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The Importance of Being Discrete (and Spatial)

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We consider and compare four approaches to modeling the dynamics of spatially distributed systems: mean field approaches (described by ordinary differential equations) in which every individual is considered to have equal probability of interacting with every other individual; patch models that group discrete individuals into patches without additional spatial structure; reaction-diffusion equations, in which infinitesimal individuals are distributed in space; and interacting particle systems, in which individuals are discrete and space is treated explicitly. We apply these four approaches to three examples of species interactions in spatially distributed populations and compare their predictions. Each represents different assumptions about the biology and hence a comparison among them has biological as well as modeling implications. In the first case all four approaches agree, in the second the spatial models disagree with the nonspatial ones, while in the third the stochastic models with discrete individuals disagree with the ones based on differential equations. We show further that the limiting reaction-diffusion equations associated with particle systems can have different qualitative behavior from those obtained by simply adding diffusion terms to mean field equations.

One of the fundamental issues in the modeling of any system is the choice of level of detail. The relevance goes far beyond mathematical convenience to the heart of understanding the mechanism, specifically, which details at one level are important to the determination of phenomena at

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other levels and which can be ignored. In modeling the temporal evolution of a spatially distributed system, describing for example the interaction of species or the spread of an epidemic, one can choose several levels of description involving different levels of spatial detail. The simplest approach is to assume that the system is homogeneously mixing over its entire extent and model the dynamics by a system of ordinary differential equations or difference equations. Since each individual interacts equally with all the others we follow physicists and call this the mean field approach. Alternatively, one can recognize that spatial position is important and allow individuals to move about in continuous or discrete space; the relevant mathematical description is then a reaction diffusion system or discrete approximation to it.

The reaction diffusion approach recognizes the importance of spatial inhomogeneity and the inadequacy of mean field approaches when local interactions are nonlinear (Levin, 1974), but it does not lend itself easily to the treatment of local stochasticity (Levin and Paine, 1974; Chesson, 1981) or the fact that individuals are discrete units. Both of the above approaches are deterministic, and implicitly involve a limit in which the population size gets large or, equivalently, that individuals become infinitesimal. Models that relax these limitations within a spatial framework have received increasing attention in the ecological literature in recent years and are explored in this paper.

The usual mechanism (Levin, 1974, 1976; Levin and Paine, 1974; Chesson, 1981, 1985) is to abandon the continuum of spatial scales available in the reaction diffusion approach in favor of a subdivision of space into patches with (Levin, 1974; Durrett and Levin, 1994) or without (Levin and Paine, 1974; Chesson, 1981) further specification of the spatial arrangement and accesibility of the patches. The latter approach fits into the patch dynamics framework developed by Levin and Paine (1974) and explored later by Paine and Levin (1981) and Chesson (1981) and in metapopulation theory (Gilpin and Hanski, 1991) and aspects of life history evolution (Levin *et al.*, 1984).

Chesson, in developing a general theory to deal with the interplay between spatial localization and local stochasticity when interactions are nonlinear and individuals are discrete, extends earlier work in several ways to explore these influences. He demonstrates clearly that local stochastic phenomena "have a systematic effect on average population density and this effect does not disappear in large populations." In demonstrating the inadequacy of mean field models when local spatial interactions are important, this work complemented earlier work of Levin (1974, 1976) who showed that multiple stable states and stochastic colonization events could lead to coexistence of competitors that were incompatible in mean field theory and extended work of Levin and Paine (1974) who argued that local stochasticity (in the form of disturbance) could lead to nonequilibrium coexistence even in the absence of multiple stable states.

Chesson (1981) argues that the lack of spatial structure in the set of patches or equivalently the assumption of equal accessibility does not affect the main conclusions he wishes to draw. (See Section 6 of his paper.) It can however affect other conclusions as we show in Case 2 below. In an approach that relaxes the assumption of equal accessibility while maintaining the restriction that individuals are discrete, Durrett and Levin (1994) explicitly subdivide space into a grid of cells and directly model the interactions between individuals via an interacting particle system. The four approaches and their relationships are summarized schematically in Fig. 1; these relationships are explored in this paper. The approaches considered in this paper do not exhaust the realm of possible models for spatially distributed populations; among the alternatives are coupled map lattices (Hastings, 1993), spatially discrete analogues of reaction diffusion equations (Levin, 1974), cellular automata (Caswell and Etter, 1993; May and Nowak, 1992), and individual-based models (Pacala, 1986).

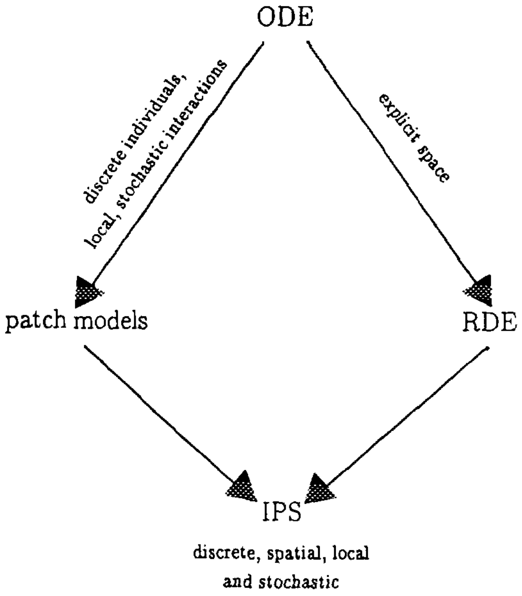

FIG. 1. Relationship of the four approaches studied. Here ODE stands for ordinary differential equation, RDE for reaction diffusion equations, and IPS for interacting particle system.

1. FOUR APPROACHES TO MODELING SPECIES INTERACTIONS

This paper was originally inspired by an attempt to understand the results of Brown and Hansell (1987) who considered a spatial version of Maynard Smith's evolutionary games. In this system there are two types of individuals, whose interaction is described by a game matrix:

$$\begin{array}{ccc} & H & D \\ H & a & b \\ D & c & d. \end{array}$$

Here, H denotes a hawk and D a dove. This nomenclature is usually reserved for Case 3 considered below, but since we find these terms a convenient way of referring to the two strategies, we use them throughout the paper even though they may be inappropriate for some biological or sociological applications.

To explain the game matrix, b is, for example, the payoff to a hawk when interacting with a dove. When the population consists of a fraction p of hawks and $1-p$ of doves then the payoff for hawks is $ap+b(1-p)$ and we interpret $ap+b(1-p)$, which may be positive or negative, as the net birth rate of hawks in this situation. The payoff matrix should be thought of more broadly than as just defining game interactions—our model applies to any situation where the growth rates are a linear function of the frequencies of the various types. Thus b is the density independent net growth rate for hawks inhabiting a region dominated by doves.

In addition to the net growth rate, we assume that there is a density dependent death rate per individual that is proportional to the density, and arrive at the following dynamical system for the densities of hawks (u) and doves (v):

$$\begin{aligned} \frac{du}{dt} &= u\left\{a\frac{u}{u+v}+b\frac{v}{u+v}-\kappa(u+v)\right\} \\ \frac{dv}{dt} &= v\left\{c\frac{u}{u+v}+d\frac{v}{u+v}-\kappa(u+v)\right\}. \end{aligned} \tag{1}$$

Note that a species specific linear term in the net birth (death) rate, r, is easily accommodated within this framework as part of a and b or c and d. We have occasion to refer to this possibility later.

The traditional (but occasionally incorrect) way to turn a dynamical system into a reaction diffusion system is to simply add diffusion terms to the two equations:

$$\begin{aligned}\frac{du}{dt} &= \Delta u + u\left\{a\frac{u}{u+v} + b\frac{v}{u+v} - \kappa(u+v)\right\}\\ \frac{dv}{dt} &= \Delta u + v\left\{c\frac{u}{u+v} + d\frac{v}{u+v} - \kappa(u+v)\right\}\end{aligned} \tag{2}$$

Here we restrict our attention to two dimensions so $\Delta u = \partial^2 u/\partial x_1^2 + \partial^2 u/\partial x_2^2$. For simplicity we have assumed that the two diffusion constants are the same and we have scaled time to make them equal to 1. When different diffusion rates are considered, an additional parameter (the ratio of the diffusion constants) enters and the range of behaviors is enlarged. (See Levin and Segel (1983).) At the end of this paper we use the viewpoint of interacting particle systems to derive alternative reaction diffusion equations that we think more accurately approximate the individual-based accounting, but for present comparisons we take (2) as the usual description. While on the subject of alternative equations, we note that Vickers (1989) and Hutson and Vickers (1992) use a different version of the death term that is motivated by Zeeman's (1981) equations for the evolution of the proportions of individuals who play various strategies.

In our first two approaches the individuals are infinitesimal. To formulate alternative systems that treat individuals as discrete units, we let S be the set of sites or "patches," and following Brown and Hansell (1987), assume that the state at time t is given by two functions η_t and ζ_t from S to $\{0, 1, ...\}$. So $\eta_t(x)$ and $\zeta_t(x)$ represent the number of hawks and doves in the patch at x at time t. In our model, we take time to be continuous, i.e., t can be any nonnegative real number; so the temporal evolution is described by specifying the rate at which things happen. Here, we say something happens at rate r if the probability of an occurrence in a short amount of time h is $rh + o(h)$, where $o(h)$ denotes a quantity with $o(h)/h \to 0$ as $h \to 0$. When an event occurs at a constant rate r (like the migrations in the models below) then the times t_i between successive occurrences have an exponential distribution with parameter r; that is, $P(t_i > t) = e^{-rt}$.

Having explained what it means for something to happen at rate r, we can now formulate our two models with discrete individuals. Three types of events occur in each model but space is treated differently.

Patch Models. Our first approach is to use the continuous time analogue of Chesson's (1981) formulation, adopting a well known technique from the physics literature (see Nicolis and Prigogine, 1977). In these models the subdivision into patches recognizes the importance of space at local scales but the collection of patches, S, has no spatial structure; thus, we choose $S = \{1, 2, ..., N\}$ where N is the number of patches.

(i) *Migration.* Each individual changes its spatial location at rate μ, and when it moves it moves to a randomly chosen patch.

(ii) *Deaths due to crowding.* Each individual at x at time t dies at rate $\kappa(\eta_t(x)+\zeta_t(x))$.

(iii) *Game step.* Let $p_t(x)=\eta_t(x)/(\eta_t(x)+\zeta_t(x))$ be the fraction of hawks at site x. Each hawk experiences a birth (or death) rate of $ap_t(x)+b(1-p_t(x))$ while each dove experiences a birth (or death) rate of $cp_t(x)+d(1-p_t(x))$. The phrase "birth (or death)" means that these numbers are interpreted as birth rates if they are positive and death rates if they are negative.

Interacting Particle Systems. Our second approach assumes that the patches can be identified with the set of lattice points $S=\mathbf{Z}^2$, the points in two-dimensional space with integer coordinates. Following Brown and Hansell (1987), the dynamics are formulated as follows:

(i) *Migration.* Each individual changes its spatial location at rate μ and when it moves it moves to a randomly chosen nearest neighbor of x; i.e., it picks with equal probability one of the four points $x+(1,0)$, $x-(1,0)$, $x+(0,1)$, and $x-(0,1)$ that differ from x by 1 in one of the coordinates.

(ii) *Deaths due to crowding.* Each individual at x at time t dies at rate $\kappa(\eta_t(x)+\zeta_t(x))$.

(iii) *Game step.* Let $\mathcal{N}$ be the interaction neighborhood for the model. In this paper we consider two choices for $\mathcal{N}$:

$\mathcal{N}_1=\{z\in\mathbf{Z}^2: \lvert z_1\rvert+\lvert z_2\rvert\leqslant 1\}$	(0, 0) and its nearest neighbors
$\mathcal{N}_2=\{z\in\mathbf{Z}^2: \lvert z_1\rvert\leqslant 2, \lvert z_2\rvert\leqslant 2\}$	a 5 × 5 square centered at (0, 0).

For any choice of $\mathcal{N}$ we let

$$\hat{\eta}_t(x)=\sum_{x\in\mathcal{N}}\eta_t(x+z) \qquad \hat{\zeta}_t(x)=\sum_{z\in\mathcal{N}}\zeta_t(x+z)$$

$$p_t(x)=\hat{\eta}_t(x)/(\hat{\eta}_t(x)+\hat{\zeta}_t(x)).$$

Here $\hat{\eta}_t(x)$ and $\hat{\zeta}_t(x)$ are the number of hawks and doves in the interaction neighborhood of x at time t, and $p_t(x)$ is the fraction of hawks. Each hawk experiences a birth (or death) rate of $ap_t(x)+b(1-p_t(x))$ while each dove experiences a birth (or death) rate of $cp_t(x)+d(1-p_t(x))$. The phrase "birth (or death)" means that these numbers are interpreted as birth rates if they are positive and death rates if they are negative.

The choice of the nearest neighborhood $\mathcal{N}_1$ for the migration and the game steps is primarily for simplicity. In most cases the qualitative features of the model do not depend upon the exact form of the neighborhood chosen. (However, see the analysis of Case 3 below.) We could make the interacting particle system model look more like the patch model by making the game step involve only individuals in the same patch but this would not affect the results very much.

2. COMPARISONS OF THE FOUR APPROACHES

We contrast the predictions of the four approaches by considering three examples. No two approaches agree in all three cases. To motivate the choice of our examples, we change variables $p = u/(u+v)$, $s = u+v$ in the dynamical system to get

$$\begin{aligned} \frac{dp}{dt} &= (a-b-c+d)\, p(1-p)\,(p-p_0) \\ \frac{ds}{dt} &= s\{\alpha p^2 + \beta p + \gamma\} - \kappa s^2 \end{aligned} \tag{3}$$

where

$$p_0 = \frac{b-d}{b-d+c-a}, \qquad \alpha = a-b-c+d, \qquad \beta = b+c-2d, \qquad \gamma = d-\kappa s.$$

The equation for dp/dt is identical to the usual equation from population genetics for weak selection with selection coefficient $a-b-c+d$. If the hawk strategy is never worse than the dove strategy, that is, $a \geqslant c$ and $b \geqslant d$, then $p_0 \geqslant 1$ or $p_0 \leqslant 0$ (ignoring the trivial case $a = c$, $b = d$). The same conclusion holds if the dove strategy dominates the hawk strategy; but if neither strategy dominates the other, p_0 represents a mixed strategy equilibrium. That is, if a fraction p_0 of the players play the hawk strategy and a fraction $1-p_0$ play the dove strategy, both strategies have the same payoff. To check this note that

$$p_0 a + (1-p_0) b = p_0 c + (1-p_0)\, d \qquad \text{if and only if } p_0 = \frac{b-d}{b-d+c-a}.$$

When $p_0 \in (0, 1)$, it may be (i) an attracting or (ii) a repelling fixed point. In accord with the situation in population genetics when the heterozygote is superior or inferior, this occurs when (i) $a < c$ and $b > d$, or (ii) $a > c$ and $b < d$. These are the first two cases we consider below. The third and most interesting case we consider is (iii) $0 > a > c$, $b > d > 0$. To keep the discussion simple we consider only a single numerical example of each case.

Case 1: *All Four Approaches Agree.*

$$a = 0.4 \qquad b = 0.8$$
$$c = 0.6 \qquad d = 0.3$$

In this case the two types have an apparent symbiotic relationship because the fitness of each is enhanced by the presence of the other. Note, however, that the terms a, b, c, and d could represent the sum of a constant growth rate and negative effects of competition:

$$\begin{pmatrix} 0.4 & 0.8 \\ 0.6 & 0.3 \end{pmatrix} = \begin{pmatrix} 1 & 1 \\ 2 & 2 \end{pmatrix} + \begin{pmatrix} -0.6 & -0.2 \\ -1.4 & -1.7 \end{pmatrix}.$$

This would then correspond to the competition situation in which each species inhibits itself more than it inhibits the other, for which it is well known that coexistence results and that a globally stable internal equilibrium exists. (See, e.g., Slobodkin, 1962).

In this situation all four methods of analysis (dynamical systems, reaction-diffusion equations, patch models, and interacting particle systems) reach the same conclusion: there is a unique equilibrium that is the limit starting from any initial state in which both species have positive density. The graph in Fig. 2 shows the behavior of the dynamical system.

THEOREM 1.1. *From any starting point* (u_0, v_0) *with both coordinates positive the system converges to the unique fixed point* (u^*, v^*) *in the positive quadrant.*

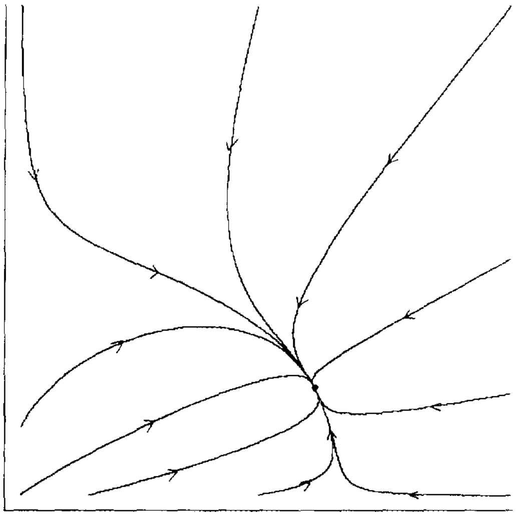

FIG. 2. Dynamical system for Case 1.

Proof. This is easy to see from (3). The equation for p is a one-dimensional ordinary differential equation with a fixed point p_0 that is globally attracting in $(0, 1)$, so $p(t) \to p_0$. Once we know this, it is easy to see that $s(t) \to (\alpha p_0^2 + \beta p_0 + \gamma)/\kappa$ as $t \to \infty$. ∎

Because the frequency dependent dynamics promote coexistence locally, it is not surprising that coexistence also results in the other approaches as well. For the reaction diffusion equation, we make the following conjecture.

Conjecture 1.2. If $u(0, x)$ and $v(0, x)$ are nonnegative, continuous, and not identically 0, then as $t \to \infty$, $(u(t, x), v(t, x))$ converges to (u^*, v^*) uniformly on compact sets.

Support for this conjecture can be found in the work of Durrett (1993), which by building on the results of Redheffer *et al.* (1988) and many others proves a convergence theorem for reaction diffusion equations when the associated dynamical system has a convex Lyapunov function.

To determine the behavior of the patch models and interacting particle system, we have to resort to simulation. Figure 3 shows a simulation of the

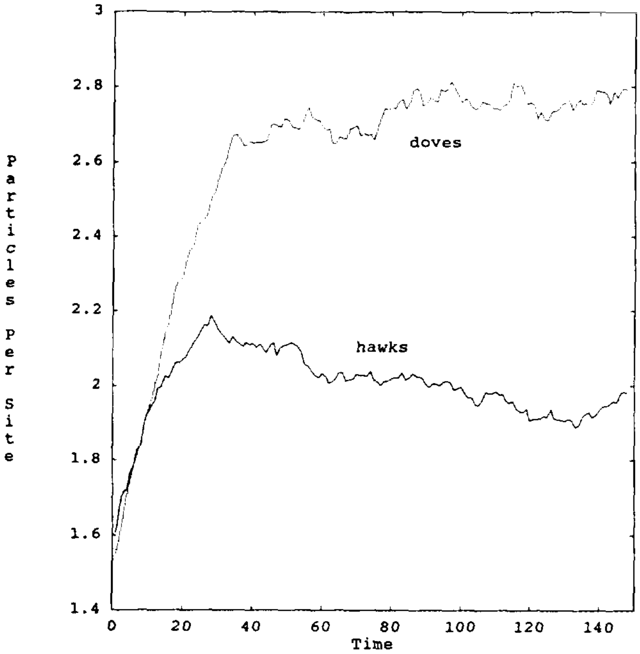

FIG. 3. Average number of hawks and doves per site in Case 1 for a simulation of the patch model with 2500 sites.

patch model with $N = 2500$ patches when $\kappa = 0.08$ and $\mu = 1$ and we start from an initial condition in which the initial numbers of hawks and doves at site x were $[4 * U_x]$ and $[4 * V_x]$, where $[y]$ is the integer part of y and the U_x and V_x are independent random variables that are uniformly distributed on $(0, 1)$. All of our initial states have this structure, so in what follows we simply refer to the 4, 4 initial condition, indicating the numbers we used to multiply U_x and V_x. This choice makes the number of hawks or doves at each site independent and $= 0, 1, 2, 3$ with probability $\frac{1}{4}$ each, for an expected value of 1.5. As the simulation indicates, the numbers of hawks and doves rise from initial levels near 1.5 to equilibrate near 2.0 and 2.7 respectively, although there are fluctuations coming from the fact that there are only 2500 patches.

To determine the behavior of the interacting particle system, we simulated the process on a 100×100 system with periodic boundary conditions. (That is, sites on the left edge of the square are considered to be neighbors of those on the right, and those on the top edge are considered to be neighbors of those on the bottom.) Figure 4 shows the evolution of the system with $\kappa = 0.08$ and $\mu = 0.4$ starting from the 7.5, 7.5 initial condition. As the figure indicates the densities of hawks and doves converge exponentially fast to their equilibrium values, although again there are some fluctuations in the densities due to the fact that there are only 10,000 sites. Based on the simulation and on theoretical results due to Neuhauser

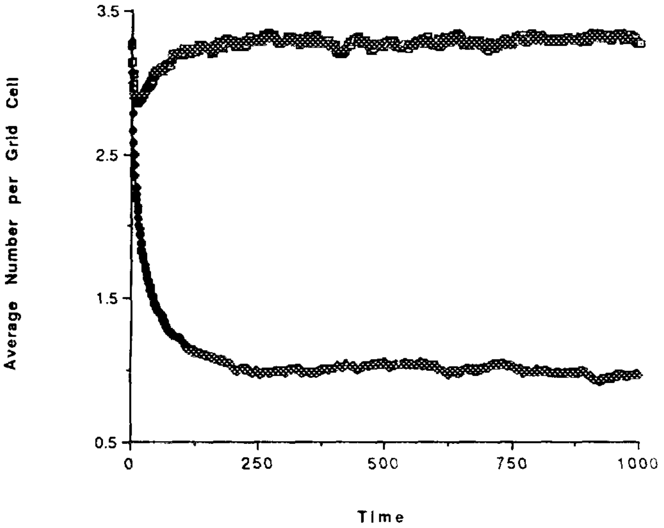

FIG. 4. Average number of hawks (□) and doves (◆) per site in Case 1 for a simulation of the interacting particle system on a 100 by 100 lattice.

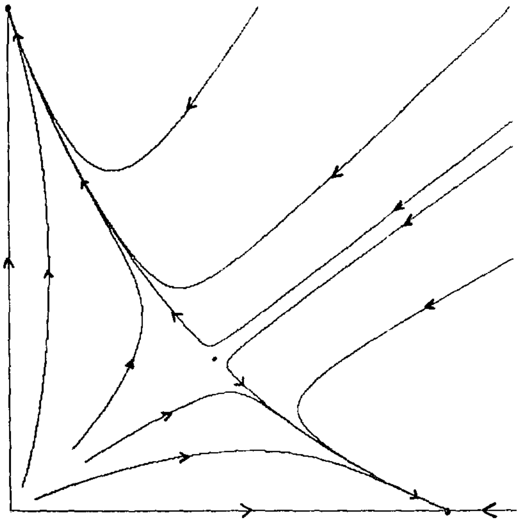

FIG. 5. Dynamical system for Case 2.

(1990) and Ding *et al.* (1990) for a closely related model of Schlögl (1972) (see Part IV of Chen (1992) for a survey), we make the following conjecture.

Conjecture 1.3. The interacting particle system has a unique equilibrium state that is the limit starting from any initial state (a) that is translation invariant and (b) in which each species has a positive density.

That is, it is the limit starting from any initial state in which (a) for any finite set $\{y_1, ..., y_k\}$, the joint distributions of $\eta_t(x+y_1), ..., \eta_t(x+y_k)$ and of $\zeta_t(x+y_1), ..., \zeta_t(x+y_k)$ do not depend on x, and (b) the probabilities $P(\eta_t(x)=0)$ and $P(\zeta_t(x)=0)$, which by assumption do not depend upon x, are both strictly less than 1. Since only hawks can give birth to hawks and only doves can give birth to doves, the second assumption is clearly necessary to get an interesting limit. Assumption (a) comes up several more times below, so we add a few more words of explanation. This condition says that the random initial state is spatially homogeneous; i.e., the random picture looks the same (i.e., has the same distribution) no matter where we stand.

Case 2: *The Importance of Being Spatial.*

$$a=0.7 \qquad b=0.4$$

$$c=0.4 \qquad d=0.8$$

This may be thought of as two species competing for use of the same resource and in which the competition of each inhibits the other species more than it does itself. Again, of course, other interpretations are possible since a, b, c, and d represent net growth terms. In this situation, the non-spatial models disagree with the ones that treat space explicitly. As Fig. 5 suggests, and one can prove easily using (3), we have the following.

THEOREM 2.1. *The dynamical system has two stable equilibria* $(\bar{u}, 0)$ *and* $(0, \bar{v})$ *on the axes, and their basins of attraction contain the whole positive quadrant except for a line through the origin containing the equilibrium* (u^*, v^*), *which is a saddle point.*

The details of the proof are similar to those for Theorem 1.1 and are left to the reader.

Figures 6 and 7 show simulations of the patch model with $\kappa = 0.8$ and $\mu = 1$ for the 5, 5 and 7, 3 initial configurations, respectively. In the first case the hawks died out at time 211, while in the second the doves died out at time 237. Thus in the patch model, as in the ordinary differential equations, the species that wins out depens on the initial densities.

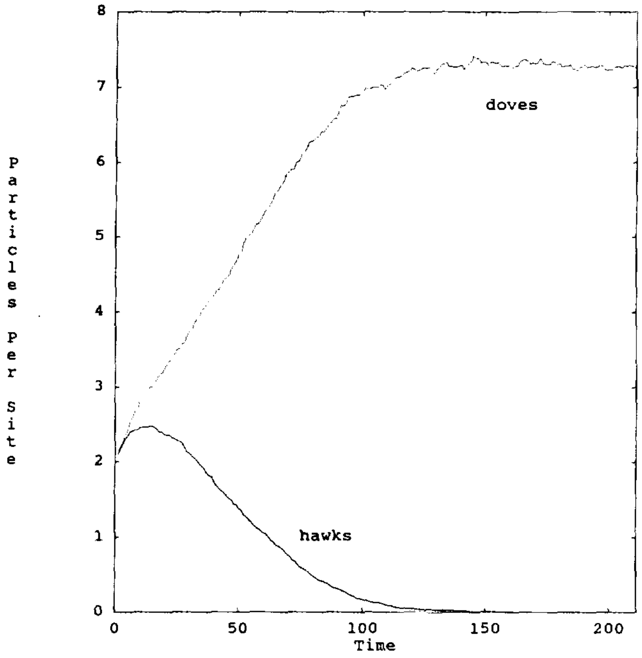

FIG. 6. Average number of hawks and doves per site in Case 2 for a simulation of the patch model with 2500 sites and the 5,5 initial condition. The hawks die out at time 211.

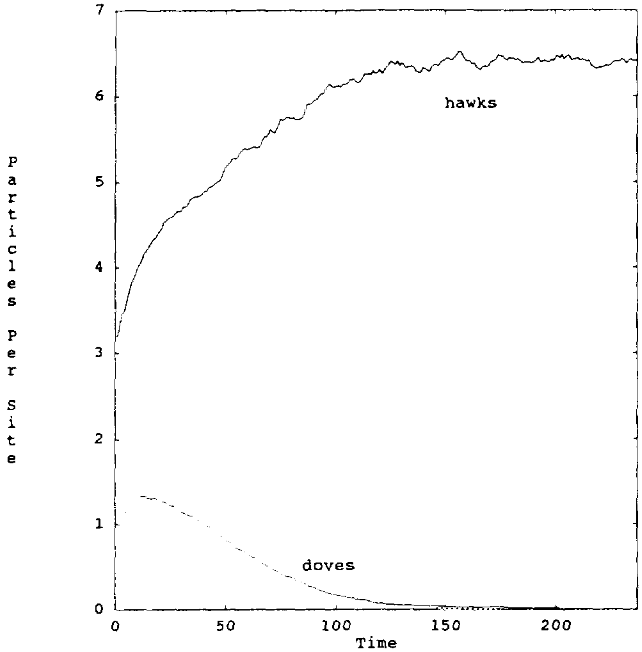

FIG. 7. Average number of hawks and doves per site in Case 2 for a simulation of the patch model with 2500 sites and the 7,3 initial condition. The doves die out at time 237.

The last conclusion is not true for the reaction diffusion equation. In this case for "generic" initial conditions $(u(t, x), v)t, x))$ converges to $(0, \bar{v})$ uniformly on compact sets. To explain this, we note that results of Gardner (1982) imply that the reaction diffusion equation has a travelling wave solution $u(x, t) = U(x - \rho t)$, $v(x, t) = V(x - \rho t)$, where U and V are monotone functions with $U(-\infty) = 0$, $U(\infty) = \bar{u}$, $V(-\infty) = \bar{v}$, $V(\infty) = 0$. Since $b = c$ and $d > a$, it is not hard to see that in our case the velocity $\rho > 0$. The positivity of ρ in this case indicates that (at least for this very special initial condition) an interface between a region of all doves and a region of all hawks moves in a direction that favors the doves. Based on this observation, it should not be too surprising that the doves win. A slight modification of the proof of Theorem 2.2 in Gardner (1982) shows the following.

THEOREM 2.2. *There are* $\varepsilon > 0$ *and* $L < \infty$ *so that if* $|u(0, x)| < \varepsilon$ *and* $|v(0, x) - \bar{v}| < \varepsilon$ *when* x *is in a ball of radius L centered at some point* x_0 *then* $(u(t, x), v(t, x))$ *converges to* $(0, \bar{v})$ *uniformly on compact sets.*

It is the last result on which the first conclusion in this paragraph is based, since a "generic" initial configuration can satisfy this condition somewhere in space.

Figures 8 and 9 show the behavior of the number of hawks per site and the number of doves per site for the 10,5 and 11,4 initial configurations. Again $\kappa = 0.08$ and $\mu = 1$. In Fig. 8 the doves win, while in Fig. 9 the hawks win. At first glance, this may appear to agree with the predictions of the dynamical system and patch models, but the picture changes if we consider the second initial condition on a 200×200 lattice. In the simulation in Fig. 10, the doves are clearly winning but our allotment of time for this run on the Cornell supercomputer elapsed before a complete takeover by doves could occur. The explanation of the behavior of the interacting particle system is related to our analysis of the reaction diffusion equation. If a large enough pocket of doves (i.e., a region in space that contains mostly doves) forms then that region will grow linearly in radius and take over the system. On a small system this pocket may not have a chance to form, but if we consider the system on the infinite lattice $\mathbf{Z}^2$ and start with a translation invariant initial distribution with a positive density of doves, such a pocket forms with probability one and the hawks would die out. Thus, we make the following.

Conjecture 2.3. Starting from any initial state that is translation invariant and in which each type has positive density, the hawks die out; i.e., $P(\eta_t(x) > 0) \to 0$.

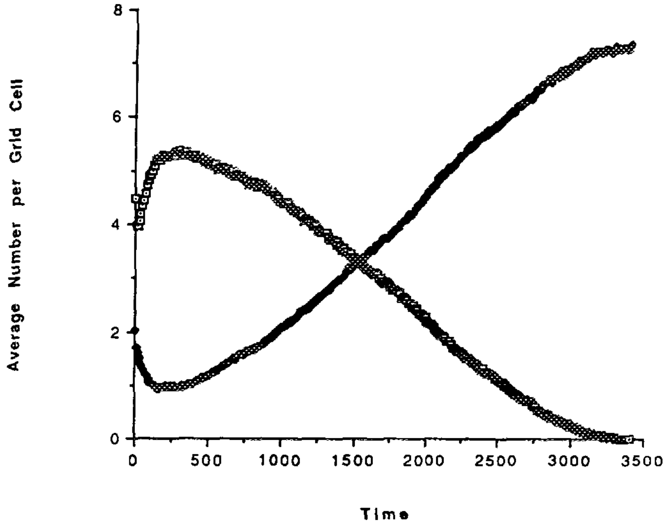

FIG. 8. Average number of hawks (⊡) and doves (◆) per site in Case 2 for a simulation of the interacting particle system on a 100 by 100 lattice with 10,5 initial condition. Note that the hawks die out just before time 3500.

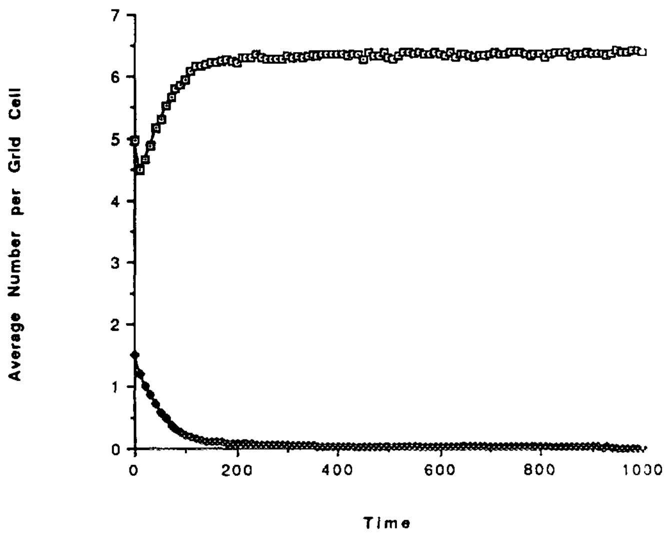

FIG. 9. Average number of hawks (⊡) and doves (◆) per site in Case 2 for a simulation of the interacting particle system on a 100 by 100 lattice with the 11,4 initial condition. Note that the doves die out before time 400.

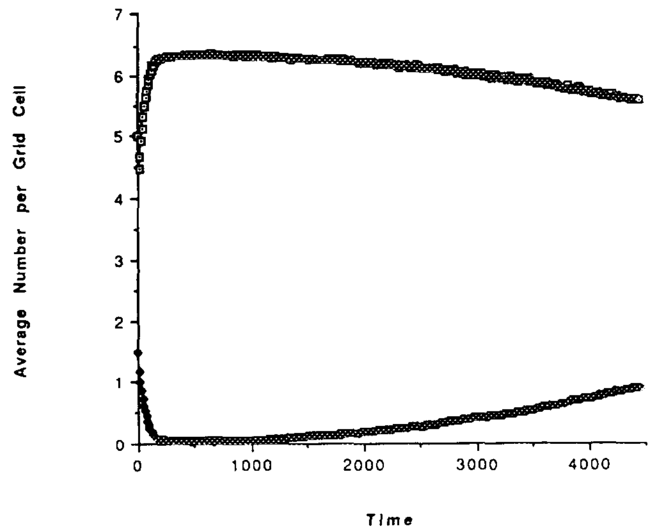

FIG. 10. Average number of hawks (⊡) and doves (◆) per site in Case 2 for a simulation of the interacting particle system on a 200 by 200 lattice with the 11,4 initial condition. The doves are starting to take over by the end of the simulation at time 4500.

Support for this conjecture can be found in the work of Durrett and Swindle (1993), who consider a model of the oxidation of carbon monoxide on a catalytic surface. There the corresponding ordinary differential equation has two stable fixed points and one can identify the equilibrium for the interacting particle system with fast migration by looking at the speed of the traveling wave connecting the two fixed points. Such ideas were used earlier for particle systems with state space $\{0, 1\}^S$ by Durrett and Neuhauser (1993). The idea that one should look at the speed of the traveling wave to determine the relative stability of equilibria can also be found in Hutson and Vickers (1992).

Case 3: *The Importance of Being Discrete.* Cases 1 and 2 considered the two possibilities when neither strategy dominates the other. We now consider what happens when the hawk strategy dominates the dove strategy. If the matrix entries a and b are positive, this case is boring: the hawks reproduce faster than the doves and drive them to extinction. The case in which a and d are both negative is even less interesting: all entries are negative and both species die out. Things get quite interesting when $a < 0 < d$, however.

$$a = -0.6 \qquad b = 0.9$$

$$c = -0.9 \qquad d = 0.7$$

In this case, the hawks always do better than the doves, but a population consisting purely of hawks dies out. (For this it is important that $a < 0$.) This case may be though of as a classic fugitive species (Huffaker, 1958) in a spatial mosaic or as two competitors sharing a resource along a successional gradient (Levin and Paine, 1974; Whittaker and Levin, 1977). In each case the dominant species eliminates the weaker one locally but then dies out itself, and the vacant space is recolonized by the inferior species.

In Case 3, the dynamical system and reaction diffusion system agree that both populations die out, but both of the interacting particle systems tell us that the hawks and doves can coexist in an equilibrium. Figure 11 shows the dynamical system. As can be easily seen from the equation (3), the fraction of hawks increases with time, and once it gets too large the total density of hawks and doves decreases to 0.

THEOREM 3.1. *If the initial condition for the dynamical system has* $u(0) > 0$ *then* $(u(t), v(t)) \to (0, 0)$.

Again this can be demonstrated by imitating the proof of Theorem 1.1 and the proof is omitted.

A similar fate occurs for the reaction diffusion equation.

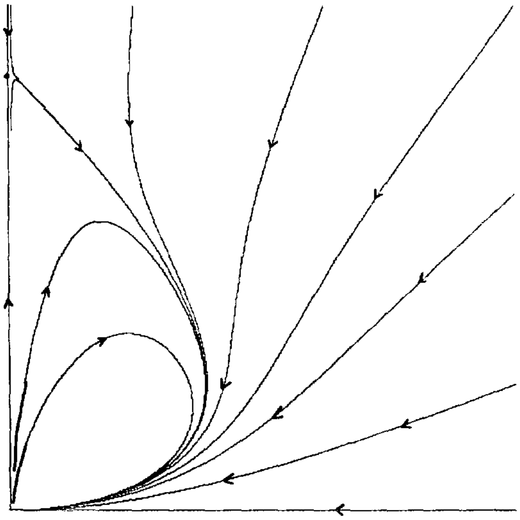

FIG. 11. Dynamical system for Case 3.

THEOREM 3.2. *If we consider the system in a bounded domain with Neumann (no flux) boundary conditions, then*

$$\min_x \frac{u(t,x)}{u(t,x)+v(t,x)} \to 1 \qquad \max_x \{u(t,x)+v(t,x)\} \to 0.$$

Proof. Inspired by the simplificaction in passing from (1) to (3) we let $p = u/(u+v)$ and $s = u+v$. Using subscripts to denote partial derivatives

$$p_x = \frac{u_x(u+v) - u(u_x+v_x)}{(u+v)^2} = \frac{u_x v - v_x u}{s^2}$$

$$p_{xx} = \frac{u_{xx} v - v_{xx} u}{s^2} - \frac{2(u_x+v_x)(u_x v - v_x u)}{s^3}.$$

In one dimension using (2) we have

$$p_t = \frac{u_t v - v_t u}{s^2} = \frac{u_{xx} v - v_{xx} u}{s^2} + pq\{(a-c)p + (b-d)(1-p)\}$$

$$= p_{xx} + \frac{2}{s} s_x p_x + pq\{(a-c)p + (b-d)(1-p)\}$$

and it follows easily that in general

$$\frac{\partial p}{\partial t} = \Delta p + \frac{2}{s} \nabla s \cdot \nabla p + pq\{(a-c)\, p + (b-d)\,(1-p)\}.$$

To analyze the last equation we look at $\rho(t) = \min_x p(t, x)$ and let $x(t)$ be a point where the minimum is achieved. $\nabla p(t, x(t)) = 0$ and $\Delta p(t, x(t)) \geqslant 0$ so it follows that

$$\frac{d\rho}{dt} \leqslant \rho(1-\rho)\,\{(a-c)\rho + (b-d)\,(1-\rho)\}.$$

In Case 3, $a > c$ and $b > d$, so a routine comparison argument shows that $\rho(t) \to 1$ as $t \to \infty$. This is the first conclusion and the second follows easily. Adding the two equations in (2),

$$\frac{\partial s}{\partial t} = \Delta s + s\{ap^2 + (b+c)\, p(1-p) + (1-p)^2\, d\} - \kappa s^2.$$

To analyze the last equation we look at $\sigma(t) = \max_x s(t, x)$ and let $y(t)$ be a point where the maximum is achieved. $\Delta p(t, y(t)) \leqslant 0$ so it follows that

$$\frac{d\sigma}{dt} \leqslant \sigma\{ap^2 + (b+c)\, p(1-p) + d(1-p)^2\} - \kappa\sigma^2$$

where p is short for $p(t, y(t))$. Now when ρ is close enough to 1 the expression in braces is negative so another comparison argument shows $\sigma \to 0$. ▮

In contrast, the hawks and doves coexist in the two stochastic models with discrete individuals. Figure 12 shows a simulation of the patch model with $\kappa = 0.02$ and $\mu = 1$ for the 2,8 initial condition. After an initial dramatic increase in the number of doves, the system settles down to an equilibrium. Some indication of how the equilibrium is maintained can be found in Fig. 13 which describes the state of the system at time 300 for the realization pictured in Fig. 12. At some sites the fraction of hawks is small and the number of individuals increases in one time step, while at some sites the fraction of hawks is low and the number of individuals decreases.

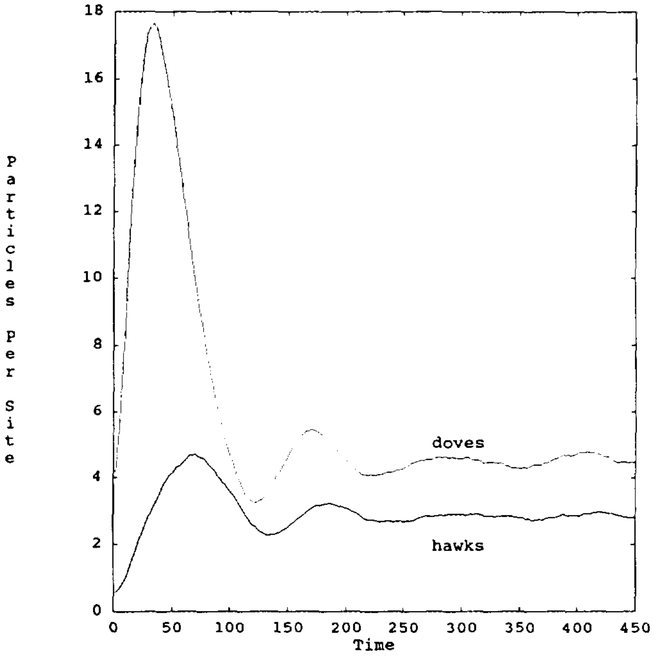

FIG. 12. Average number of hawks and doves per site in Case 3 for a simulation of the patch model with 2500 sites and the 2,8 initial condition.

	hawks	0	1	2	3	4	5	6	7	8	≥ 9
doves	total	116	366	539	579	424	287	113	56	13	7
0	31	0	11	6	11	3	0	0	0	0	0
1	142	7	22	26	32	26	15	11	1	1	1
2	270	10	38	57	69	54	32	9	1	0	0
3	388	10	56	86	101	65	38	19	8	3	2
4	439	14	64	97	89	68	64	27	12	3	1
5	381	17	46	82	87	70	47	21	9	2	0
6	308	21	37	69	76	46	39	6	13	1	0
7	197	7	33	44	45	33	18	10	3	3	1
8	150	10	25	28	32	30	15	3	6	0	1
9	84	9	12	19	13	12	12	4	2	0	1
10	52	5	13	5	13	9	5	2	0	0	0
11	32	2	4	11	7	5	1	1	1	0	0
12	11	2	1	4	2	1	1	0	0	0	0
13	9	1	3	2	1	2	0	0	0	0	0
14	4	1	0	2	1	0	0	0	0	0	0
≥ 14	2	0	1	1	0	0	0	0	0	0	0

FIG. 13. A look at the distribution at time 300 in the simulation in Fig. 12. To explain the table, there are 424 sites with 4 hawks and 33 sites with 4 hawks and 7 doves.

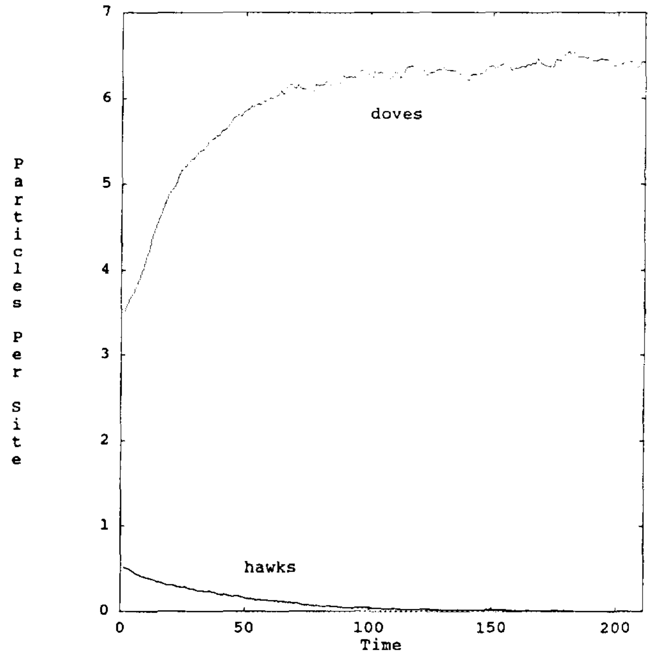

FIG. 14. Average number of hawks and doves per site in Case 3 for a simulation of the patch model with 2500 sites and the 2,8 initial condition. The parameter κ here is 0.08 instead of the 0.02 used in Fig. 12, and the hawks die out at time 211.

Observant readers may have noticed that in the last simulation we took $\kappa = 0.02$ instead of $\kappa = 0.08$. Figure 14 shows the reason for this: if we set $\kappa = 0.08$ (keeping $\mu = 1$ and the 2.8 initial condition) the hawks die out at time 211. The effect of lowering κ is to decrease the number of individuals per site. Our computer experiments indicate that when the number of individuals per site is too low then the situation depicted in Fig. 13, where there is a balance of growth at some sites and a decrease at others, cannot become established. We leave it to others more skilled in the study of these models to resolve this mystery.

A typical simulation of the interacting particle system in Case 3 begins with a period in which the hawk population grows faster than the dove population until the fraction of hawks is too large and both species start to die out. When the density gets low we have a few doves who are completely isolated and give birth at rate $d = 0.7$. These doves start colonies that grow and would fill up the space to the doves, preferred equilibrium density, except for the fact that along the way they encounter a few hawks that managed to escape extinction. These hawks reproduce faster than the doves, the fraction of hawks grows, and the cycle begins again.

Figure 15 gives a graph of the density of hawks vs time for a simulation on a 50 × 50 grid. At first glance this figure might seem to indicate a much more exotic (or, gasp, chaotic) behavior than simple convergence to equilibrium, but this is simply a "finite size effect." Figures 16 and 17 show the hawk density vs time on 100 × 100 and 150 × 150 systems. As the system sizes increase the oscillations decrease. The explanation for this is simple: if we look at a 150 × 150 grid then the cycle of growth of the hawks' fraction, decrease of the population, and regrowth from isolated doves in any 50 × 50 subsquare is much like that of the simulation on the 50 × 50 grid. However, the 150 × 150 system consists of nine 50 × 50 subsquares which do not oscillate in a synchronized fashion, so the cycles cancel each other out to some extent. If we had the patience and computer time to simulate this model on a very large system we would see a graph much like the one in Fig. 4 where the densities converge exponentially fast to an equilibrium level.

Conjecture 3.3. If we start the particle system from an initial translation-invariant distribution in which each species has positive density, then the system will converge to an equilibrium state in which each species has positive density.

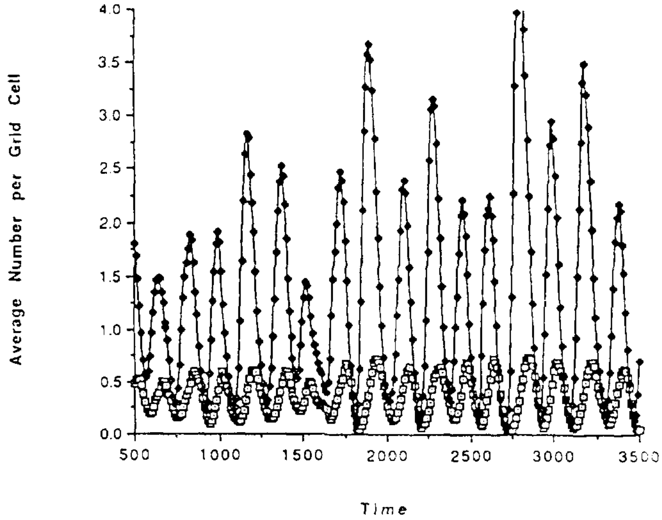

FIG. 15. Average number of hawks (☐) and doves (◆) per site in Case 3 for a simulation of the interacting particle system on a 50 by 50 lattice. The neighborhood of a point x is a 5 by 5 square centered at x.

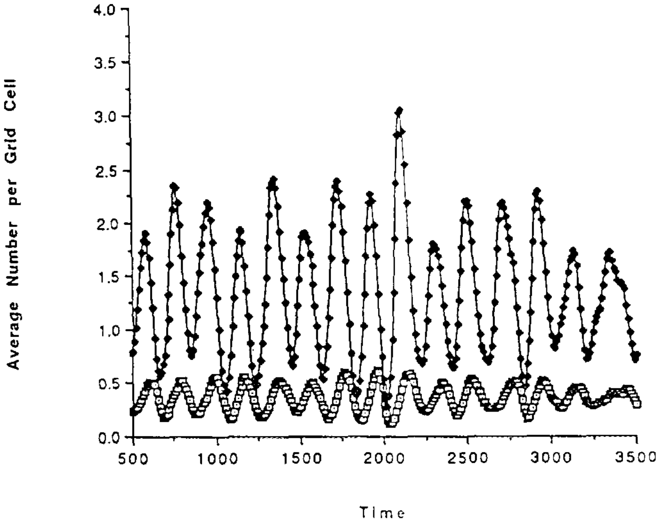

FIG. 16. Average number of hawks (⊡) and doves (◆) per site in Case 3 for a simulation of the interacting particle system on a 100 by 100 lattice. The neighborhood of a point x is a 5 by 5 square centered at x.

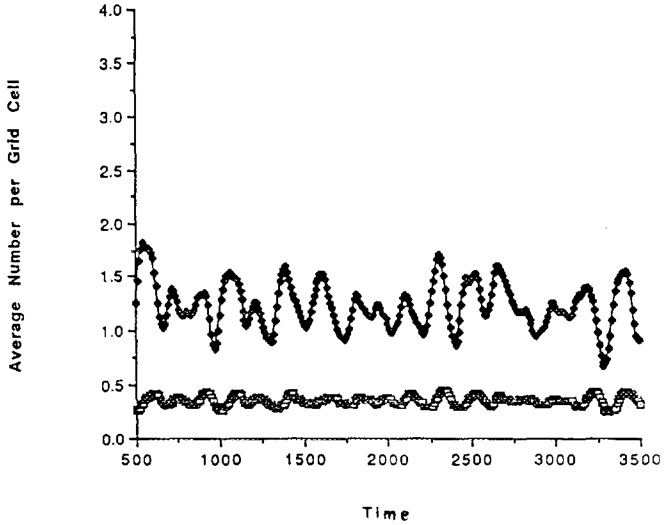

FIG. 17. Average number of hawks (⊡) and doves (◆) per site in Case 3 for a simulation of the interacting particle system on a 150 by 150 lattice. The neighborhood of a point x is a 5 by 5 square centered at x. Comparing with Figs. 8 and 9 we see that increasing the system size greatly reduces the oscillations.

The last conjecture is similar to the behavior of the patch model (when the hawks do not die out there) but there is one substantial difference. The equilibrium state for the particle system displays an interesting spatial structure which is responsible for local oscillations in the density of the hawks and doves. Such phenomena are of course impossible unless the patches have some spatial relationship.

In the simulations reported in the last paragraph we have taken $\mathcal{N} = \mathcal{N}_2$, a five-by-five square centered at the origin. If instead we use the nearest neighbors $\mathcal{N} = \mathcal{N}_1$ then there are almost no oscillations. See Fig. 18 for a simulation using the neighborhood $\mathcal{N}_1$ on a 100×100 grid. The reason for this difference is simple: the larger neighborhood over which the averages are taken makes the local fraction of hawks less random and makes the system behave more like the dynamical system. To explain the last remark, consider our system on an $N \times N$ grid and suppose (i) each site uses an interaction neighborhood equal to the entire lattice and (ii) each particle experiences deaths at rate $\kappa(\hat{u}_t^N + \hat{v}_t^N)$, where $\hat{u}_t^N$ and $\hat{v}_t^N$ are the number of hawks and doves per site at time t. Then it is easy to show that as $N \to \infty$, $\hat{u}_t^N$ and $\hat{v}_t^N$ converge to the solution of the differential equation (1).

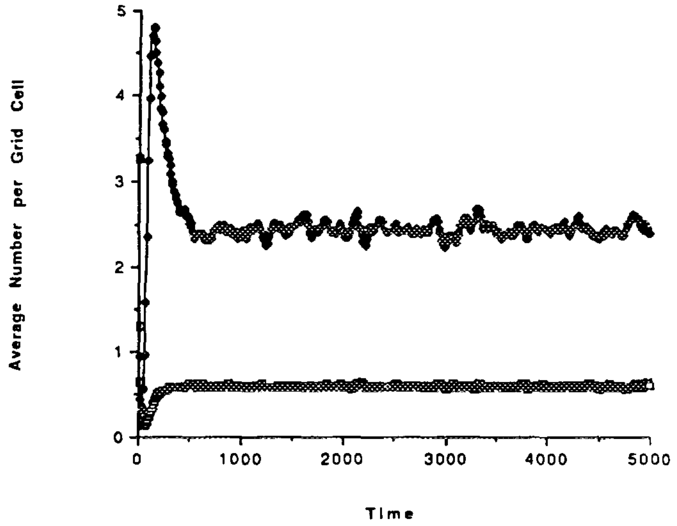

FIG. 18. Average number of hawks (▨) and doves (◆) per site in Case 3 for a simulation on a 50 by 50 lattice. The neighborhood of a point x now contains x and its four nearest neighbors. Note that the densities no longer oscillate.

3. Partial Differential Equation Limits of Particle Systems

The last paragraph explains the connection between the interacting particle system and the dynamical system. To complete the circle of ides we now explain how to get a reaction diffusion equation as a limit of an interacting particle system by making the migration fast and scaling the lattice appropriately. That is, we take the diffusion constant to be $\mu = 4\varepsilon^{-2}$ and consider a lattice $\varepsilon\mathbf{Z}^2$ with spacing ε between the points. Suppose we start with $\eta_0^\varepsilon(x)$ and $\zeta_0^\varepsilon(x)$, $x \in \varepsilon\mathbf{Z}^2$, independent and having Poisson distributions with means $u(0, x)$ and $v(0, x)$. [Recall that if X is "Poisson (λ)," that is, has a Poisson distribution with mean λ, then $P(X=k) = e^{-\lambda}\lambda^k/k!$ for $k = 0, 1, 2, \ldots$] Let $u^\varepsilon(t, x) = E\eta_t^\varepsilon(x)$ and $v^\varepsilon(t, x) = E\zeta_t^\varepsilon(x)$ be the mean number of hawks and doves at x at time t.

Claim 4.1. As $\varepsilon \to 0$, $u^\varepsilon(t, x) \to u(t, x)$ and $v^\varepsilon(t, x) \to v(t, x)$ where u and v are the solutions of

$$\begin{aligned} \frac{\partial u}{\partial t} &= \Delta u + u \left\{ a\left(h + (1-h)\frac{u}{u+v}\right) \right. \\ &\qquad \left. + b(1-h)\frac{v}{u+v} - \kappa(1+u+v) \right\} \\ \frac{\partial v}{\partial t} &= \Delta v + v \left\{ c(1-h)\frac{u}{u+v} \right. \\ &\qquad \left. + d\left(h + (1-h)\frac{u}{u+v}\right) - \kappa(1+u+v) \right\} \end{aligned} \tag{4}$$

with

$$h = h(u, v) = \frac{1 - e^{-|\mathcal{N}|(u+v)}}{|\mathcal{N}|\,(u+v)},$$

where $|\mathcal{N}|$ is the number of points in the interaction neighborhood.

Explanation of the Claim.

It is easy to see the source of the Δu. Individual hawks perform random walks at rate $4\varepsilon^{-2}$ on a lattice with spacing ε so the central limit theorem implies that in the limit the particles perform Brownian motions. The constant 4 in the jump rate has been chosen so that the limiting diffusion constant is 1.

The first step in deriving the reaction term is to recall that if we consider particles performing independent random walks on $\mathbf{Z}^2$ then under suitable assumptions[1] the joint distribution of the number of particles at any finite set of points converges to independent Poisson random variables with mean λ. See Dobrushin (1956) or Stone (1968). Combining the last observation with the fact that the migration occurs on a much faster time scale than the game interaction, it follows that in the limit as $\varepsilon \to 0$, sites near x at time t are independent and have a Poisson number of hawks and doves with means $u(t, x)$ and $v(t, x)$.

Proving the last claim rigorously is difficult. See Boldrighini, *et al.* (1987) for a proof of the analogous result for Schlögl's model, and see Spohn (1991) and DeMasi and Presutti (1991) for general surveys on the topic of these "hydrodynamic limits." If we accept the conclusion that in the limit all the sites in an interaction neighborhood are independent and have the indicated Poisson distributions then it is straightforward to compute how the density of hawks and doves will change with time.

Let U and V be the number of hawks and doves at x, and let U' and V' be the total number of hawks and doves at the neighbors $y \neq x$. Suppressing the (t, x) and letting $N = |\mathcal{N}|$ be the number of points in the interaction neighborhood (which by definition contains 0) we see that in the limit U, V, U', and V' will be independent Poissons with means u, v, $(N-1)u$, and $(N-1)v$. Letting $T = U + U' + V + V'$, the rate of change of the density of hawks due to the game interaction is

$$E\left(U\left\{a\cdot\frac{U+U'}{T}+b\cdot\frac{V+V'}{T}\right\}-\kappa UT\right).$$

To compute the expected value we condition on the value of T and use the fact that the distribution of $(U, U', (V+V'))$ conditional on $T = m$ is multinomial $(m; p, q, r)$ with $p = u/(Nu + Nv)$, $q = (N-1)u/(Nu + Nv)$, and $r = v/(u + v)$. That is, the vector has the same distribution as the number of occurrences of three disjoint events with probabilities p, q, and r in n independent trials. Basic facts about the multinomial distribution imply

$$E(U \mid T = m) = pm \qquad E(U^2 \mid T = m) = mp(1-p) + (mp)^2$$

$$E(UU' \mid T = m) = m(m-1)\,pq.$$

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[1] Specifically, we refer to the assumptions that the initial state is translation invariant and ergodic with density λ. Loosely, ergodic means that the initial state is not a mixture of two different initial states, e.g., having no particles anywhere with probability $\frac{1}{2}$ and having 2λ particles at every site with probability $\frac{1}{2}$.

Conditioning on the value of T we have

$$\begin{aligned} E\left(aU \cdot \frac{U+U'}{T}\right) &= a \sum_{m=1}^{\infty} e^{-(Nu+Nv)} \frac{(Nu+Nv)^m}{m!} \\ &\quad \times E\left(\frac{U^2+UU'}{m} \,\middle|\, T=m\right) \\ &= a \sum_{m=1}^{\infty} e^{-(Nu+Nv)} \frac{(Nu+Nv)^m}{m!} \\ &\quad \times \{p(1-p-q)+mp(p+q)\} \\ &= a\{pr(1-e^{-(Nu+Nv)})+(Nu+Nv)\,p(p+q)\} \\ &= au\left(h+(1-h)\frac{u}{u+v}\right). \end{aligned}$$

Similar computations, which are left to the interested reader, give the other terms in the first equation. The result for dv/dt follows by symmetry.

Comparing (4) and (2) reveals two differences: there is an extra 1 in the death term (which comes from the fact that $E(X^2)=\lambda^2+\lambda$, not λ^2), but more importantly, the form of the game term has changed. To examine the second difference, we note that $h(u, v)$ converges to 1 as $(u+v) \to 0$ and decreases to 0 as $(u+v) \uparrow \infty$. When h is close to 0 (which occurs for example if $N=|\mathcal{N}|$ is large) the game term is almost what it was before. When h is close to 1, the game term is almost a in the first equation and d in the second equation, reflecting the fact that when the density is small most individuals are isolated and think that the universe consists exclusively of their own type.

The changes in the limiting equation bring about a drastic change in the behavior of the reaction diffusion equation and the associated dynamical system. As Fig. 19 shows, we have the following.

Conjecture 4.2. The dynamical system now has a globally attracting fixed point.

Using the reasoning employed for Conjecture 1.2, we make the following.

Conjecture 4.3. Consider the reaction diffusion equation starting from any initial state in which $u(0, x)$ and $v(0, x)$ are nonnegative, continuous, and not identically 0. Then $u(t, x) \to \rho_1$ and $v(t, x) \to \rho_2$ uniformly on compact sets.

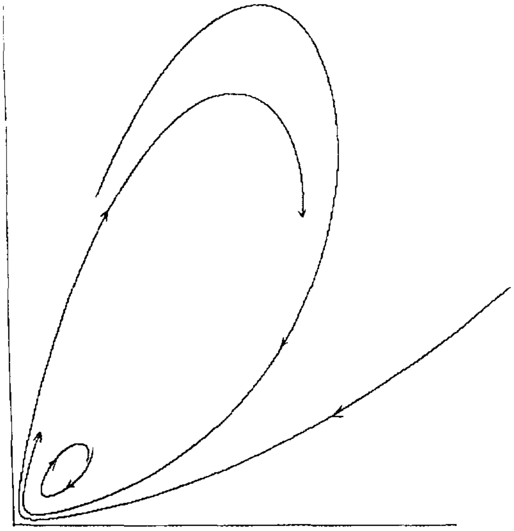

FIG. 19. Picture of dynamical system for (4) indicating the presence of an attracting fixed point.

Equation (4) is not the only limit that we can obtain. One can argue that in computing the death rate due to crowding you should not count yourself, and likewise in the game step you shoul not play the game against yourself. Thus, isolated hawks should give birth at rate r, and hawks that have at least one other individual in their interaction neighborhoods should give birth at rate

$$r + a\tilde{p}_t(x) + b(1 - \tilde{p}_t(x)) \qquad \text{where} \quad \tilde{p}_t(x) = \frac{\hat{\eta}_t(x) - 1}{\hat{\eta}_t(x) - 1 + \hat{\zeta}_t(x)},$$

where $\hat{\eta}_t(x)$ and $\hat{\zeta}_t(x)$ are the total number of hawks and doves in the neighborhood of x at time t. If we make similar changes in the birth rates for doves and take the limit as before we have the following.

Claim 4.4. As $\varepsilon \to 0$, $u^\varepsilon(t, x) \to u(t, x)$ and $v^\varepsilon(t, x) \to v(t, x)$ where u and v are the solutions of

$$\begin{aligned} \frac{\partial u}{\partial t} &= \Delta u + u\left\{r + g \cdot \left(a\frac{u}{u+v} + b\frac{v}{u+v}\right) - \kappa(u+v)\right\} \\ \frac{\partial v}{\partial t} &= \Delta v + v\left\{s + g \cdot \left(c\frac{u}{u+v} + d\frac{v}{u+v}\right) - \kappa(u+v)\right\}, \end{aligned} \tag{5}$$

where

$$g = g(u, v) = 1 - e^{-|\mathcal{N}|(u+v)}$$

is the probability of having someone else in our interaction neighborhood.

Most of the reasoning used in the explanation of Claim 4.1 applies verbatim, so we omit the details.

The dynamical system associated with (5), like the one with (4), has an attracting fixed point; however, it is easier to analyze since it responds better to the change of variables $p = u/(u+v)$ and $s = u + v$. We do not enter into a detailed analysis of the equations in (5) since the point we wanted to make is that even if you do not want to use interacting particle systems as models, their viewpoint is useful for deriving appropriate reaction diffusion equations. Of course, the other point we have tried to make is that you should add interacting particle systems to your repertoire of models. For more propaganda on the last point see Durrett and Levin (1994).

4. SUMMARY AND DISCUSSION

It has long been recognized (Huffaker, 1958; Levin, 1974; Smith, 1972) that heterogeneous space can enhance the coexistence of species and (Levin, 1974; Chesson, 1981) that corresponding consideration of space will alter the outcome of models of population interactions. There are, however, a number of different ways that space makes its influence felt and different modeling approaches isolate or emphasize the importance of particular mechanisms. Levin (1974) discusses the interplay of spatial and temporal scales, and focuses attention on "local uniqueness" (intrinsic differences among habitats), "phase differences" (timing differences in potentially identical environments), and the effects of dispersal. Locally stochastic colonization and extinction phenomena, coupled with the enhancement of differences through nonlinear dynamics, can lead to coexistence through nonuniform patterns in space and time. Chesson (1981) explores the interplay between nonlinearity, inhomogeneous interaction (including the effect among patch variability, local uniqueness, and dispersal), and within-patch variability (including phase differences). The major new aspects of Chesson's work were in broadening the range of stochastic phenomena permitted, and in the recognition of the quantum nature of populations—that is, individuals come in discrete units. In this paper we extend both of these approaches through the introduction of interacting particle systems, which capture features of both (see Fig. 1).

In recent years the importance of spatial phenomena has been recognized increasingly in discussions of the ecology and evolution of species (Comins and Noble, 1985; Levin, *et al.*, 1984; Comins *et al.*, 1980; Pacala 1986) and in terms of modeling approaches (Levin, 1976; Okubo, 1980; Chesson, 1985); May and Nowak, 1992; Hastings, 1993). Each approach has its advantages and disadvantages and leads to unique conclusions. In this paper we select three prototypical spatial approaches from among this bestiary and compare the predictions with the null model of no spatial detail. Specifically, our focus is on the comparison of four different approaches to modeling the dynamics of spatially distributed systems:

1. mean field approaches (described by ordinary differential equations) in which every individual is considered to have equal probability of interacting with every other individual;
2. patch models that group discrete individuals into patches without other levels of spatial structure (i.e., individuals interact equally with all individuals in the same patch and there is between-patch migration that treats all other patches equally;
3. reaction-diffusion equations, in which infinitesimal individuals diffuse in space and undergo purely local interactions;
4. interacting particle systems, in which individuals are discrete and space is treated explicitly.

To compare and contrast these four approaches we examined three examples of interactions in spatially distributed populations. As the remarks below should indicate, the differences we have observed in the four approaches are of interest beyond the models and point to the consequence of particular influences such as localization of interactions or discreteness of individuals.

In the first case where the fitness of one type of individual is enhanced by the presence of the other, all four approaches reach the same conclusion: there is a unique equilibrium that is the limit starting from any initial state in which both species have positive density. More generally, we expect this consensus of opinion to occur in most cases in which the ordinary differential equation has a globally attracting fixed point.

In the second case where two individuals compete for the same resource, the spatial models disagree with the nonspatial ones. The ordinary differential equation has two stable equilibria on the axes and their basins of attraction contain the whole positive quadrant except for a boundary line which is attracted to the interior equilibrium. Similarly, in the patch model, the species that wins depends on the initial densities of the two types. By contrast, in the reaction diffusion equation and in the interacting particle system there is one species that is the winner whenever it is present at a positive density. In the spatial models, the victorious type first establishes itself in some region which then grows linearly in time and covers the entire space. A general picture that covers this case is that when we have two stable equilibria, their relative stability in the reaction-diffusion equation can be determined by examining the speed of the traveling wave connecting the two equilibria. Results of Durrett and Neuhauser (1993) and Durrett and Swindle (1993) show that the last reasoning is valid for interacting particle systems with fast migration.

In the third case, the first type (hawks) always reproduces faster than the second type (doves) but a population of pure hawks dies out. In this case, the deterministic models die out since even when the density of hawks is 10^{-6} and the density of doves is 10^{-9} their mixing assumptions imply that each individual thinks that 99.9% of the world is hawks. In contrast, in the patch model, since there is only local mixing, an equilibrium can become established in which growth at some patches is balanced by decrease at others. The interacting particle system in this case equilibrates by a similar mechanism. Simulations of the particle system begin with a period in which the hawk population grows faster than the dove population until the fraction of hawks is too large and both species start to die out. When the density gets low there are some doves that are isolated and start colonies that grow until they encounter hawks that have managed to escape extinction; the cycle then begins again. Even though this case goes under the heading of "the importance of being discrete," we should note that the equilibrium for the spatial model has interesting spatial structure not possible in the patch model. The most familiar biological examples are fugitive species (see Huffaker, 1958; Levin, 1974) and the coexistence of species sharing a successional gradient (Levin and Paine, 1974).

Finally, we show that particle systems are a vehicle for deriving limiting reaction-diffusion equations. The key to this derivation, which the reader might find useful in other circumstances, is that if the migration is fast compared to the other rates, we can obtain a reaction-diffusion equation by assuming that the states of our sites are independent Poisson random variables and then computing how the densities change. When we apply this procedure to the example in Case 3, the new reaction term has an interior equilibrium point, in contrast to the ordinary differential equation which has a family of homoclinic orbits that begin and end at (0, 0).

ACKNOWLEDGMENTS

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Theorem 3.2 and thank Odo Diekmann for suggesting the version of the system investigated in Claim 4.4 and analyzing the associated dynamical system. The authors thank Peter Chesson for urging that we include patch models to complete the square in Fig. 1.

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