	44 9	30	18
24	24	10 x 10			
		60 28		48	50
Data [*]		17 11		17	11
Lumped Discrete Event [*]		28 15		28	15

⁺Other parameter values: $GRT_1 = 20$ days, $DCT_1 = 20$ days, $GRT_2 = 5$ days,
 $DCT_2 = 2$ days, $RT = 44$ days

^{*}From Table A.2

event model and the real system data.

In sum, this between model comparison seems to indicate that the random-phase condition is only approximately being satisfied in the lumped discrete event model and the real system. While the occupancy and RPS models predict that coexistence is possible within the allowed parameter space, they do not do very well in predicting the observed occupancy cell averages unless the number of cells is considerably increased.

CAPTIONS

Figure 1. A data element of a frame $E_{\text{food,prey/pred}}^{\text{global,total}}$ is shown in Fig. 1b) (redrawn from Fig. 8, Huffaker, 1958). The universe consists of four oranges embedded in an array of rubber balls (oranges are the darkened circles in Fig. 1a). The hatched initial portion of Fig. 1b) is the data element belonging to the frame $E_{\text{food,prey/pred}}^{\text{local,total}}$ where the subset referred to by the "local" designation is the set of oranges indicated in Fig. 1a).

Figure 2. Experimental frames organized according to planes of abstraction. Degree of abstraction increases from top to bottom. Nodes represent frames and lines (implicitly directed from top to bottom) represent the derivability relation.

Figure 3. Discrete-event representation of the base model. The discrete states are: E(empty, no food), ER(empty, food replenished), PREY(pre colony established), PREY'(pre colony at maximum size), PRED(predators invaded), MAXPD(predator colony at maximum size). Scheduling times are: GRT(growth time of prey colony), PYPECT(decay time of prey colony), MAXPYT(time to reach maximum prey size after predator invasion), PAXPDT(time to reach maximum predator population from maximum prey population) and JOINTDECT(time from maximum predator to end of cycle).

Figure 4. Typical trajectories in the prey-predator (x,y) plane with food $r > 0$ (Fig. 4a) and $r = 0$ (Fig. 4b).

Figure 5. State update and scheduling curves obtained by simulation of Eq. 1. Symbols shown are keyed to Fig. 4.

Figure 6. The occupancy model. Discrete states are: 0(empty, food replenished), 1(some prey), 2(some predator), E(empty, no food).

Figure 7. The organization of models ~~N_0~~ ^{t = 1977}. Also shown are the experimental frames applicable to the various models.

Figure 8. The cumulative number of cells hit versus the number of samples from the random walk distribution with parameters typical in the case of extended predator-prey persistence. The numbers pd and py indicate upper bounds on the numbers of predators and preys emigrating in a migration episode as estimated in Table 7.