Predator-Mediated Coexistence: A Nonequilibrium Model

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PREDATOR-MEDIATED COEXISTENCE: A NONEQUILIBRIUM MODEL

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THE EMPIRICAL PROBLEM

One of ecology’s central problems is the coexistence of species. Within a trophic level, explanations for coexistence are usually framed in terms of competition by asking what properties of the species, and of their environment, prevent competition from excluding some members of the assemblage. Predation, impinging on a group of (presumably) competing species, has been implicated as a potentially important factor which might allow coexistence.

Observations of such “predator-mediated coexistence” are by now commonplace, including Darwin (1859) on mowing of grassland plants, Summerhayes (1941) on voles and grassland plants, Paine (1966, 1971) and Dayton (1971) on starfish and intertidal invertebrates, Harper (1969) on grazers and plants, Slobodkin (1964) on harvesting of laboratory hydrids, Neill (1972) on fish and laboratory zooplankton, and Porter (1972) on starfish and corals. Brooks and Dodson (1965), Wells (1970), and Hall et al. (1970) showed that fish predation could mediate zooplankton coexistence, although it is not certain that the interaction being affected is purely competitive (Dodson 1974). Finally, predation has also been shown to contribute to the coexistence of different genetic morphs within single species, e.g., zooplankton (Zaret 1972) and moths (Kettlewell 1955; Lees and Creed 1975).

There are also studies that have failed to demonstrate predator-mediated coexistence or actually have shown a decrease in the number of coexisting species under the impact of predation (e.g., Harper 1969; Paine and Vadas 1969; Hurlbert et al. 1972; Adicott 1974; Janzen 1976). These studies are particularly useful as tests of any theory devised to explain predator-mediated coexistence. Not only must such a theory be able to generate the observed positive effect of predation on coexistence, but it should also explain the conditions under which the effect is not seen or is negative.

The empirical observations of predator-mediated coexistence have led naturally to the suggestion that it may play a major role in structuring communities (Paine 1966; Janzen 1970; Connell 1970) and thus to attempts to incorporate it into the mathematical framework of population biology. These attempts to date have been frustrating. While the possibility of predator-mediated coexistence has been demonstrated, most analyses make its occur-
rence seem very unlikely. The following brief review builds a framework for presenting a new model for predator-mediated coexistence.

THEORETICAL APPROACHES

Population models can be conveniently classified according to the kinds of systems they are designed to mimic. I distinguish first closed population systems from open population systems. A closed system is one in which the population exists in a single, closed, roughly homogeneous volume of habitat. There is no migration into or out of this single habitat cell. An open system consists, in its simplest form, of a set of habitat cells coupled by migration. The flux of population between cells must be small enough that the cells retain some measure of independence but large enough that the cells are not totally isolated. Notice that an open population system, considered as a whole, may itself be closed. In this sense the distinction between open and closed systems might be described equally well as between subdivided and nonsubdivided systems. Also note that the terms "open" and "closed" are not used here in their thermodynamic sense, in which an open system is one which exchanges energy with its environment. All populations are thermodynamically open.

The bottle ecosystem studies pioneered by Gause (1934) have provided an experimental paradigm for closed systems, and the vast majority of ecological theory is based on the properties of such systems. The most important of these properties is that zero is an absorbing state for a population in such a system. Extinction is final, permanent, irreversible.

For open systems, an experimental paradigm can be found in the multicelled systems of Huffaker (1958), mites on connected oranges; Pimentel et al. (1963), wasps and houseflies in connected cages; or Neill (1972), algae, zooplankton, and fish in connected aquaria. The most crucial distinction between closed and open systems is that in open systems local extinction is not an absorbing state. Recolonization of a local population that becomes extinct is now a possibility.

A second way to classify population models is as equilibrium or nonequilibrium theories. Equilibrium theories focus their attention on the properties of the system at an equilibrium point. Such theories abstract time out of the picture completely, since a system at equilibrium exhibits no temporal dynamics at all. A nonequilibrium theory, by contrast, would be concerned with the transient behavior of the system away from equilibrium and would be intimately concerned with time.

These two categories generate four classes of population systems within which the effect of predation on coexistence can be examined. The most straightforward way to do this is to construct a model of interacting prey species and then study the coexistence properties of the model with and without predators. Some results follow.

The Predation Effect: Closed, Equilibrium Systems

In a closed system, zero is an absorbing state for any population. This means that coexistence is assured only by a stable equilibrium point at which all species have positive values (or a limit cycle which does not get too close to
Moreover, laboratory studies suggest that unless there is a stable equilibrium extinction occurs relatively rapidly. From this the inference is commonly drawn that in nature one will see primarily or exclusively equilibrium situations. Most of theoretical community ecology is devoted to seeking conditions on the properties of the species and their environment that will assure a positive stable equilibrium. In fact, it is customary, when looking for predator-mediated coexistence, to refer to the problem as one of predator-generated stability. We will see later that the two cannot be equated.

Several attempts have been made to model predator-mediated coexistence in closed, equilibrium systems. The results depend on the form in which the predation process is modeled. Let $N_1$ and $N_2$ be the population sizes of two competing prey species, and $N_3$ that of the predator. Equations for the system dynamics can be written

\[
\frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 - N_1 - \alpha N_2}{K_1} \right) - f_1(N_1, N_2, N_3),
\]

\[
\frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 - N_2 - \beta N_2}{K_2} \right) - f_2(N_1, N_2, N_3),
\]

\[
\frac{dN_3}{dt} = g(N_1, N_2, N_3),
\]

where the function $f_i(N_1, N_2, N_3)$ expresses the losses to population $i$ due to predation. These losses in general depend on the densities of all three species.

Constant dilution rate [$f_i(N_1, N_2, N_3) = k_i N_i$]—This is the simplest possible model of "predation," in which a constant fraction of the prey population is continuously removed. It is more appropriately termed dilution than predation, since there is no feedback from the abundance of the prey to the predation process.

Slobodkin (1961) analyzed this case graphically and found that such predation easily could reverse the outcome of competition if the losing competitor had a higher growth rate at low densities. In order to maintain both species in stable coexistence, however, the coefficients in the model must be very precisely balanced indeed.

Yodzis (1976) has recently analyzed an even simpler analogue of predation: harvesting at a constant rate, where $f_i(N_1, N_2, N_3) = k_i$. He found that, in a deterministic environment, such harvesting can eliminate competitive dominance and result in stable coexistence. When the environment is subject to random fluctuations, however, harvesting at a constant rate increases the niche separation required for stable coexistence, leading to the loss of species from the community (Yodzis 1977).

Lotka-Volterra predation [$f_i(N_1, N_2, N_3) = k_i N_i N_3$].—This description of predation adds a little more realism to the situation; the intensity of predation now depends on the densities of both the predator and the prey. May (1973) and Cramer and May (1971) have studied the coexistence properties of this model. As in the previous case, it turns out that predation can stabilize the system but that this requires a delicate balancing of the parameters. Over most
of the parameter space, the stability properties of the model with and without predators are identical.

The results for both of these models can be understood qualitatively in terms of Ayala's (1972) analysis of frequency dependence in competition systems. In order for a competitive equilibrium to be stable, the fitnesses of the competing species must exhibit reverse frequency dependence near the equilibrium point. That is, a perturbation away from equilibrium which increases the frequency of \( N_1 \) relative to \( N_2 \) must decrease the fitness of \( N_1 \) relative to that of \( N_2 \). Only in this case will the relative frequencies move back in the direction of the equilibrium.

Neither the constant dilution rate nor the Lotka-Volterra predation terms are frequency dependent; the predation intensity on one prey species is independent of the abundance of the other. Thus predator-generated stability in these cases requires that the addition of a non-frequency-dependent predation pressure to a non-frequency-dependent situation results in frequency dependence. This is possible (since fitnesses depend on the absolute as well as the relative values of the \( N_i \) and because the system with predation is three rather than two dimensional), but it does not seem very likely.

**Frequency-dependent predation.**—A frequency-dependent form of predation, in which the \( f_i(\cdot) \) would depend explicitly on all the \( N_i \), might be more successful at stabilizing competitive interactions. What is needed is a form of predator switching in which any prey species that begins to dominate the system receives a disproportionate increase in predation pressure, while a species that begins to disappear gets a correspondingly disproportionate decrease. This process has not been extensively analyzed, but Roughgarden and Feldman (1975) have shown that if predator preference increases with the relative density of the prey then the permissible niche overlap between prey can be significantly increased.

The theories of Janzen (1970) and Connell (1970) for predator-mediated coexistence in tropical trees can be interpreted in frequency-dependent terms. The frequency dependence is generated by the dispersal and searching abilities of seed and/or seedling predators. A local high-density aggregation of seedlings near the parent tree will be decimated by predation; isolated seedlings have a much higher probability of escaping. Because of the spatial element involved, this hypothesis can also be interpreted in open-system terms (see below).

It is worth noting that reverse frequency-dependent predation can occur in which rare species are preyed upon especially heavily. This can happen any time that the competitive pressure in the community is lowered to the point that a very unpalatable (or inedible) species can persist. If such a species begins to become abundant, the predator has no choice but to continue to seek out the ever-rarer palatable forms. This has been found to happen in certain heavy grazing situations (Harper 1969), in certain cases of physical disturbance due to elephant populations in Africa (Laws 1970), and in a generalized form seems to be responsible for the “disclimax” situations caused by practicing swidden agriculture in areas of insufficient moisture (Geertz 1969).

The most encouraging of the attempts to explain predator-mediated coexist-
ence in terms of equilibria in closed systems seem to be Yodzis’s (1976) analysis of the reversal of competitive dominance and Roughgarden and Feldman’s (1975) work on frequency-dependent predation. The major weakness of both of these attempts is the neglect of the predator population dynamics. In those models which have included the predator population, this form of predator-mediated coexistence seems to require a very strict balancing of parameters.

*The Predation Effect: Open, Equilibrium Systems*

Several authors recently have examined the properties of sets of competitive systems connected by migration (e.g., Levins 1970; Levins and Culver 1971; Cohen 1970; Horn and MacArthur 1972; Levin 1974; Slatkin 1974). This is usually approached by switching attention from $N_1$ and $N_2$, the abundances of the competing species, to the proportions of cells ($P_1$ and $P_2$) in which the two species occur. Local extinction, within a single cell, is no longer an absorbing state. Overall extinction ($P_i = 0$) is, of course, still absorbing, and in these studies coexistence has been equated with a stable equilibrium with both $P_1$ and $P_2$ positive.

The effect of predation on such equilibria has not been extensively investigated, but some hints are forthcoming from the preceding analyses. The models of Levins and Culver (1971), and Horn and MacArthur (1972) turn out to be formally equivalent to the Lotka-Volterra competition equations. Frequencies of occurrence take the place of abundances, and immigration and extinction rates replace birth and death rates. This suggests that the effects of predation may be similar to those outlined above, depending on the form in which it is modeled.

Slatkin (1974) considered briefly the effect of predation on an open system at equilibrium. He found that if competition acted only through colonization probability or only through extinction probability then increased extinction rates (as by a predator) could stabilize an otherwise unstable system. Again, no predator dynamics were included in the model.

*The Predation Effect: Closed, Nonequilibrium Systems*

The possibility of nonequilibrium (and thus, of course, temporary) coexistence in closed systems has received little attention in ecology. The crucial quantity in a nonequilibrium theory of competition is the rate of competitive exclusion, or, equivalently, extinction time. This contrasts with the equilibrium theory in which temporal dynamics are abstracted out of the picture by taking limits as $t \to \infty$.

The factors affecting the rate of competitive exclusion have not been thoroughly studied. Some simulation work (Caswell, unpublished) suggests, however, that the rate of exclusion decreases with increasing similarity of the competing species and is higher for interference than for exploitation competition (agreeing with data summarized by Miller [1969]). The possibility to be explored here is that predation might increase extinction time to the point that the competitors would appear to coexist indefinitely.
Preliminary analyses (Caswell, unpublished simulation data) suggest that predation may slow down competitive exclusion. Parrish and Sails (1970) reported that predation (Lotka-Volterra type) stabilized an otherwise unstable competitive system, but Cramer and May (1971) later showed analytically that their example was actually unstable even under the impact of predation. Predation had, however, prolonged coexistence of the prey dramatically enough that it was mistaken for stability.

Hutchinson (1953, 1961) proposed nonequilibrium coexistence as a possible explanation for the persistence of ecologically similar plankton species. In such a situation, Hutchinson distinguishes three cases: depending on whether the time required for competitive exclusion is much less than, approximately equal to, or much greater than the time scale on which the environment fluctuates. In the first case, a competitive equilibrium would be established, and there would be no coexistence. The third case would lead to an equilibrium obtained by time averaging of the rapidly varying environmental conditions, and again one species would be excluded. In the second case, however, nearly permanent nonequilibrium coexistence may result.

It seems entirely possible that a fluctuating predator population could provide a varying environment on precisely the right time scale to keep competition from reaching its equilibrium. In Parrish and Sails's (1970) simulation results, the decline of the prey species which is being excluded becomes apparent as soon as the predator's oscillations die out. On the other hand, Caswell (1972) examined the interaction of predation and competition in a complex model including time lags, predator satiation, and prey refuges. This system oscillated violently, and the competitors appeared to coexist indefinitely. How general such phenomena are in nature is unknown.

While these closed system, nonequilibrium results look promising, there are still problems with generalizing them to explain predator-mediated coexistence in nature. Local extinction is still an absorbing state, and it is not yet clear that predation can delay that extinction for ecologically relevant lengths of time. Nature, moreover, is not organized in closed system fashion.

The Effect of Predation: Open, Nonequilibrium Systems

Nonequilibrium coexistence in open systems can be phrased as a special case of a more general problem. Consider a system composed of a large number of similar components, each of which interacts with some of its fellows. How long does it take such a system to reach equilibrium (the usual nonequilibrium theory question) as a function of the number of components, the time required for each component to reach its local equilibrium, and the pattern of connection between components? This question has arisen in the study of adaptive behavior in the nervous system (Ashby 1960), in the study of general hierarchical system theory (Simon 1962), in design theory (Alexander 1964), and in the study of epigenetic control networks (Kauffman 1969). The answer in each case is the same: for even very simple components in reasonably small numbers, high levels of connectedness lead to astronomically long delays in reaching
equilibrium. Consider this simple example from Ashby (1960). The system is a set of 100 light bulbs, each of which is in one of two states (on or off). For each bulb, in each second, the transition (on → off) occurs with probability .5. For each bulb, in each second, the reverse transition (off → on) occurs with probability .5 if at least one bulb in the “on” state is connected to the bulb in question, otherwise the probability is zero. The equilibrium for the system is the state with all bulbs off; this equilibrium is stable. If the system is started with all 100 lights on, how long will it take to reach equilibrium?

If there are no connections among the bulbs at all, the expected time required to reach equilibrium is on the order of $2^4 \times s = 2 s$. At the other extreme, when the system is totally connected, with every bulb interacting with every other bulb, the time to equilibrium is on the order of $2^{100} \times s = 10^{22} \text{ yr}$. This is an immensely long time; the estimated age of the universe is only $10^{10} \text{ yr}$. For all practical purposes this system, containing a reasonable number of components, each of which reaches its own equilibrium on a time scale of seconds, will never reach equilibrium at all.

This suggests that in an open system of population cells joined by migration, nonequilibrium conditions might last long enough to be ecologically relevant—perhaps even more relevant than the equilibrium conditions.

In the following sections of this paper I will examine in some detail the effect of predation on nonequilibrium coexistence in open systems. To show the possibility of predator-mediated coexistence in such a system, I have built a simple but very general model from which the closed-system equilibrium, closed-system nonequilibrium, and open-system equilibrium effects of predation are eliminated. After demonstrating the possibility of predator-mediated coexistence in this system, I will try to make some deductions about its probability in nature and then examine some observed cases of predator-mediated coexistence in light of the model results.

A MODEL

The model consists of a set of cells (the number of cells is an independent variable whose effect is to be studied) connected stochastically by migration. A model of an entire ensemble of cells is generated from a description of the within-cell population interactions and between-cell migrations.

The description of population dynamics within a single cell is an abstraction of the results typically observed in closed, single-cell systems in the laboratory. In figure 1 the top panel shows the model for single-species population growth; the logistic curve has been abstracted into a discrete binary variable registering presence (1) or absence (0). The middle panel shows the model for the competitive interaction of two such populations. (The losing competitor, species $A$, coexists with the winning competitor, species $B$, for $TC$ time units and then becomes extinct.) The bottom panel shows the model for predation. Over the course of $TP$ time units the predator population increases, decimates its prey, and then crashes to extinction ($TC$ is the competitive exclusion time and $TP$ the predatory decimation time; these are also independent variables
whose effect is of interest). Time units in the model could be measured either in generations or calendar time.

The instantaneous situation in each cell is described by a five-dimensional state variable:

\[XA = \text{abundance of the losing competitor (0 or 1)},\]
\[XB = \text{abundance of the winning competitor (0 or 1)},\]
\[XC = \text{abundance of the predator (0 or 1)},\]
\[tc = \text{competitive "clock," } 0 \leq tc \leq TC, \text{ and}\]
\[tp = \text{predatory "clock," } 0 \leq tp \leq TP.\]
The competitive and predatory clocks keep track of how long competitive and predatory interactions have been going on. In a sense, they are alarm clocks; when $tc = TC$ or $tp = TP$ the losing competitor or the prey, respectively, goes extinct.

Migration between cells is modeled in similarly abstract fashion. The probability of a given species colonizing a cell from which it is absent and which is suitable for colonization (as specified below) is given by

$$P[\text{colonization}] = D_i \times \frac{\text{no. of cells occupied by species } i}{\text{total number of cells}}; \quad i = A, B, C.$$  

Dispersal is thus directly proportional to the number of cells occupied by a given species. The proportionality constant ($D_A$, $D_B$, and $D_C$) measures the “per cell” dispersal ability of the species. This version of the model does not incorporate the spatial configuration of the cells, so there is no proximity effect on colonization. This will be added to future versions of the model.

Coupling the within-cell dynamics with the migration process, and adding a few additional details to complete the descriptions of predation and competition, results in an overall set of state-transition rules (table 1). Note particularly the following points: (i) Competitive exclusion of species $A$ by species $B$ is total. A cell can be invaded by species $A$ only if species $B$ is absent; the presence of the predator does not affect this restriction. (ii) The presence of the predator cannot result in permanent coexistence of the prey within a single cell (the closed system, equilibrium effect). (iii) The presence of the predator cannot even extend coexistence within a single cell (the closed system, nonequilibrium effect). In a cell containing all three species, species $A$ becomes extinct when $tc = TC$, regardless of the presence of the predator. (iv) The system as a whole is a finite-state Markov process with three absorbing states: (1) species $B$ present in every cell and both other species extinct, (2) species $A$ present in every cell and both other species extinct, (3) all three species extinct. The system will eventually end up in one of these states with probability 1.0 (see, e.g., Feller 1968; Karlin 1966). Thus there is no possibility of overall equilibrium coexistence (or its stochastic analogue, a limiting probability distribution) with all species present (the open-system equilibrium effect).

In establishing these transition rules, I have purposely made it as difficult as possible for the presence of the predator to generate coexistence of the prey, by eliminating all modes of predator-mediated coexistence except the open system, nonequilibrium effect. This is not because I am convinced that the other effects never operate in nature (they probably do), but simply to maximize the power of any demonstration of this mode of coexistence.

**RESULTS**

The independent variables of interest in this model are the number of cells in the system ($NC$), the per cell dispersal rates of the three species ($D_A$, $D_B$, $D_C$), the competitive exclusion time ($TC$), and the predatory decimation time ($TP$). It is interesting to note that the first four of these are of interest because the model describes an open system, the last two because I am concerned with
### Table 1

**State-Transition Rules**

<table>
<thead>
<tr>
<th>State Variable</th>
<th>Transition Rule</th>
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| $XA$ (the losing competitor): | If $XB = 1$ and $t_c = TC$ or $XC = 1$ and $t_p = TP$  
1 $\rightarrow$ 0  
1 $\rightarrow$ 1  
0 $\rightarrow$ 1  
0 $\rightarrow$ 0  | Otherwise  
With probability $D_A P_A$ if $XB = 0$  
with probability 0 if $XB = 1$  
With probability $1 - D_A P_A$ if $XB = 0$  
with probability 1 if $XB = 1$ |
| $XB$ (the winning competitor): | If $XC = 1$ and $t_p = TP$  
1 $\rightarrow$ 0  
1 $\rightarrow$ 1  
0 $\rightarrow$ 1  
0 $\rightarrow$ 0  | Otherwise  
With probability $D_B P_B$  
With probability $1 - D_B P_B$ |
| $XC$ (the predator): | If $XA = 0$ and $XB = 0$  
1 $\rightarrow$ 0  
1 $\rightarrow$ 1  
0 $\rightarrow$ 1  
0 $\rightarrow$ 0  | With probability $D_C P_C$  
With probability $1 - D_C P_C$ |
| $t_c$ (competitive clock) | The competitive clock is started as soon as species $A$ and $B$ are both present and is incremented each time unit until it reaches $TC$ |
| $t_p$ (predatory clock) | The predatory clock is started as soon as species $C$ and either $A$ or $B$ are both present and is incremented each time unit until it reaches $TP$ |

**Note.** $P_A$ = the proportion of cells containing species $A$, similarly for $P_B$ and $P_C$; $D_A$ = the per colony dispersal ability of species $A$, similarly for $D_B$ and $D_C$; $TC$ = the time required for competitive exclusion of $A$ by $B$; $TP$ = the time required for predatory decimation of $A$ and/or $B$ by $C$.

nonequilibrium dynamics, in which the time scale cannot be abstracted out of the picture. A fully general treatment of this problem would also include the spatial configuration of the cells; the dispersal rates would then be defined in terms of dispersal over distance.

The mere possibility of predator-mediated coexistence is easy to demonstrate. Figure 2 shows the results of a single realization of the model, with predators present. All three species persisted until the simulation was terminated after 1,000 generations. In fact, all three species persisted for the full 1,000 generations in each of 10 replicates of this particular system. In contrast, in the absence of the predator the persistence time of species $A$ averaged only 64 generations (range in 10 replicates 53–80). In fact, in 160 replications using 16 different parameter combinations (see fig. 3), the maximum persistence time for species $A$ was 92 generations, an order of magnitude less than that demonstrated in figure 2 under the impact of predation.

Species $A$, the otherwise doomed competitor, is not necessarily being maintained as a rare species. In the 10 replicates using the parameter set of figure 2,
Fig. 2.—Simulation results showing long-term coexistence of all three species in a 50-cell system (species A–C from top to bottom). The simulation was terminated after 1,000 generations, although all three species were present and showed no signs of disappearing. The ordinate measures frequency of occurrence. Parameter values: \( NC = 50, D_A = .25, D_B = .10, D_C = .25, TC = 20, TP = 20 \). In the absence of predators, species A was eliminated in less than 80 generations under these conditions.
the frequencies (mean ± SE) for the three species at the end of 1,000 generations were $A$, $0.68 \pm 0.034$; $B$, $0.48 \pm 0.13$; $C$, $0.75 \pm 0.24$. Species $A$ was actually more frequent than the superior competitor, $B$.

To explore the effect of the model parameters, a statistical examination of the parameter space was carried out. Each of the independent variables was examined at two values, generating a $2^6$, fixed effect, factorial design. The results were examined by analysis of variance. This design is standard for exploring the effect of a large number of variables simultaneously (Kirk 1968); it sacrifices information on nonlinearities for the ability to examine and screen a large number of variables.

The dependent variable of interest in this analysis is extinction time. This creates some operational problems, since the only way to evaluate extinction time is to let the simulation run until extinction occurs. This can take a lot of computer time, since this system may persist for any time short of infinity. To get around this problem, I used the following procedure. For each combination of parameter values I ran 10 replicates of the system, terminating the simulation after 1,000 generations. From these replicates I calculated the median extinction time and used this as the response variable in the analysis of variance. Unlike the mean, the median can be unambiguously calculated if more than half of the extinction times are less than 1,000. The region of the parameter space to be explored was chosen, after some pilot runs, so that the
median extinction time of species $A$ was almost always less than 1,000 generations. In the few cases where it exceeded 1,000 generations, its value was set equal to 1,000.

Using the median as the response variable means that there is only a single value per cell in the analysis of variance. The four-, five-, and six-way interactions were pooled and used as an error term (Kirk 1968). This assumes that these interactions are negligible; if the assumption is violated, the significance tests are conservatively biased due to inflation of error mean squares.

Three response variables were measured and analyzed: the extinction time of species $A$ without predators, the extinction time of species $A$ with predators present, and the effect of predation on the extinction time of species $A$. The latter quantity was defined as the difference between the median extinction time of species $A$ with and without predators. Positive values indicate that predation increased persistence.

Initial conditions for the simulations were arbitrarily defined by randomly and independently allocating species $A$, $B$, and $C$ into 50% of the cells. A few spot checks revealed no great sensitivity to different initial conditions.

Figures 3–5 show the main effects and significance levels for the three dependent variables. The extinction of species $A$ in the absence of predators is determined by how long it takes species $B$ to disperse to all of the cells, since there is no mechanism to remove the winning competitor once it occupies a cell. Thus there are significant positive effects on persistence time of the number of cells and $TC$, and a negative effect of $D_p$. The dispersal rate of species $A$ has a marginally nonsignificant ($P = .079$) positive effect; in this situation there is little advantage to a high dispersal rate for species $A$, since species $B$ permanently occupies any cell it colonizes.

In the presence of predation (fig. 4), the persistence time of species $A$ is increased significantly by increases in the number of cells, its own dispersal rate and that of the predator, and the time required for within-cell interaction (either predation or competition) to be completed. The dispersal rate of species $B$ has, as would be expected, a significant negative effect.

The results for the measure of predation effect (fig. 5) parallel those for persistence under predation. The fact that this effect is significantly greater than zero is statistical proof of the possibility of open-system, nonequilibrium, predator-mediated coexistence. This demonstration is particularly powerful because the analysis is triply biased against demonstrating the effect. First, the parameter space investigated was chosen to result in median extinction times of less than 1,000 generations. Then those parameter combinations which resulted in more than 1,000 generations of coexistence were constrained to equal 1,000. Finally, there is the complication of predator extinction. Strictly speaking, a demonstration of predator-mediated coexistence could be made conditional on the continued presence of the predator, not merely its presence at the beginning of the simulation. In fully 40% of these runs, the predator went extinct before species $A$. These cases speak not of the failure of the predator to generate coexistence of the prey but rather of the inability of the predator to maintain a viable population, yet they were included in the analysis.
The Likelihood of Predator-mediated Coexistence:  
A Crude Evolutionary Argument

The possibility of open-system, nonequilibrium, predator-mediated coexistence is established, but how likely is it to occur? The answer to this question requires a prediction of the course of evolution to predict where in the parameter space real systems are likely to be located. To make a crude attempt at answering this question, I will use the treatment effects shown in figures 3–5, as well as similar data on the extinction time of the predator which is not included here.

The only measure of fitness available in this model is persistence time. Since
Fig. 5.—Main effects and significance levels for the effect of predation on the coexistence of species A. Note change in scale from those of figs. 3 and 4.

the system is open, it is possible to select (interdemic selection) for delayed extinction. Genotypes leading to shorter extinction times will disappear and be replaced by those with longer extinction times (see Gilpin [1975] for a detailed example). The evolution of decreased virulence by myxomatosis virus in Australian rabbits (Ratcliffe 1959) is a model case.

From the treatment effects in figures 3 and 4 and the data on species C it is possible to predict that those parameters likely to be under the genetic control of either species A or C (D_A, TC, TP, and D_C) should all be increased by selection for persistence. Predictions about species B cannot be made from this data; it seldom went extinct. The crucial point is that these increases all tend to increase the effect of predation. That is, this form of selection will act to increase the importance of predation in maintaining coexistence of the prey.
This first-order analysis can be extended somewhat by examining the
two-way interactions. All the interactions involving combinations of $D_A$, $TC$,
$TP$, and $D_C$ are of the reinforcing type. That is, the effect of one of the variables
is increased by an increase in the level of the other. Thus these second-order
interactions will only act to increase selection pressure for an increased effect of
predation.

This analysis is crude in several respects (ignoring species $B$, considering only
extinction time as a measure of fitness, and particularly in ignoring possible
nonlinear responses), but it does suggest that this type of coexistence can be
selected for.

SOME GENERALIZATIONS

The model used here is highly abstracted—cells are discrete permanent
fixtures, species are modeled by binary switches, etc. As I have repeatedly
pointed out, however, the abstractions have been designed to stack the deck
against predator-mediated coexistence whenever possible. In addition, the
model can be generalized easily, suggesting that the results obtained could be of
widespread occurrence and importance in natural communities.

What Is a Predator?

In this model, the predator opens up otherwise closed cells for colonization
by the inferior competitor. There is no reason why this function must be
performed by an actual predator. Physical disturbance would serve equally
well. Forest fires have been implicated as having a major role in maintaining
coeexistence of trees in northern temperate forests (e.g., Loucks 1970; Taylor
1973; Wright and Heinselman 1973) and in maintaining the precarious exist-
tence of the Kirtlands warbler in Michigan (Mayfield 1960). Osman (1977) has
documented the importance of physical disturbance by wave action on the
maintenance of coexistence in a marine epifaunal community, and Abele (1976)
has shown that physical disturbance generates an increase in diversity in the
crustacean community inhabiting coral heads. The major difference between
actual predation and abiotic physical disturbance is in the feedback between
the abundance of the “prey” and the activity of the disturbing agent. This
would lead to different dynamics of the system but would probably make
the coexistence effect more dramatic because the “predator” could not become
extinct.

The role of the predator can also be taken by nonpredatory biological
disturbance. Werner (1972) introduced a rosette-forming biennial plant species
(teasel, *Dipsacus sylvestris*) into several old fields and found an increase in the
number of plant species in the plots to which the teasel had been added. Close
investigation revealed that this increase was due to the colonization of open-
ings in the field generated by the teasel rosettes. The colonizing species were
clearly nonequilibrial, since they were found only in the teasel-generated
openings and were unable to reestablish themselves on the site through
reproduction. It is hard to guess how generally important this type of biological disturbance is, but it seems likely to occur in certain stages of succession, where one life form invades a community dominated by a few species of another life form. Platt (1975) has documented an even more dramatic case in which a well-defined assemblage of plants persists in the Iowa prairie only because of the generation of open space by badger mounds.

It is even possible for competitors to act as predators in this model. A nonlinear competitive hierarchy (e.g., \(A\) excludes \(B\), \(B\) excludes \(C\), \(C\) excludes \(A\)) would have the same basic properties as the predator-prey system modeled here: between-cell interactions would perturb the progress to local equilibrium. Jackson and Buss (1975) report such an interaction among coral reef invertebrates and suggest that it might be partly responsible for the high diversity of coral reefs.

**What Is a Cell?**

This model is applicable directly to situations with discrete, permanently defined, habitat patches (islands, lakes, mountaintops, host plants, etc.), but there are a variety of manifestations of this idea in different form.

In many cases, the cells are formed by the action of the “predator” itself (e.g., forest fires, badger mounds). Levin and Paine (1974) have modeled the generation of open cells in the rocky intertidal by starfish grazing. Coupling a model like theirs for patch formation with something like my model for species interaction within and between patches would generate a first approximation to a model of community dynamics in the intertidal.

An important generalization of the model would be to include cells of more than one type. Of particular importance is the division of a habitat into areas which the predator can reach and those which he cannot. The latter areas form a particular type of cell—a prey “refuge.” Such refuges are known to be important in maintaining coexistence of predator-prey systems (e.g., Gause 1934; Caswell 1972).

The most important result of the division of an area into cells is the maintenance of nonuniformity from one spot to another. Since extinction must happen everywhere at once to be final, this nonuniformity acts to prolong coexistence. This effect also can occur in a homogeneous expanse of habitat simply because of the time-lag inherent in the propagation of ecological effects over distance. This continuous form of “cells” would stand in the same relation to my discrete model as the “isolation-by-distance” to the “stepping-stone” model in population genetics (see, e.g., Crow and Kimura 1970). Earlier (Caswell 1972) this phenomena was implicated as a way to obtain refuges for prey populations. I am inclined to view Luckenbill's (1973, 1974) experiments as examples of this, although he might not. Dubois (1975) and Levin and Segel (1976) have begun work on modeling the generation of nonuniform conditions in ecological systems in homogeneous media. The much more general work of Glansdorff and Prigogine (1971), Iberall (1972), and Thom (1975) may ultimately provide a framework for this sort of phenomenon.
If cell-like phenomena can be generated by temporal asynchrony over large expanses of uniform habitat, then the results of this analysis become extremely general. They suggest that nonequilibrium coexistence may occur not only in obviously patchy habitats, but in such apparently uniform areas as large lakes or oceans.

In the model presented here, cells are cells to all three species involved. This clearly need not be the case in nature (see, e.g., Janzen [1967] in a different context). A whole spectrum of locally effective population areas may exist with interactions occurring between species at all levels. This will make any direct application of the model to a real community very difficult but is no deterrent to applying the model's qualitative conclusions.

Hierarchical arrangements of cells are an interesting possibility. Such a hierarchy would consist of sets of clusters of cells, each cluster being described by a model like the one developed here. Nonequilibrium coexistence in a hierarchy will be extended beyond its value within a single cluster. At the second level of the hierarchy, $TC$ and $TP$ will be greatly lengthened over their values in a single cell at the first level. And, while the dispersal probability from any single cell of one cluster to any single cell of a second cluster must be small (or else the two clusters would not be divided), the probability of dispersal from some cell of one cluster to some cell of the second should be rather higher. The results in figure 5, applied to the second level of the hierarchy, suggest that predation in this case will extend coexistence beyond its already extended value at the first level.

*Interaction of TP and TC*

The closed-system, nonequilibrium effect of predation is essentially an interaction between the competitive and predatory exclusion times, $TC$ and $TP$. If the predator is present in the cell, competitive exclusion is delayed for a greater or lesser period of time. In the most extreme case, $TC$ would become equal to $TP$; that is, competitive exclusion would not occur at all while the predator was present.

This effect is not included in the model, although it may occur in nature. It would definitely occur at the cell-cluster level in the hierarchical systems discussed above. Its effect, again, will be to prolong predator-mediated coexistence. This effect could be approximated by an increase in $TC$ to somewhere between $TC$ (in the absence of predators) and $TP$, the exact location determined by the fraction of cells in which both predator and prey occur.

*Continuous and Discrete Mathematics*

How many of the results of this analysis are artifacts of the use of discrete (presence-absence) mathematics, as opposed to a continuous representation? This is a difficult question to answer, but some justifications for the use of discrete mathematics are available.

First, the logical structure underlying the modeling of dynamic systems
applies equally to continuous and to finite-state systems (Arbib 1966). Presence and absence of a species are perfectly good ecological variables, and a finite-state model describing the dynamics of these variables is certainly of ecological relevance.

However, presence and absence can also be obtained from continuous mathematical models—abundances of zero and greater than zero, respectively. To evaluate the agreement between two different models describing the same quantities, we need more than just a formal equivalence between discrete and continuous modeling approaches; we need to look for properties of the particular system under consideration that will guarantee that we draw the same conclusions from the two analyses.

Rosen’s (1968) analysis of this problem showed that a discrete representation is obtained by a decomposition of the state space and input space of the continuous system into equivalence classes. The equivalence classes of states correspond to the basins of the stable orbits in the continuous state space; the equivalence classes of inputs are groups of inputs which transfer the continuous system from one basin to another. The transition rules for my model correspond exactly to such a decomposition. Attaching single values to competitive exclusion and predatory decimation times tacitly assumes that the basins in the continuous state space are very steep sided, a condition which Rosen (1968) points out results in a system with strong digital characteristics.

My results thus will be most quantitatively accurate for systems in which competition and predation generate extinction abruptly and at rates relatively independent of initial conditions. When these conditions are not met, the time scale of the model will become blurred, but the qualitative results will be unaffected.

It is worth noting briefly here the relation between my model and the similar models of epigenetic control networks studied by Kauffman (1969, 1972). Modeling the switching of genetic control systems, he coupled randomly defined Boolean functions in a randomly selected pattern and followed the approach of the systems to stable cycles of behavior. In Kauffman’s systems, the components of the network are specified at random, and the system then operates deterministically. The components of my networks, on the other hand, are specified deterministically but are operated stochastically. The lags involved in competitive and predatory extinction are another phenomenon which does not appear in Kauffman’s nets, in which elements switch on and off instantaneously.

A LOOK AT THE REAL WORLD

This model can be tested against real-world observations in several ways. Since it predicts the existence of predator-mediated coexistence, all of the examples cited in the opening section, as well as the cases involving nonpredatory disturbance mentioned above, can be taken as corroborating the model. More interesting, however, are those predictions of the model that distinguish it from the other three types of predator-mediated coexistence.
The first of these is the prediction that the observed effect of predation will vary with the scale of observation. If an investigator happens to focus his attention within a single cell, predation will have a negative effect on coexistence. (Total extermination of all prey, in the limiting case described in the model.) On the other hand, if a study takes in an area large enough to contain a whole ensemble of cells, it should demonstrate a positive predation effect. Neither of the closed-system theories predicts an area effect of this sort.

In addition, the model relies on the temporary action of predation, opening up new cells for colonization and then releasing the predation pressure to allow nonequilibrium population growth. If the predation pressure does not disappear periodically, the nonequilibrium effect will not be seen. Instead, a new equilibrium will be established within the cell—with no more, perhaps fewer, species than in the absence of predation. Neither of the equilibrium models of predator-mediated coexistence makes this prediction.

A number of examples in the literature which have failed to show predator-mediated coexistence seem to be explained by these predictions. Adicott (1974) searched for predator-mediated coexistence in the protozoan communities in pitcher plant leaves under the impact of mosquito larva predation. The isolated water bodies in a single pitcher plant are clearly single cells for both the prey and the predator. Within these cells, Adicott demonstrated a significant negative relationship between predation intensity and the number of coexisting protozoans. Unfortunately, he presents no data on the effect of predation at the multicell level in these systems. However, it would not be surprising if it also were small or nonexistent, because the predation pressure does not seem to be intermittent. Mosquito larvae occupy a given cell more or less continuously throughout the summer. Abele (1976) studied a similar system: the crustacean community inhabiting heads of the coral Pocillopora damicornis. He contrasted the diversity of this community in two sites differing in the level of abiotic environmental variability and found that the disturbance generated no increase in diversity within a single coral head, but at the multicell level it generated a 50% increase in species numbers in a sample of 35 heads.

The rocky intertidal communities studied by Paine and his students also provides an interesting comparison. The work on the starfish/molluse system (Paine 1966, 1971; Dayton 1971) clearly demonstrated a positive predation effect on a spatial scale of tens of meters of coastline. It would probably not occur to anyone to study this system within a single cell; this would involve following a starfish around and studying the patches he leaves behind him after feeding. Paine and Vadas (1969), however, seem to have found a within-cell effect in another intertidal system, this one involving grazing by sea urchins on tide-pool benthic algae. When the urchins were removed from individual tidal pools, the immediate response was an increase in the number of algal species, which eventually decreased as a few species became dominant. I suspect that a single tidal pool functions as a cell to a group of grazing sea urchins. If there is some mechanism available to occasionally remove urchins from pools, thus making predation intermittent, urchin grazing could be responsible for maintaining the diversity of algal species over stretches of shoreline. It turns out that there is such a mechanism. The starfish *Pycnopodia* occasionally enters pools,
consuming some urchins and stampeding the rest out of the pool (see also Dayton 1972).

Fish predation has been clearly implicated in maintaining coexistence among zooplankton in ponds (Hall et al. 1970) and lakes (Brooks and Dodson 1965; Wells 1970). Such systems are large and spatially complex enough to contain many “cells” for zooplankton, and predation is made locally intermittent by the fact that the fish cannot be everywhere at once. In contrast to these systems, Hurlbert et al. (1972) reported on the effect of fish predation (by the mosquitofish, Gambusia) on zooplankton in small plastic wading pools. In this system, where the fish were almost certainly treating the pool as a single cell, and in which there was no fluctuation in predation intensity, the fish totally decimated their prey. They eliminated all aquatic insects and all zooplankton species larger than rotifers. Neill (1972) also studied the effect of fish predation on zooplankton in microcosms (1.5-liter aquaria in this case). He found a significant increase in the number of coexisting zooplankton under the impact of fish predation, but his system differed from Hurlbert’s in two respects. Neill generated migration of prey species between aquaria, thus creating an open, multicelled system, and he made predation locally intermittent by periodically removing the fish from the aquaria. Thus Neill’s system fits somewhere between Hurlbert’s closed system and the complexity of a real lake.

When grazing herbivores are fenced into enclosed pastures, both the density of grazers and the temporal pattern of the grazing will affect the pattern of predator-mediated coexistence. At high densities, the entire pasture will be treated as a single cell, receiving uniformly high predation pressure. In this situation the nonequilibrium model predicts that predation will have a positive effect on coexistence only if it is interrupted by removal of the grazers. Harper (1969) cites several such cases. At much lower densities of grazers, or in situations where they are not enclosed, predator movement will generate intermittent predation pressure in a patchy fashion over the landscape and thus increase coexistence. Harper (1969) and Summerhayes (1941) discuss several examples; Nicholson et al. (1970) report some observations on the spatial pattern of grazing by livestock.

Janzen (1976) has proposed an interesting special case of this effect to explain the low density of snakes and lizards in Africa compared with Central America. He hypothesizes that the decline is due to a higher predation pressure in Africa caused by the availability of carrion as an alternative food source, which keeps the predation pressure constant rather than intermittent.

Cairns et al. (1971) studied the protozoan fauna colonizing artificial sponges suspended in a lake and imposed an intermittent, nonselective disturbance on the community by periodically squeezing the sponges and allowing them to refill with water. As predicted by the nonequilibrium model, they found a significant increase in the number of protozoan species in the squeezed sponges. It would be very interesting to repeat this experiment with continuous rather than intermittent “predation,” perhaps by pumping a continuous flow of water through the center of the sponge. The model predicts that this manipulation should not increase the number of coexisting species.

Finally, at a very general level the nonequilibrium model predicts that as a
community becomes more protected from the action of disturbance (biotic or abiotic) it will become less diverse. This prediction agrees with the observation that, in the absence of disturbance, population-level interactions result in decreases, not increases, in diversity (Caswell 1976).

The agreement between the open system, nonequilibrium model of predator-mediated coexistence and studies of real communities is impressive. Each of the four types of predator effect are no doubt important in some natural situations. The open-system, nonequilibrium model seems as robust as any of the others at this point since it includes the dynamics of the predator, is insensitive to environmental variation, and can make at least crude evolutionary predictions. Still, more information is needed on parameter effects than is included here, and distinguishing the different predator effects in nature should receive more attention.

EQUILIBRIUM AND NONEQUILIBRIUM CONCEPTS
IN ECOLOGICAL THEORY

The distinction between closed and open, equilibrium and nonequilibrium systems has implications extending beyond the problem of predator-mediated coexistence. The structure of ecological theory is heavily influenced by its spatial and temporal scales of reference.

A theory which focuses on a single closed cell, on a time scale corresponding to a single extinction, will view zero as an absorbing state for the system. Since extinction in such a system is permanent, this theory will devote considerable energy to the search for conditions which guarantee the existence of stable equilibria.

A theory encompassing many cells, over a time scale of many local extinctions, will have very different properties. It will differentiate, implicitly or explicitly, between the extinction of local populations and of entire species. Local extinctions will be regarded as relatively common, and, since such extinction is not an absorbing state, this theory will not be overly concerned with conditions leading to stable equilibria. Dispersal, migration, and colonization will be fundamental to such a theory, and spatial effects likely will be explicitly considered.

The arguments which raged in the 1950s over density dependence are one example of this. In addition to the empirical evidence mustered by each side, this dispute was characterized by a peculiar logical argument. The density-dependent theorists, largely inspired by closed laboratory systems (Gause 1934; Nicholson 1957), argued that density-dependent effects are necessary to generate stable equilibria and that stable equilibria are necessary to prevent extinction. The champions of density independence replied.

Nevertheless, the misconception prevails that the extinction of a population is a very rare event. This leads our colleagues who hold to the dogma of "density-dependent factors" to propound this riddle. On hearing us expound our views on ecology, they ask: "How is it, if there is no density-dependent factor in the environment, that the population does not become extinct?" This places us in a position like that of the man in the dock who was asked to answer Yes or No to the
question: “Do you still beat your wife?” We cannot answer the question until we have cleared up
the misconception in the mind of the questioner ... we can witness the extinction of local
populations, of even the most abundant species, going on all around us all the time. [Andrewartha
and Birch 1954, pp. 663 ff.]

That they were defending an open-system, nonequilibrium theory of popula-
tion dynamics can be seen in their explicit distinction between extinction of
local populations and of entire species, and in their insistence (reflected in the
title of their book) that distribution and abundance be considered together.

The frequency of local extinction has since been documented in studies of
island communities (Mayr 1965; MacArthur and Wilson 1967; Simberloff and
Wilson 1969; Diamond 1969; Simberloff 1974) although the quality of some of
these data is now in doubt (Lynch and Johnson 1974). The theory of island
biogeography (MacArthur and Wilson 1967; Simberloff 1974) maps this
open-system nonequilibrium view of populations upward to the community
level. This theory focuses on an equilibrium in species number, generated by an
implicit, open-system, nonequilibrium conception of the dynamics of the
species. The unexpectedly high species turnover rates discovered in these
studies are clearly a nonequilibrium phenomenon.

While the problem of succession is only beginning to be rigorously for-
mulated in terms of population theory, it also seems to involve open-system,
nonequilibrium phenomena. Successional development is strewn with the
corpses of locally extinct populations (not species); this fact is so obvious that it
excites little attention until a conceptual framework is available in which it is
important. The process of dispersal, necessary to supply colonists to open
systems, has always figured prominently in succession theory (Thoreau 1860;
Keever 1950; Drury and Nisbet 1973; Horn 1975). There is recent evidence
strongly suggesting that in the mature stages of succession diversity declines in
the absence of disturbance (Loucks 1970; Auclair and Goff 1971; Wright and
Heinselman 1973; Caswell 1976).

With the seeming defeat of density independence, equilibrium theory became
the dominant mode of explanation in population biology in the late 1960s.
Nonequilibrium ideas remained in evidence (Hutchinson [1951, 1961, 1965] in
particular seems to have been well aware of the distinction), but until very
recently the mainstream of ecological thought has regarded them as special
cases and sought explanations for community structure primarily in terms of
equilibria of species interactions.

The fact that nonequilibrium situations in multicell connected systems can
persist for immense periods of time (Ashby 1960), and that such systems can be
easily interpreted in terms of ecological communities, suggests the need to
evaluate the importance of nonequilibrium coexistence. It certainly will not do
to suggest that communities as a whole are entirely equilibrium or entirely
nonequilibrium systems. It seems more reasonable to view the populations
within a community as existing in a spectrum of cell sizes, reflecting within-cell
equilibria and between-cell disequilibria, modified by biotic and abiotic distur-
bance on a variety of levels. Perhaps a community consists of a core of
dominant species, which interact strongly enough among themselves to arrive
at equilibrium, surrounded by a larger set of nonequilibrium species playing out their roles against the backdrop of the equilibrium species (see, e.g., Diamond 1975).

Certainly, to evaluate this requires looking at the whole spectrum of abundance in the community. The diversity trends analyzed by Loucks (1970), and Auclair and Goff (1971), and Caswell (1976) are a promising approach. The correlation of rarity with spatial clumping demonstrated in soil mites (Hastion 1959), periodical cicadas (Dybas and Davis 1962), and snails in Egyptian and Sudanese canals (Hastion, personal communication) is also suggestive. Developing these ideas rigorously will require much more work on the transient behavior of ecological systems, the topological properties of multispecies interactive models, and the properties of open systems.

SUMMARY

There is now convincing evidence, from a variety of ecological systems, that predation is capable of maintaining coexistence among a set of competing prey species, some of which would be excluded in its absence. This interaction has been suggested as a major factor determining the structure of some communities, but attempts to incorporate it into the mathematical framework of population theory have been frustrating. Although the possibility of predator-mediated coexistence is easily shown, parameter-space studies of simple three-species models suggest that it is an improbable occurrence, requiring a very delicate balancing of parameter values.

To attack this problem, I classify population systems as open or closed, and equilibrium or nonequilibrium. Closed systems consist of a single homogeneous patch of habitat; open systems, in their simplest form, are a collection of such patches (or cells) connected by migration. Equilibrium theories are restricted to behavior at or near an equilibrium point, while nonequilibrium theories explicitly consider the transient behavior of the system. Almost all of the work on predator-mediated coexistence has been limited to closed, equilibrium systems. In such studies conditions are sought which guarantee that predation results in a stable equilibrium at which all species are present.

A general property of open systems is that transient, nonequilibrium behaviors may persist for extremely long periods of time. A model is presented which uses this fact to generate long-term, but nonequilibrial, coexistence among competitors under the impact of predation. The model is a discrete, or logical, model, in which presence and absence of each of two competitors and a predator is followed in a set of stochastically connected local population cells. The predator acts to open up new cells for nonequilibrium growth of the prey species. All forms of predator-mediated coexistence other than the open-system, nonequilibrium effect were purposely eliminated from the model.

The results of the model clearly demonstrate the possibility of long-term predator-mediated coexistence in such a system. In spite of stacking the deck against it, the positive effect of the predator on coexistence is statistically highly significant. Moreover, a crude evolutionary analysis suggests that the effect is not only possible, but probable. These results can be generalized far beyond the
highly abstracted framework of the model. Such generalizations suggest that this phenomenon may be of major importance in natural systems.

The predictions of the model can be tested against the real world in several ways. First, it predicts the possibility of predator-mediated coexistence, which agrees with the numerous observations of that phenomenon. More importantly, it makes predictions (concerning the spatial and temporal organization of the predation process) that distinguish it from the other modes of predator-mediated coexistence. These predictions are corroborated by observations of a number of cases where predation has failed to generate coexistence.

The distinction between closed and open, equilibrium and nonequilibrium, population systems has an important impact on the form and substance of ecological theory.

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