Stochastic Spatial Models

Rick Durrett
Cornell University
Ithaca NY 14853 USA

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Introduction and summary.

In a stochastic spatial model space is represented by a grid of sites, usually the d-dimensional integer lattice $\mathbf{Z}^d$. Each site can be in one of a set of states S and changes its state at a rate that depends on the states of neighboring sites. This framework is appropriate for a large number of situations in biology, so it has seen a diverse range of applications. See Durrett and Levin (1994a) and references therein.

In six 45 minute lectures it would be impossible to survey the field, so we will concentrate on two aspects. The first is the process that mathematicians call *the voter model with mutation*, but which biologists would call a spatial version of the Wright-Fisher or Moran models. Adopting the first viewpoint we can describe the dynamics by saying that (i) each voter at rate one decides to change its mind and adopts the opinion of a randomly chosen neighbor, (ii) each voter mutates at rate α creating a new type. To implement (ii) it is convenient to take S to be the unit interval and choose the new types at random from S.

The homogenizing force of (i) and the introduction of new types in (ii) create a stochastic equilibrium state for the process. Since in many situations the rate at which new types enter the system due to migration or genetic mutation is small, it is interesting to investigate the limiting behavior of this equilibrium state as $\alpha \to 0$. Here, we will concentrate on two aspects motivated by classical questions in biology: species-area curves and the abundance of species.

To define the species-area curves for the equilibrium state, let N_r be the number of different types in the box of side L^r centered at the origin. Since most research suggests a power law relationship between species and area, we plot log species versus log area, considering $\varphi_L(r) = \log N_r / \log(L^2)$. Results on the limiting behavior of this curve when $L = 1/\sqrt{\alpha}$ and $\alpha \to 0$ are given in Section 2 and the relationship with data on species area curves in nature is discussed.

In addition to the number of species seen in a viewing window, one can be concerned about their relative abundances. In this case experimental work suggests that we should look at abundances on a logarithmic scale, and many theoretical papers suggest that when we do this the result will be a log normal distribution. In Section 3 we show that the species abundance distribution for our model, when viewed on logarithmic scale, has a non-normal limit which is similar to Hubbell's data from Barro Colorado Island in having an

over abundance of rare species when compared with the normal distribution.

In the last four lectures, we switch from the detailed study of one model to a much broader perspective. Durrett and Levin (1994b) proposed that the behavior of stochastic spatial models could be determined from the properties of the mean field ODE (ordinary differential equation), i.e., the equations for the densities that result from pretending that adjacent sites are independent. In their scheme there are three cases depending upon the properties of the ODE:

Case 1. *One attracting fixed point with all components positive.* There will be coexistence in the ODE and in the stochastic spatial model.

Case 2. *Two locally attracting fixed points.* In the ODE, the limiting behavior depends on the initial densities. However, in the stochastic spatial model, there is one stronger equilibrium that is the winner starting from generic initial conditions. To determine the stronger equilibrium, one can start with one half plane in each equilibrium and watch the direction of movement of the front that separates the two equilibria.

Case 3. *Periodic orbits in the ODE.* In the spatial model densities fluctuate wildly on small length scales, oscillate smoothly on moderate length scales, and after an initial transient are almost constant on large scales. That is, there is an equilibrium state with an interesting spatial structure.

These principles are a heuristic, designed to allow one to guess the behavior of the system under consideration, but there is a growing list of examples where the conclusions have been demonstrated by simulation or proved mathematically. In the last four sections of these notes, we will explain some of the results that have been obtained in support of this picture.

I. The Versatile Voter Model

Our first two lectures are concerned with the voter model. It is one of the simplest interacting particle systems, so it has been used as a model in many different contexts. We begin by defining the model and describing the basic results of Holley and Liggett (1975) then proceed to more recently developments concerning species-area curves and species-abundance distributions

1. Basic Results

The state of the voter model at time t is given by a function $\xi_t : \mathbf{Z}^d \to S$, where S is the set of possible types. The dynamics of the voter model are simple, perhaps the simplest possible:

The voter at x at times of a rate one Poisson process $\{T_n^x, n \geq 1\}$, decides to change its opinion and adopts the opinion of the voter at y with probability $p(x, y) = \varphi(y - x)$.

To avoid complications in proofs, we will assume that the neighbor choice function φ has the following properties:

(A1) *finite range:* $\varphi(z) \neq 0$ for only finitely many z.

(A2) $\mathbf{Z}^d$-*symmetric:* $\varphi(z) = \psi(|z|)$ where $|z| = (z_1^2 + \cdots + z_d^2)^{1/2}$.

It is sensible to require also that:

(A3) *irreducible:* for any $x, y \in \mathbf{Z}^d$ the opinion at y can by some chain of effects get to x. Formally, there is a sequence of sites $x_0 = x, x_1, \ldots, x_n = y$ so that $\varphi(x_k - x_{k-1}) \neq 0$.

A common concrete example is the *nearest neighbor case:*

$$\varphi(z) = \begin{cases} 1/2d & \text{if } |z| = 1 \\ 0 & \text{otherwise} \end{cases}$$

However, with applications in mind, we will be interested in allowing more general distributions and obtaining an understanding of how the quantities we compute depend on the underlying distribution. We assume finite range out of laziness. That way we do not worry about the minimal moment conditions needed for the results to be hold or investigate exotic cases that occur e.g., transient two dimensional random walks.

a. Construction and Duality

For $x \in \mathbf{Z}^d$ let $\{T_n^x, n \geq 1\}$ be independent rate one Poisson processes and let $\{Y_n^x, n \geq 1\}$ be independent random variables taking values in $\mathbf{Z}^d$ with $P(Y_n^x = y) = p(x, y)$. Intuitively, at time T_n^x the voter at x imitates the one at Y_n^x. To implement this in a graphical way we draw an arrow from (x, T_n^x) to (Y_n^x, T_n^x). Since there are infinitely many Possion processes and hence no first arrival, we have to do a little work to show that this recipe gives rise to a well defined process. To accomplish this, but more importantly, to introduce the concept that will be the key to our analysis of the voter model, we will define a family of *dual random walks* $\{S_s^{x,t}, 0 \leq s \leq t\}$ that trace the origin of the opinion at x at time t. These will have the property

$$(1.1) \qquad \qquad \xi_t(x) = \xi_{t-s}(S_s^{x,t})$$

In words, the opinion at x at time t is the same as the one at $S_s^{x,t}$ at time $t - s$.

The paths $S_s^{x,t}$ are easy to describe in words: we work our way down the Poisson processes from time t to time 0, jumping to the head of an arrow whenever we encounter its tail. For an example, see Figure 1.1, where the thick lines indicate the duals $S_s^{x,t}$ and $S_s^{y,t}$. Formally, the dual random walks are defined by the requirement that $S_s^{x,t} = y$ if and only if there is a sequence of sites $x_0 = x, x_1, \ldots x_n = y$ and times $0 = r_0 < r_1 \ldots < r_n \leq r_{n+1} = s$ so that

(i) for $1 \leq i \leq n$ there is an arrow from x_{i-1} to x_i at time $t - r_i$

(ii) for $1 \leq i \leq n$ there is no Poisson arrival at x_{i-1} in $[t - r_{i-1}, t - r_i)$

(iii) there is no Poisson arrival at x_n in $[t - r_n, t - r_{n+1}]$.

Note. The closed interval in (iii) is there so that the state will change at the time a Poisson arrival occurs, and we will have a traditional right continuous Markov process.

To analyze the voter model, it is convenient to extend the definition of the dual process to subsets $A \subset \mathbf{Z}^d$ by

$$\zeta_s^{A,t} = \{S_s^{x,t} : x \in A\} \quad \text{for } 0 \leq s \leq t$$

To see how this system behaves we note that

(a) If $S_r^{x,t} = S_r^{y,t}$ then $S_s^{x,t} = S_s^{y,t}$ for $r \le s \le t$.

(b) Two random walks $S_s^{x,t}$ and $S_s^{y,t}$ move independently until they hit.

Again the reader can consult Figure 1.1 for an example. Visually, we imagine that when one particle lands on another one, the two particles combine into one, so we call the process $\zeta_s^{A,t}$, $A \subset \mathbf{Z}^d$, *coalescing random walks*.

The processes $S_s^{x,t}$, $0 \le s \le t$ are nice since their properties have a direct (almost sure) relationship with corresponding properties of ξ_t, e.g.,

$$\{\xi_t(x) = i\} = \{\xi_0(S_t^{x,t}) = i\}$$

For some purposes, such as the proofs of Theorems 1.1 and 1.2 below, it is convenient to combine these processes which are defined for $0 \le s \le t$ into two that are defined for all time by requiring that for any t

$$\{S_s^x, 0 \le s \le t\} \stackrel{d}{=} \{S_s^{x,t}, 0 \le s \le t\}$$
$$\{\zeta_s^A, 0 \le s \le t\} \stackrel{d}{=} \{\zeta_s^{A,t}, 0 \le s \le t\}$$

and noting that these equations give us consistent finite dimensional distributions to which Kolmogorov's theorem can be applied.

b. Basic Dichotomy

Combining the duality described in the last few paragraphs with the idea that some random walks are recurrent while others are transient, leads to a dichotomy in the behavior of the voter model between dimensions $d \le 2$ and $d > 2$ discovered by Holley and Liggett (1975).

Theorem 1.1. *Clustering occurs in $d \le 2$.* For any set of possible states S, any initial configuration ξ_0, and any sites $x, y \in \mathbf{Z}^d$ we have

$$P(\xi_t(x) \ne \xi_t(y)) \to 0 \text{ as } t \to \infty$$

Theorem 1.2. *Coexistence is possible in $d > 2$.* Let ξ_t^θ denote the process with values in $S = \{0, 1\}$ starting from an initial state in which the events $\{\xi_0^\theta(x) = 1\}$ are independent and have probability θ. In $d > 2$ as $t \to \infty$, $\xi_t^\theta \Rightarrow \xi_\infty^\theta$, a translation invariant stationary distribution in which $P(\xi_\infty^\theta(x) = 1) = \theta$.

Remark. Here $\Rightarrow$ stands for weak convergence, which in this setting is just convergence of *finite dimensional distributions*: $P(\xi_t(x_1) = i_1, \ldots \xi_t(x_k) = i_k)$. By *translation invariant*, we mean that the probabilities

$$P(\xi_t(x + y_1) = i_1, \ldots \xi_t(x + y_k) = i_k)$$

do not depend on x.

Proof of Theorem 1.1 If the two sites x and y trace their opinions back to the same site at time 0 then they will certainly be equal at time t so

$$P(\xi_t(x) \neq \xi_t(y)) \leq P(S_t^x \neq S_t^y)$$

Now the difference $S_s^x - S_s^y$ is a random walk stopped when it hits 0, and the random walk has jumps that have mean 0 and finite variance. Such random walks are *recurrent*, and since ours is also, by (A3), an irreducible Markov chain, it will eventually hit 0. Since 0 is an absorbing state for $S_s^x - S_s^y$ it follows that $P(S_t^x \neq S_t^y) \rightarrow 0$ and the proof is complete. □

Proof of Theorem 1.2 The inclusion-exclusion formula implies that all of the finite dimensional distributions are determined if we know $P(\xi_t(x) = 0$ for all $x \in B)$ for each B. To show the convergence of these probabilities we observe that

$$P(\xi_t(x) = 0 \text{ for all } x \in B) = E\{(1 - \theta)^{|\zeta_t^B|}\}$$

since by duality there are no 1's in B at time t if and only if all of the sites in ζ_t^B are 0 at time 0, an event with probability $(1 - \theta)^{|\zeta_t^B|}$. Since ζ_t^B is a coalescing random walk, $|\zeta_t^B|$ is a decreasing function of t and hence has a limit. Since $0 \leq (1 - \theta)^{|\zeta_t^B|} \leq 1$ it follows from the bounded convergence theorem that $\lim_{t \to \infty} E\{(1 - \theta)^{|\zeta_t^B|}\}$ exists.

At this point we have shown that $\xi_t^\theta \Rightarrow \xi_\infty^\theta$. Since the voter model is a Feller process, it follows that ξ_∞^θ is a stationary distribution. For more details see Section 2 of Durrett (1995a). Since the ξ_t^θ are translation invariant, the limits ξ_∞^θ are. Duality implies that

$$P(\xi_t^\theta(x) = 1) = P(\xi_0(S_t^{x,t}) = 1) = \theta$$

for all t so $P(\xi_\infty^\theta(x) = 1) = \theta$. □

Remark. Holley and Liggett (1975) have shown that the ξ_∞^θ are spatially ergodic and give all the stationary distributions for the voter model with $S = \{0, 1\}$. That is, all stationary distributions are a convex combination of the (distributions of the) ξ_∞^θ. For proofs of this result see the original paper by Holley and Liggett (1975) or Chapter V of Liggett (1985).

c. The voter model with mutation.

In our new process, the state at time t is given by a function $\xi_t : \mathbf{Z}^d \to (0, 1)$, with $\xi_t(x)$ being the type (or species) of the individual at x at time t. We index our types by values w in the interval $(0, 1)$, so we can pick new types at random from the set of possibilities without duplicating an existing one. As in the voter model

(i) Each site x at times of a rate one Poisson process $\{T_n^x, n \geq 1\}$, decides to change its state and imitates the state of y with probability $p(x, y) = \varphi(|y - x|)$.

The new feature here is the spontaneous appearance of new types, which can be thought of as being genetic mutations or migration of individuals from outside the system.

(ii) Each site x mutates at rate α, changing to a new type w', chosen uniformly on $(0, 1)$.

To keep our treatment of the subject as brief, we will restrict our attention here to

(iii) *two dimensional nearest neighbor case: $d = 2$* and

$$\varphi(z) = \begin{cases} 1/4 & \text{if } |z| = 1 \\ 0 & \text{otherwise} \end{cases}$$

Results can be generalized to finite range without substantial change. Interesting new phenomena occur when we consider this system in $d > 2$, in $d = 1$, or on the complete graph, but there is not enough time to discuss them here. For details see Bramson, Cox, and Durrett (1997).

It is straightforward to modify the construction of the voter model without mutation to take care of rule (ii). We introduce independent rate α Poisson processes of "mutation events" $\{\hat{T}_n^x, n \geq 1\}$, $x \in \mathbf{Z}^d$ and independent random variables $\{U_n^x, n \geq 1\}$, $x \in \mathbf{Z}^d$ uniformly distributed on $(0, 1)$

that are the new types. That is, at time T_n^x, the type at site x is set equal to U_n^x.

Because of the last feature, when we are working backwards in time with the random walks $S_s^{x,t}$ we can stop (and kill the random walk) when we encounter a mutation event, since that will determine the state of x at time t independent of the initial conditions. This modification turns the dual starting from a finite set A, $\hat{\zeta}_s^{A,t}$, into a coalescing random walk in which each particle is killed at rate α. If $\hat{\zeta}_t^{A,t} = \emptyset$ we need no information from the initial configuration to compute the state of A at time t. Since each particle is individually killed at rate α, it is not hard to show that:

Theorem 1.3. *The multitype voter model with mutation has a unique stationary distribution ζ_∞. Furthermore, for any initial ζ_0, we have $\zeta_t \Rightarrow \zeta_\infty$ as $t \to \infty$.*

Proof See Section II.2 of Griffeath (1978).

In most situations of interest in biology the mutation/migration rate α will be small, so our aim here will be to study the spatial structure of ζ_∞ in the limit $\alpha \to 0$.

2. Species-area curves

Since almost the beginning of the subject, see Watson (1835), ecologists have been interested in the relationship between species and area. The exact dependence of species number S on area A has been the subject of much debate. Early studies (e.g., Hopkins (1955)) fitted the curve $S = a\ln(1 + bA)$, a relationship that would be expected if the individuals in a quadrant were a random sample from a larger population (Preston (1969)). The most accepted relationship, however (Kilburn (1966), MacArthur and Wilson (1967), May (1975), Connor and McCoy (1979), Coleman (1981), Sugihara (1981)), takes the logarithm of S to be proportional to log area.

Hubbell (1993) was the first to suggest that a stochastic spatial model could be used to investigate species area curves. Some of his results are reported in Hubbell (1995). Hubbell's model is somewhat complicated because he allows each site to be occupied by more than one species and these species interact via specified rules of competition. Here, we follow the approach in

Bramson, Cox, and Durrett (1997), and Durrett and Levin (1996), and replace his model by a much simpler one, the voter model with mutation, so that we can obtain analytical results about the structure of the equilibrium state.

To define species-area curves for the voter model with mutation, we let $B(K)$ be a box with side K centered at the origin, and for $0 \leq r < \infty$ let N_r be the number of different types in $B(L^r)$ in the stationary distribution ξ_∞. To plot log-species vs. log-area, we let

$$\varphi_L(r) = \frac{\log N_r}{\log(L^2)}$$

To see what to expect, we let $\bar{\alpha} = 1/\alpha$ and note that a typical $S_s^{x,t}$ will survive for time $O(\bar{\alpha})$ without being hit by a mutation and by the central limit theorem will move a distance about $L = \bar{\alpha}^{1/2}$ in that amount of time. Thus we expect sites that are separated by a large multiple of L to be distinct with high probability. This motivates part of the following result.

Theorem 2.1. *Let $L = \bar{\alpha}^{1/2}$. If $r \geq 1$, then as $\alpha \to 0$,*

(2.1)
$$\frac{N_r}{L^{2r-2}(\log L)^2} \to \frac{2}{\pi} \quad \text{in probability.}$$

Readers should note that (2.1) gives a very boring limit for the species area curve:
$$\varphi_L(r) \to (r-1)^+$$
i.e., a segment of slope 0 followed by a ray of slope 1. The ray with slope 1 is easy to understand: sites separated by $L^{1+\epsilon} = \bar{\alpha}^{(1+\epsilon)/2}$ will with high probability experience mutations before their random walks coalesce. Thus when $r \geq 1$, the number of species N_r increases in proportion to the area.

The segment of slope 0 at the beginning of the limiting curve $(r-1)^+$ was initially a major disappointment for us. However, it turned out to be a blessing: although the limiting slope is 0, when α is positive one gets slopes that agree reasonably well with data. To explain this we note that $N_1 \approx (2/\pi)(\log L)^2$ so

$$\frac{\log N_1}{2 \log L} \approx \frac{2 \log \log L + \log(2/\pi)}{2 \log L}$$

The right hand side converges to 0 but only very slowly.

α	10^{-6}	10^{-8}	10^{-10}	10^{-12}
slope	.264	.229	.202	.182

These slopes are the range of values given in Figure 2.1. We are not able to prove that the species area curve will be roughly a straight line over $0 \leq r \leq 1$ but one can demonstrate this using computer simulation. Figure 2.2 gives the results of three simulations of the system with $\alpha = 10^{-6}$ and hence $L = 1/\sqrt{\alpha} = 1000$. Since we are only interested in the behavior on boxes of size L^r with $0 \leq r \leq 1$ we have performed the simulation on a 1000×1000 grid with *periodic boundary conditions*. That is, sites on the left edge are neighbors of those on the right on the same row; those on the top edge are neighbors of those in the bottom row in the same column.

Returning to the content of Figure 2.2, the reader should notice that the three simulated curves are fairly straight and end close to the value of .264 predicted by the table above. Having a slope that depends on the mutation rate provides a new explanation of the wide variety of slopes found in species area curves, i.e., mutation/migration rates vary considerably. For more on this see Durrett and Levin (1996).

3. Species abundance distributions

In addition to the spatial arrangements of the types it is interesting to look at the distribution of the abundance (i.e., number of representatives) of the types found in a sample. Again, this question has a long history in ecology. In an influential early paper, Fisher, Corbet, and Williams (1943) considered the distribution of moth and butterfly species caught in a light trap, making the interesting observation that while there are a huge number of individuals from a few species, the majority of species were represented by a few individuals.

Preston (1948) was one of the first to suggest the use of the lognormal distribution of species abundances. The theoretical explanation for the lognormal given on pages 88-89 of May (1975) is typical. Define $r_i(t)$ to be the per capita instantaneous growth rate of the ith species at time t, that is,

$$(3.1) \qquad r_i(t) = \frac{1}{N_i(t)}\frac{dN_i(t)}{dt} = \frac{d}{dt}\ln N_i(t).$$

The last equation integrates to

$$(3.2) \qquad \ln N_i(t) = \ln N_i(0) + \int_0^t r_i(s)\, ds.$$

If, as May (1975) says, "the ever-changing hazards of a randomly fluctuating environment are all important in determining populations," then one might reason that the integral is a sum of random variables to which the central limit theorem can be applied, and the distribution of abundances should follow a lognormal law.

While the last argument is simple, and possibly convincing, there are a number of data sets that do not fit the lognormal distribution very well. The tropical rain forest data in Hubbell (1995) is an example (see Figure 3.1). In the rain forest, the abundances of various plant species are not independent since individuals compete for a limiting resource, light. A static approach to this competition is provided by *MacArthur's broken stick distribution* (see his (1957) and (1960) papers). He imagines that the proportions $(p_1, p_2, \ldots, p_n)$ of the area occupied by n given species to be chosen at random from the set of all possible vectors of proportions, i.e., those with nonnegative coordinates that sum to one. For this reason, Webb (1974) calls this the *proportionality space model*. A simple way of generating such p_i's is to put $n - 1$ independent uniform random variables on (0,1) and look at the lengths of the intervals that result, hence, the name "broken stick distribution." Quoting May's (1975) survey again, "This distribution of relative abundance is to be expected whenever an ecologically homogeneous group of species apportion randomly among themselves a fixed amount of some governing resource." Broken stick abundance patterns have been found in data for birds by MacArthur (1960), Tramer (1969), and Longuet-Higgins (1971).

One of the weaknesses of the "broken stick" approach is that it simply chooses a nice distribution based on symmetry, without a direct consideration of the underlying mechanisms. Engen and Lande (1996) have recently (see their pages 174–175) introduced a dynamic model in which new species enter the community at times given by a Poisson process, and where the log abundances of the species $Y_t^i = \log(X_t^i)$ evolve according to the independent diffusion processes

$$(3.3) \qquad dY_t^i = (r - g(\exp(Y_t^i)))\, dt + \sigma(\exp(Y_t^i))\, dB_t^i.$$

Here, $r > 0$ is a fixed growth rate, $g(x)$ is a "density regulation function", and $\sigma(x) = \sigma_e^2 + \sigma_d^2 e^{-x}$, with σ_e being the environmental and σ_d the demographic

stochasticity. Engen and Lande then showed that, if $g(x) = \gamma \ln(x + \nu)$, with $\nu = \sigma_e^2/\sigma_d^2$, the species abundances in equilibrium are given by the lognormal distribution. Although the last approach is dynamic, the reader should note that the sizes of the different species there (as well as in May's derivation of the lognormal) are independent. That is, there is no competition between the species, as there is, at least implicitly, in the broken stick model.

Here we will use the voter model with mutation to derive a new species abundance distribution. To explain precisely what we will study requires several definitions. We define the *patch size in A* for the type i at time t to be the number of sites y in A with $\xi_t(y) = i$. Let $N(A, k)$ be the number of types in ξ_∞ with patch size in A equal to k, and, for $I \subset [0, \infty)$, let $N(A, I) = \sum_{k \in I} N(A, k)$ be the number of types with patch sizes in A that lie in the interval I.

Here, we only consider the case in which the viewing window A is $B(L)$, the square of side L centered at the origin. Let $|B(L)|$ be the number of points of the integer lattice $\mathbf{Z}^2$ that are in the square $B(L)$. It is convenient to divide the number of species observed by the number of sites, $|B(L)|$, to obtain the species abundance per site. That is, we consider the frequency of types with patch sizes in the interval I:

$$N^L(I) = \frac{N(B(L), I)}{|B(L)|}.$$

One immediate advantage of computing densities per site is that by invoking an appropriate law of large numbers, (see e.g., Theorem 9 on page 679 of Dunford and Schwarz (1957)), we can conclude that as the observation window, $B(L)$, gets large our estimate becomes close to the underlying mean.

Proposition 3.1. *For all sets I,*

$$N^\infty(I) = \lim_{L \to \infty} N^L(I)$$

exists and is a nonrandom constant.

We refer to $N^\infty(I)$ as the underlying *theoretical abundance distribution.*

Proposition 3.1 implies that when L is large, the observed species abundance frequencies in the square $B(L)$ will be close to the theoretical frequency,

so we next inquire how large L needs to be so that $N^L(I) \approx N^\infty(I)$. It is easy to see that some L are too small. The time until mutation along the line of descent of a given individual is an exponential random variable with mean $\bar{\alpha} = 1/\alpha$. Since offspring are displaced by independent and identically distributed amounts from their parents, the family tree of an individual behaves like a random walk and will move a distance of order $\bar{\alpha}^{1/2}$ in time $\bar{\alpha}$.

The arguments in the last paragraph indicate that we will need an observation window whose length is at least of order $\bar{\alpha}^{1/2}$ to get an accurate idea of the distribution of sizes. In our first result, we will we will take our observation window to have this smallest possible size. To be precise, we will let $\beta > 0$ and suppose that $L \geq \beta\bar{\alpha}^{1/2}$. This will turn out to be large enough to look at patch sizes on a logarithmic scale. That is, we will consider $N^L([1, \bar{\alpha}^y])$, the number of species (per site) with sizes between 1 and $\bar{\alpha}^y$.

When the mutation rate gets small then the individual species have a large number of individuals and the number of species per site is small. Thus to get a sensible asymptotic statement when $\alpha \to 0$ we have to divide $N^L([1, \bar{\alpha}^y])$ by something that tends to 0.

$$(3.4) \qquad F_\alpha^L(y) = \frac{N^L([1, \bar{\alpha}^y])}{\alpha(\log \bar{\alpha})^2/2\pi}$$

The exact form of the denominator may look mysterious, but our results given below will show that it is the right choice. Readers curious about why this is the right normalization can consult Bramson, Cox, and Durrett (1997) for a more detailed explanation.

To state our result about the asymptotic behavior of the distribution of sizes $F_\alpha^L(y)$, we need to define the limiting distribution function V. Let

$$V(y) = \begin{cases} 0, & y \leq 0, \\ y^2, & 0 \leq y \leq 1, \\ 1, & y \geq 1. \end{cases}$$

The nature of this distribution is clearer if we look at its density function, which is 0 unless $0 < y < 1$ in which case $v(y) = V'(y) = 2y$. The graph of $v(y)$ is a right triangle. The next result is then a "log-triangular" limit theorem for species abundances in the two dimensional voter model with mutation.

Theorem 3.1. *Let $\beta > 0$, and assume that $L = L(\alpha) \geq \beta \bar{\alpha}^{1/2}$. Then, for any $\epsilon > 0$,*

$$(3.5) \qquad P\left(\sup_y |F_\alpha^L(y) - V(y)| > \epsilon\right) \to 0 \quad \text{as } \alpha \to 0.$$

An obvious first reaction to the triangular limiting density $v(y)$ is that it does not look very much like Hubbell's data given in Figure 3.1. We will return to this point when we discuss the simulations below. The key to connecting our result with the Hubbell's data lies in a more refined result than Theorem 3.1 which we will now introduce.

Theorem 3.1 does not apply directly to the histograms of abundance counts reported in the literature. For example, in Preston (1948), abundance counts are grouped into "octaves," 1–2, 2–4, 4–8, 8–16, 16–32, ..., splitting in half the observations that are exactly powers of 2. To avoid trouble with the boundaries, some later investigators (see e.g., Chapter 3 of Whittaker (1972)) viewed the 1 cell as an interval [0.5,1.5], and then multiplied by 3 to get disjoint classes [1.5,4.5], [4.5,13.5], etc.

To treat such histograms, as well as other possibilities, we could fix an $r > 1$ to be the width of the cells, and look at the area-normalized abundance of species, $N^L([ar^k, ar^{k+1}))$ where a is some constant, which can always be chosen so that $r^{-1} < a \leq 1$. For example, in this setting Whittaker's cells have $a = 0.5$, $r = 3$, and Preston's correspond roughly to $a = 1$, $r = 2$. One can easily generalize what we are about to do too $a \neq 1$. However, our formulas are already too messy, so we will try to suppress clutter by restricting our attention to the case $a = 1$.

Theorem 3.2 below provides the refinement of Theorem 3.1 needed to analyze the histograms that are used to estimate the densities. To see what form the result should take, we note that $r^k = \bar{\alpha}^y$ where $y = \log(r^k)/\log(\bar{\alpha})$ so if in Theorem 3.1 convergence of the underlying density functions also holds, then we would have

$$\frac{N^L([r^k, r^{k+1}))}{\alpha(\log \bar{\alpha})^2/2\pi} \approx \int_{\log(r^k)/\log \bar{\alpha}}^{\log(r^{k+1})/\log \bar{\alpha}} 2y \, dy$$

Rearranging and then evaluating the integral, we have

$$(3.6) \qquad \begin{aligned} N^L([r^k, r^{k+1})) &\approx \frac{\alpha(\log \bar{\alpha})^2}{2\pi}\left\{\left(\frac{\log(r^{k+1})}{\log \bar{\alpha}}\right)^2 - \left(\frac{\log(r^k)}{\log \bar{\alpha}}\right)^2\right\} \\ &= \frac{\alpha}{2\pi} \cdot (2k+1)(\log r)^2 \approx \frac{\alpha k}{\pi}(\log r)^2 \end{aligned}$$

Our next result, Theorem 3.2, shows that the counts $N^L([r^k, r^{k+1}))$ are simultaneously well approximated by the formula just derived over a wide range as $\alpha \to 0$. Fix $r > 1$ and $\varepsilon > 0$, and let $E_{L,\varepsilon}(k)$ be the event that our approximation in the kth cell, $[r^k, r^{k+1})$, is off by at least a factor of ε from what we expect. That is, $E_{L,\varepsilon}(k)$ is the event

$$(3.7) \qquad \left| N^L([r^k, r^{k+1})) - \frac{\alpha k}{\pi}(\log r)^2 \right| > \varepsilon \alpha k.$$

Note that we have simplified the right hand side by dispensing with $(\log r)^2/2\pi$ which for fixed r is a constant.

Unfortunately, the approximation in (3.6) does not apply to large patch sizes. To say how large is too large, we introduce the cutoff size $\hat{\alpha} = \pi\bar{\alpha}/\log\bar{\alpha}$.

Theorem 3.2. *Let $r > 1$, $\beta > 0$, and assume that $L \geq \beta\bar{\alpha}^{1/2}(\log\bar{\alpha})^2$. Then, for any $\varepsilon > 0$ we can pick δ small enough so that*

$$\limsup_{\alpha \to 0} P\left(E_{L,\varepsilon}(k) \text{ for some } k \text{ with } r^k \in [\delta^{-1}, \delta\hat{\alpha})\right) \leq \varepsilon$$

The form of the conclusion of Theorem 3.2 is dictated by the fact that the approximation given in (3.6) does not apply well when k is small or k is of order $\hat{\alpha}$. Thus, we have to pick δ small to restrict the range of values considered, in order to get a small error in the limit as $\alpha \to 0$.

The additional restriction $L \geq \beta\bar{\alpha}^{1/2}(\log\bar{\alpha})^2$ in Theorem 3.2, compared to the requirement $L \geq \beta\bar{\alpha}^{1/2}$ in Theorem 3.1, comes from the fact that we are considering abundance sizes rather than their logarithms, so losing that fraction of the mass of a patch which is outside of the observation window can have a significant effect. Thus, to have the sampled distribution agree with the underlying theoretical distribution, we need to choose L substantially larger than $\bar{\alpha}^{1/2}$. A second complication is that we are making a statement simultaneously for about $\log\bar{\alpha}$ histogram cells, so we need $L/\bar{\alpha}^{1/2} \to \infty$ with at least a certain rate to be able to control the errors for all of the cells simultaneously.

The restriction to $r^k \geq 1/\delta$, in Theorem 3.2, is needed in order to use the asymptotics employed in our proof. Small patches are formed due to rare events, and require a separate analysis. The largest patch size covered by Theorem 3.2 is $[r^k, r^{k+1})$, where r^k is small relative to $\hat{\alpha}$. The distribution

of larger patch sizes, i.e., those of the form $[a\hat{\alpha}, b\hat{\alpha})$, differs in a fundamental way from the distribution of the smaller patch sizes.

Theorem 3.3. *Let* $\beta > 0$, *and assume that* $L = L(\alpha) \geq \beta\bar{\alpha}^{1/2}(\log \bar{\alpha})^2$. *Then, for any* $\varepsilon > 0$, *and* a, b *with* $0 < a < b$,

$$\lim_{\alpha \to 0} P\left(\left| \hat{\alpha} N^L([a\hat{\alpha}, b\hat{\alpha}]) - \int_a^b u^{-1} e^{-u}\, du \right| > \varepsilon \right) = 0.$$

Some readers may be disturbed by the limiting density $u^{-1}e^{-u}$ above, which has an infinite integral over $(0, \infty)$. This behavior must, in fact, occur, since the scale in Theorem 3.3 for the frequency of patch sizes of interest is $1/\hat{\alpha} \approx \alpha \log \bar{\alpha}$, while Theorem 3.1 tells us that the scale for the total frequency is $\alpha(\log \bar{\alpha})^2$, which is of greater order of magnitude for small α.

Theorem 3.3 is a close relative of Theorem 3.4 which is taken from Sawyer (1979), Theorem 1.2.

Theorem 3.4. *Let* $\nu(O)$ *be the number of sites with the same type as the origin. As the mutation rate* $\alpha \to 0$,

$$P\left(\nu(O) \leq b\hat{\alpha}\right) \to \int_0^b e^{-u}\, du, \qquad \text{for all } b \geq 0.$$

The same result obviously holds for any other fixed site x replacing the origin O, or for a site chosen at random from $B(L)$. Now, when a site is chosen at random, a patch has probability of being chosen which is proportional to its size. Removing this "size-bias" from Sawyer's result introduces the factor u^{-1} into the limiting density in Theorem 3.

Simulation results. To help to understand the results and to what extent the results apply when α is only moderately small, we will simulate the system with $\alpha = 10^{-4}$. By the heuristics above, the time for a typical line of descent to encounter a mutation will be of order $\bar{\alpha} = 10^4$, and it will move a distance of order $\bar{\alpha}^{1/2} = 100$ units over this time. Multiplying this distance by 10, we choose our experimental universe to be a 1000×1000 grid. To avoid edge effects we will again use *periodic boundary conditions*.

The first statistic we investigate is one that comes from the "size-biased" viewpoint. Introduce histogram bins $[1, 500], [501, 1000], \ldots$, and then, for a

given bin, throw in all of the individuals that belong to species with patch sizes in that range. Each patch of size k is counted k times, so Theorem 3.4 implies that the distribution we observe will be approximately an exponential with mean $\hat{\alpha}$. To compute this mean, we note that

$$(3.8) \qquad \hat{\alpha} = \frac{\pi\bar{\alpha}}{\log\bar{\alpha}} \approx \frac{10,000\pi}{9.21034} \approx 3411.$$

Figure 3.2 shows the average of 10 histograms for our parameters. The agreement with the exponential distribution with mean 3411 predicted by Theorem 3.4 (the curve of diamonds in Figure 3.2) is fairly good.

To investigate the ordinary (not size-biased) species abundances, we introduce histogram bins $[1, 2)$, $[2, 4)$, $[4, 8)$, ..., and count the number of species with patch sizes in the indicated ranges. Figure 3.3 displays the average of 20 replications of the experiment (which are independent of the 10 given above). To compare with theory, we begin with Theorem 3.3. If, for example, we want to know the number of species with patch sizes in $[2^k, 2^{k+1})$, then our estimate, based on Theorem 3.3, will be

$$(3.9) \qquad \frac{L^2}{\hat{\alpha}} \int_{2^k/\hat{\alpha}}^{2^{k+1}/\hat{\alpha}} u^{-1} e^{-u}\, du\,.$$

Evaluating the integral numerically for the cells of interest gives the line of diamonds in Figure 3.3. The fit is good for cells $k \geq 7$. From the remarks after Theorem 3.3, we should not necessarily expect this approximation to work well for cells too far to the left where Theorem 3.2 gives a different answer.

We now turn to Theorem 3.2. In (3.7), we employed the estimate

$$N^L([r^k, r^{k+1})) \approx \alpha k (\log r)^2 / \pi$$

for the abundance counts. Recalling that N^L is the number of species per site, we multiply by $|B(L)| \approx L^2$ to get

$$(3.10) \qquad N(B(10^3), [2^k, 2^{k+1})) \approx 10^6 \cdot 10^{-4} \cdot \frac{(\log 2)^2}{\pi}\, k \approx 15.29\, k$$

This formula, the line of squares in Figure 3.3, provides a poor fit for the simulation data. One of the problems with the prediction from Theorem

3.2 is that the proof of (3.7) already contains approximations based on the assumption that k is large. The error can be reduced by going back into the proof of Theorem 3.2 in Bramson, Cox and Durrett (1997), and pulling out the following formula for the number of species per site:

$$(3.11) \qquad N^L([2^k, 2^{k+1})) \approx \alpha \int_0^\infty p_t \left(e^{-2^k p_t} - e^{-2^{k+1} p_t} \right) dt.$$

See the discussion at the end of Section 6 there.

Here, p_t is the density at time t of a system of coalescing random walks started from all sites occupied. A complete description of coalescing random walks can be found in Bramson, Cox, and Durrett (1997). There, we employed the asymptotics $p_t \approx (\log t)/\pi t$, as $t \to \infty$, from Bramson and Griffeath (1980), to reduce the right side of (3.11) to $\alpha k (\log 2)^2/\pi$. One can instead use simulations to estimate p_t for small t, and then using the asymptotic formula after that to numerically evaluate the integral in (3.11).

In order to estimate $N(B(1000), [2^k, 2^{k+1}))$, we use simulations on a 1000×1000 grid to estimate p_t for times up to time 5000, and then the asymptotic formula after that. The result is given by the circular symbols in Figure 3.3. This results in a drastic improvement over Theorem 3.2. The value predicted by (3.11) for the $k = 0$ cell is only about 60% of the observed value, but the fit at the other cells $1 \le k \le 9$ is now good. Note that if we combine the formulas in (3.11) and (3.9) by taking the minimum of the two expressions, the result is accurate for all cells except $k = 0$.

The shapes of the distributions for the simulation data in Figure 3 and the field data in Figure 1 from Hubbell (1995) are quite similar. Besides being on the same scale, they exhibit related departures from lognormality — the distributions are not symmetric about their greatest value, and they have an over-abundance of species with small numbers. Such similarity is not necessarily evidence of a common underlying cause, of course. However, there are reasons to suggest that this agreement is not an accident. In the rain forest and in our model, species compete for a fixed amount of a limiting resource (e.g., light or area).

II. Stochastic Spatial Models vs. ODEs

In the last four sections we will describe a number of examples to illustrate Durrett and Levin's (1994b) idea that the behavior of stochastic spatial models can be determined from properties of the mean field ODE, which is obtained by pretending that neighboring sites are independent.

4. Case 1. Attracting Fixed Point

We begin with a simple but fundamentally important example. Our treatment will be brief. The reader can find the facts we quote and much more in Liggett (1985) or Durrett (1988).

Example 4.1. Contact process. This system was introduced by Harris (1974). Each site can be in state $0 =$ vacant or $1 =$ occupied. The system evolves according to the following rules:

(i) An occupied site becomes vacant at a rate δ.

(ii) A occupied site gives birth at rate β. A particle born at x is sent to y with probability $p(x, y) = \varphi(y - x)$.

(iii) The site y becomes occupied if it was vacant, and stays occupied if it was occupied.

One of the simplest and most studied cases is the two dimensional nearest neighbor model which has $\varphi(1, 0) = \varphi(0, 1) = \varphi(-1, 0) = \varphi(0, -1) = 1/4$. In words, offspring are sent to one of the four nearest neighbors chosen at random.

The contact process as formulated above has two parameters but only needs one. By scaling time we can and will suppose that $\beta = 1$. In this case, particles die at rate δ and give birth at rate at most 1 since births onto occupied sites are lost. From this it is easy to see that if we start with a finite number of occupied sites and $\delta > 1$ then the contact process will *die out*, i.e., reach the all 0 configuration with probability 1. We define the critical value δ_f, for survival from finite sets, to be the supremum of all of the values of δ so that dying out has a probability < 1 for some finite initial state.

There is a second slightly more sophisticated notion of "survival" for the contact and other process: the existence of a stationary distribution for the Markov chain which does not concentrate on the absorbing state in which

all sites are vacant. To see when such a stationary distribution will exist, we start with the observation that the contact process is *attractive*: i.e., increasing the number of 1's increases the birth rate and decreases the death rate. Then we quote

Lemma 4.1. *Let ξ_t^1 denote the process starting from all 1's. If the process ξ_t is attractive then as $t \to \infty$, $\xi_t^1 \Rightarrow \xi_\infty^1$, a stationary distribution.*

Here $\Rightarrow$ is short for *converges in distribution*, which means that for any sites $x_1, \ldots, x_n$ and possible states $i_1, \ldots, i_n$ we have convergence of the *finite dimensional distributions*

$$P(\xi_t^1(x_1) = i_1, \ldots \xi_t^1(x_n) = i_n) \to P(\xi_\infty^1(x_1) = i_1, \ldots \xi_\infty^1(x_n) = i_n)$$

This result and all the others we cite for the contact process can be found in any of the four books on the subject: Liggett (1985), Griffeath (1978), Durrett (1988) and (1995b).

Of course the limit in Lemma 4.1 could assign probability 1 to the all 0 configuration, and it will if δ is too large, e.g., $\delta > 1$. Let δ_e be the supremum of the values of δ for which the limit is not all 0's. For the quadratic contact process, Example 6.1, we will have

$$0 = \delta_f < \delta_e < \infty$$

However, for the contact process these two critical values coincide. To explain why this is true, we note that by using an explicit construction and working backwards in time, much as we did for the voter model one can show:

Lemma 4.2. *Let $p_t(A, B)$ be the probability some site in B is occupied at time t when we start with 1's on A (and 0's elsewhere) at time 0. Then $p_t(A, B) = p_t(B, A)$.*

Taking $A = $ all sites and $B = $ a single point we see that the density of occupied sites at time t is the same as the probability that the process survives until time t starting from a single occupied site. Thus $\delta_e = \delta_f$ and we denote their common value by δ_c, where the c stands for *critical value*.

Mean Field Theory. If we consider the contact process on a grid with n sites and modify the rules so that all sites are neighbors then the number of

occupied sites at time t is a Markov chain $N(t) \in \{0, 1, \ldots, n\}$ with transition rates:

$N(t) \to N(t) - 1$ at rate $\delta N(t)$.

$N(t) \to N(t) + 1$ at rate $N(t)\left(1 - \frac{N(t)}{n}\right)$.

If we let $u_n(t) = N(t)/n$ be the fraction of occupied sites and let $n \to \infty$ then it is not hard to show (e.g., using (7.1) of Chapter 8 of Durrett (1996)) that the u_n converge to the solution of the *"mean field"* *ordinary differential equation.*

$$(4.1) \qquad\qquad \frac{du}{dt} = -\delta u + u(1 - u)$$

The term in quotes comes from the physics. It refers to the fact that each site only feels the density of occupied sites. Writing 0 for vacant and 1 for occupied the density is then the mean value of the occupancy variables. The mean field equation can also be obtained from the spatial model by letting $u(t)$ be the fraction of sites occupied at time t and assuming that adjacent sites are independent. Under this assumption the rate at which new particles are produced is $u(1 - u)$, while particles disappear at rate $-\delta u$. Since the second recipe is simpler we will use it for all of the other computations.

The mean field ODE for the contact process predicts that δ_c is 1 and for $\delta < \delta_c$ the equilibrium density of occupied sites is $1 - \delta$. In the nearest neighbor contact process there is a significant positive correlation between the states of neighboring sites (see Harris (1977)) so this overestimates the critical value. Numerical results tell us the critical value of the two dimensional nearest neighbor contact process is about 0.607. See Brower, Furman and Moshe (178) and Grassberger and de la Torre (1979).

Although the nearest neighbor case has been the most studied, it turns out that the contact process gets simpler when we consider

(4.2) **Long Range Limits.** Let $\psi \geq 0$ be a continuous function that is integrable and not identically 0, and define the dispersal kernel in part (ii) of the definition of the contact process to be $\varphi(z) = c_r\psi(z/r)$ where c_r chosen to make the probabilities add up to one.

Bramson, Durrett, and Swindle (1989), have shown (see also Durrett (1992) for the weaker version stated here)

Theorem 4.1. *As* $r \to \infty$, $\delta_c(r) \to 1$ *and*

$$P(\xi^1_\infty(x) = 1) \to 1 - \delta$$

Note that as $r \to \infty$ the critical value and equilibrium densities converge to those predicted by mean field theory.

Example 4.2. Grass Bushes Trees. In our second model, the possible states are $0 = $ grass, $1 = $ bushes, $2 = $ trees. 0's are thought of as vacant sites. Types 1 and 2 behave like contact processes subject to the rule that 2's can give birth onto sites occupied by 1's but not vice versa. In formulating the dynamics, we are thinking of the various types as species that are part of a successional sequence. With Tilman's (1994) work in mind we define the model for an arbitrary number of species.

(i) If $i > 0$, type i individuals die at a constant rate δ_i and give birth at rate β_i.

(ii) A particle of type i born at x is sent to y with probability $p_i(x, y) = \varphi_i(y - x)$.

(iii) If number of the invading type is larger it takes over the site.

Starting our analysis with the case of two types, we note that 2's don't feel the presence of 1's, so they are a contact process and will survive if $\delta_2/\beta_2 < \delta_c$. The main question then is: when can the 1's survive in the space that is left to them?

To investigate this question Durrett and Swindle (1991) considered what happens when long range limits are taken as described in (4.2) above. As in the case of the long range contact process, the motivation is that in this case the densities will behave like solutions to the mean field ODE, which is obtained by pretending that adjacent sites are always independent

$$(4.3) \quad \begin{aligned} du_1/dt &= u_1 \left\{ \beta_1(1 - u_1 - u_2) - \delta_1 - \beta_2 u_2 \right\} \\ du_2/dt &= u_2 \left\{ \beta_2(1 - u_2) - \delta_2 \right\} \end{aligned}$$

For example in the du_1/dt equation the first term represents births of 1's onto sites in state 0 (vacant), the second term represents constant deaths, and the third births of 2's onto sites occupied by 1's.

From the second equation in (4.3) the equilibrium density of 2's will be

$$\bar{u}_2 = \frac{\beta_2 - \delta_2}{\beta_2}$$

Inserting this into the first equation and solving one finds there is an equilibrium with $\bar{u}_1 > 0$ if

$$(4.4) \qquad \beta_1 \cdot \frac{\delta_2}{\beta_2} - \delta_1 - \{\beta_2 - \delta_2\} > 0$$

As written, this condition can be derived by asking the question: "Can the 1's invade the 2's when they are in equilibrium?" That is, will u_1 increase when it is small enough. To see this note that in the absence of 1's, the 2's have an equilibrium density of $\bar{u}_2 = (\beta_2 - \delta_2)/\beta_2$. Plugging this into the first equation and ignoring the $-\beta_1 u_1^2$ term gives

$$\frac{du_1}{dt} = u_1 \left(\beta_1 \frac{\delta_2}{\beta_2} - \delta_1 - (\beta_2 - \delta_2) \right)$$

The next two results say that when the range r is large enough the spatial model behaves like the ODE. First we need to define the behaviors that we will observe. We say that *coexistence occurs* if there is a stationary distribution that concentrates on configurations with infinitely many sites in each of the possible states. We say that *1's die out*, if whenever there are infinitely many 2's in the initial configuration $P(\xi_t(x) = 1) \to 0$ as $t \to \infty$.

Durrett and Swindle (1991). *If (4.4) holds then coexistence occurs for large range.*

Durrett and Schinzai (1993). *Suppose that the quantity on the left-hand side of (4.4) is < 0. If the range is large 1's die out.*

Remarks. The results in Durrett and Schinazi (1993) also apply to the Crawley and May's (1987) model of the competition between annuals and perennials. In this case the perennials are a nearest neighbor contact process but annuals have a long dispersal distance. For another competition model that has been analyzed using long range limits, see Durrett and Neuhauser (1997).

5. Rapid Stirring Limits

In the previous section we saw that stochastic spatial models simplify considerably when the range is large. Our next goal is to explain that this also occurs when the particles are subject to fast stirring. Formally, a stirring event involving x and y will change the state of the process from ξ to $\xi^{x,y}$ where

$$\xi^{x,y}(y) = \xi(x) \qquad \xi^{x,y}(x) = \xi(y) \qquad \xi^{x,y}(z) = \xi(z) \quad z \neq x, y$$

In words, stirring exchanges the values found at x and y.

The stirring mechanism has product measures as its stationary distributions. See Griffeath (1978), Section II.10. So when it acts at a rapid rate we expect that nearby sites will be almost independent. To keep the particles from flying out of our field of vision as the stirring rate is increased, we scale space by multiplying by $\epsilon = \nu^{-1/2}$. Since this is the usual diffusion scaling, it should not be surprising that the particle system converges to the solution of a reaction diffusion equation.

To state a general result, we consider processes $\xi_t^\epsilon : \epsilon \mathbf{Z}^d \to \{0, 1, \ldots, \kappa - 1\}$ that have

(i) *translation invariant finite range flip rates.* That is, there are sites $y_1, \ldots y_N$ and for each state i a function h_i so that

$$c_i(x, \xi) = h_i(\xi(x), \xi(x + \epsilon y_1), \ldots, \xi(x + \epsilon y_N))$$

(ii) *rapid stirring:* for each $x, y \in \epsilon \mathbf{Z}^d$ with $\|x - y\|_1 = \epsilon$, we exchange the values at x and y at rate ϵ^{-2}.

With these assumptions we get the following *mean field limit theorem* of De Masi, Ferrari, and Lebowitz (1986). (For the version given here, see Durrett and Neuhauser (1994).)

Theorem 5.1. *Suppose $\xi_0^\epsilon(x)$ are independent and let $u_i^\epsilon(t, x) = P(\xi_t^\epsilon(x) = i)$. If $u_i^\epsilon(0, x) = g_i(x)$ where $g_i(x)$ is a continuous function of x then as $\epsilon \to 0$, $u_i^\epsilon(t, x) \to u_i(t, x)$ the bounded solution of*

$$(5.1) \qquad \partial u_i / \partial t = \Delta u_i + f_i(u) \qquad u_i(0, x) = g_i(x)$$

where

(5.2) $f_i(u) = \; < c_i(0, \xi) 1_{(\xi(0) \neq i)} >_u - \sum_{j \neq i} < c_j(0, \xi) 1_{(\xi(0) = i)} >_u$

and $< \varphi(\xi) >_u$ denotes the expected value of $\varphi(\xi)$ under the product measure in which state j has density u_j, i.e., when $\xi(x)$ are i.i.d. with $P(\xi(x) = j) = u_j$.

To explain the form of the reaction term, we note that when ϵ is small, stirring operates at a fast rate and keeps the system close to a product measure. The rate of change of the densities can then be computed assuming adjacent sites are independent.

Theorem 5.1 only concerns expected values, but once it is established we can easily demonstrate the next result which says that in the fast stirring limit on a suitably rescaled lattice, the particle system becomes deterministic and looks like solutions of the PDE.

Theorem 5.2. *If $f(x, t)$ is a continuous function with compact support in $\mathbf{R}^d \times [0, \infty)$ then*

$$\epsilon^d \sum_{x \in \epsilon \mathbf{Z}^d} \int_0^\infty f(x, t) 1_{(\xi_t^\epsilon(x) = i)} \, dt \to \iint_0^\infty f(x, t) u(t, x) \, dt \, dx \quad \text{in probability}$$

Our main interest in the PDE limit described in Theorems 5.1 and 5.2 is to obtain information about the particle system with fast (but finite) stirring rate. To do this we need one more result. The main assumption may look strange. Its form is dictated by the "block construction" technique we use to prove things. A complete discussion of this technique can be found in Durrett (1995b). Here we content ourselves to simply state one useful result.

($\star$) There are constants $A_i < a_i < b_i < B_i$, L, and T so that if $u_i(0, x) \in (A_i, B_i)$ when $x \in [-L, L]^d$ then $u_i(T, x) \in (a_i, b_i)$ when $x \in [-3L, 3L]^d$.

Durrett and Neuhauser (1994) have shown:

Theorem 5.3. *If ($\star$) holds for the PDE then there is coexistence for the particle system with fast stirring.*

At this point we have reduced the task of proving theorems for particle systems to proving a specific type of result $(\star)$ for the associated PDE. Leaving the reader to meditate on whether or not this is progress, we turn to the first of several concrete examples that can be treated by this method.

Example 5.1. Predator Prey Systems. Each site can be in state $0 =$ vacant, $1 =$ fish, or $2 =$ shark. If we let f_i be the fraction of the nearest neighbors of x (i.e., y with $\|y - x\|_1 = \epsilon$) that are in state i then we can write the flip rates as follows:

$$
\begin{array}{llll}
0 \to 1 & \beta_1 f_1 & 1 \to 2 & \beta_2 f_2 \\
1 \to 0 & \delta_1 & 2 \to 0 & \delta_2 + \gamma f_2
\end{array}
$$

Here we have shifted our perspective from occupied sites giving birth, to vacant sites receiving particles from their neighbors. After this translation is made, the two rates on the left say that in the absence of sharks, the fish are a contact process.

The third rate says that sharks can reproduce by giving birth onto sites occupied by fish, an event which kills the fish. This transition is more than a little strange from a biological point of view, but it has the desirable property that the density of sharks will decrease when the density of fish is too small. The final rate says that sharks die at rate δ_2 when they are isolated and the rate increases linearly with crowding.

To be able to use our results about rapid stirring limits we also of course have to suppose that the sharks and fish swim around. That is, for each pair of nearest neighbors x and y stirring occurs at rate ϵ^{-2}. Applying Theorem 5.1 we see that if $\xi_0^\epsilon(x)$, $x \in \epsilon \mathbf{Z}^d$ are independent and $u_i^\epsilon(t, x) = P(\xi_t^\epsilon(x) = i)$ for $i = 1, 2$ then as $\epsilon \to 0$, $u_i^\epsilon(t, x) \to u_i(t, x)$ as $\epsilon \to 0$, the bounded solution of

$$
(5.3) \qquad
\begin{array}{l}
\frac{\partial u_1}{\partial t} = \Delta u_1 + \beta_1 u_1 (1 - u_1 - u_2) - \beta_2 u_1 u_2 - \delta_1 u_1 \\
\frac{\partial u_2}{\partial t} = \Delta u_2 + \beta_2 u_1 u_2 - u_2 (\delta_2 + \gamma u_2)
\end{array}
$$

with $u_i(0, x) = f_i(x)$. To check the right-hand side, we note that if x is vacant and neighbor y is occupied by a fish, an event of probability $(1 - u_1 - u_2)u_1$ when sites are independent, births from y to x occur at rate $\beta_1/2d$ and there are $2d$ such pairs. The $-\beta_2 u_1 u_2$ in the first equation and the $\beta_2 u_1 u_2$ in the second come from sharks giving birth onto fish. The last term in each equation comes from the death events.

When the initial functions $f_i(x)$ do not depend on x, we have $u_i(t, x) = v_i(t)$ where the v_i's satisfy the ODE

(5.4)
$$\frac{dv_1}{dt} = v_1\{(\beta_1 - \delta_1) - \beta_1 v_1 - (\beta_1 + \beta_2)v_2\}$$
$$\frac{dv_2}{dt} = v_2\{-\delta_2 + \beta_2 v_1 - \gamma v_2\}$$

Here we have re-arranged the right hand side to show that the system is an example of the standard predator-prey equations for species with limited growth. See e.g., page 263 of Hirsch and Smale (1974).

The first step in understanding (5.3) is to look at (5.4) and ask: "What are the fixed points, i.e., solutions of the form $v_i(t) \equiv \rho_i$?" It is easy to solve for the ρ_i. There is always the trivial solution $\rho_1 = \rho_2 = 0$. In the absence of sharks the fish are a contact process, so if $\beta_1 > \delta_1$ there is a solution $\rho_1 = (\beta_1 - \delta_1)/\beta_1$, $\rho_2 = 0$. Finally, if we assume that the $\rho_1, \rho_2 \neq 0$, we can solve two equations in two unknowns to get

$$\rho_1 = \frac{(\beta_1 - \delta_1)\gamma + \delta_2(\beta_1 + \beta_2)}{\beta_1\gamma + \beta_2(\beta_1 + \beta_2)} \qquad \rho_2 = \frac{(\beta_1 - \delta_1)\beta_2 - \delta_2\beta_1}{\beta_1\gamma + (\beta_1 + \beta_2)\beta_2}$$

which has $\rho_2 > 0$ if

(5.5)
$$(\beta_1 - \delta_1)/\beta_1 > \delta_2/\beta_2$$

To understand this condition we note that if the fish are in equilibrium and the sharks have small density, then neglecting the $-\gamma v_2$ term and inserting the equilibrium value for v_1, the second equation in (5.4) becomes

(5.6)
$$\frac{dv_2}{dt} = v_2\left\{-\delta_2 + \beta_2 \cdot \frac{\beta_1 - \delta_1}{\beta_1}\right\}$$

The condition (5.5) says that the quantity in braces is positive, i.e., the density of sharks will increase when it is small.

Having found conditions that guarantee the existence of an interior fixed point, the next step is to check that it is attracting. Figure 5.1 shows an example of the ODE, which confirms this in the special case considered there. However, one does not need to use a computer to see that this will occur. To prove this, one begins with the easy to check fact that

$$H(v_1, v_2) = \beta_2(v_1 - \rho_1 \log v_1) + (\beta_1 + \beta_2)(v_2 - \rho_2 \log v_2)$$

is a Lyapunov function, i.e., it is decreasing along solutions of the ODE (5.4). A simple argument by contradiction then shows that all orbits starting at points with each density $v_i > 0$ converge to (ρ_1, ρ_2). The presence of a globally attracting fixed point leads us to guess that

Theorem 5.4. *Suppose that* $(\beta_1 - \delta_1)/\beta_1 > \delta_2/\beta_2$. *If* ϵ *is small there is a nontrivial translation invariant stationary distribution in which the density of sites of type* i *is close to* ρ_i.

In view of Theorem 5.3 it suffices to prove $(\star)$. For details see Durrett (1993). The proof involves Brownian motion in a minor role, but is otherwise an analytic proof built on results of Redheffer, Redlinger, and Walter (1988) who considered the problem in a bounded domain with Neumann boundary conditions.

Example 5.2. Predator Mediated Coexistence. Here the possible states of a site are $0 =$ vacant, 1, 2 = two prey species, 3 = predator. Types $i = 1, 2$ behave like a contact process, dying at a constant rate δ_i and being born at vacant sites at rate β_i times the fraction of neighbors in state i. 3's die at a constant rate δ_3, are born at sites occupied by 1's at rate β_3 times the fraction of neighbors in state 3, and are born at sites occupied by 1's at rate β_4 times the fraction of neighbors in state 3. Finally, of course, there is stirring at rate ν: for each pair of nearest neighbors x and y we exchange the values at x and at y at rate ν.

In the absence of predators, this system reduces to the competing contact process, where the stronger species, identified by the larger of the two ratios β_i/δ_i, will competitively exclude the other. (See Neuhauser (1992) where the result is proved under the assumption that $\delta_1 = \delta_2$.) However, if the predators feeding rate on the stronger species is larger, its presence may stabilize the competition between the two species.

One way of seeing this is to consider the mean field ODE:

$$
\begin{aligned}
du_1/dt &= u_1 \left\{ \beta_1 u_0 - \delta_1 - \beta_3 u_3 \right\} \\
du_2/dt &= u_2 \left\{ \beta_2 u_0 - \delta_2 - \beta_4 u_3 \right\} \\
du_3/dt &= u_3 \left\{ \beta_3 u_1 + \beta_4 u_4 - \delta_3 \right\}
\end{aligned}
$$

Here one can solve three equations in three unknowns to find conditions for an interior fixed point but a more fruitful approach is to derive conditions from an *invadability analysis*. Half of this may be described as follows.

By results for predator prey systems above, 2's and 3's can coexist if

$$\frac{\beta_2 - \delta_2}{\beta_2} > \frac{\delta_3}{\beta_4}$$

and when this holds their equilibrium densities will be $v_2 = \delta_3/\beta_4$ and

$$v_3 = \frac{(\beta_2 - \delta_2)\beta_4 - \beta_2}{(\beta_2 + \beta_4)\beta_4}$$

Examining the behavior of the ODE near $(0, v_2, v_3)$ we see that 1's can invade the (2,3) equilibrium if

$$\beta_1 - \delta_1 - \beta_1 v_2 - (\beta_1 + \beta_3)v_3 > 0$$

In a similar way one can derive conditions for the (1,3) equilibrium to exist and for the 2's to be able to invade it. When both sets of conditions hold we say there is *mutual invadability*. It is easy to prove that in this case that the ODE has an interior fixed point. By considerably extending the methods of Durrett (1993), Shah (1997) has shown

Theorem 5.5. *If mutual invadability holds for the ODE then coexistence occurs for the stochastic spatial model with fast stirring.*

To get a feel for the resulting phase diagram, set $\beta_3 = 4$, $\beta_4 = 3/2$, all the $\delta_i = 1$, and vary β_1 and β_2. The formulas above imply that 1 and 3 coexist if $\beta_1 > 4/3$, 2 and 3 coexist if $\beta_2 > 3$, and finally all three species can coexist inside the region bounded by the equations.

$$\beta_1 > \beta_2, \quad \beta_2 < \frac{17}{32}\beta_1 + \frac{5}{8}, \quad \beta_2 > \frac{9}{14}\beta_1 + \frac{15}{14}$$

The last few lines are summarized in Figure 5.3. Note that there is a region where all three species can coexist but 2's and 3's cannot. Upon reflection this is not surprising: it simply says the 2's are not a sufficiently good food source to maintain the predator by themselves.

6. Case 2. Two Locally Attracting Fixed Points

As in our consideration of Case 1, we will begin with an example that has two states: $0 = $ vacant and $1 = $ occupied. The rules are like the contact

process but now it takes two particles to make a new one. For this reason many of the early papers refer to this as the sexual reproduction process. However to emphasize that here the birth rate is quadratic instead of linear we will use the more modest name.

Example 6.1. Quadratic contact process. This system is also sometimes called Schlogl's second model. See Schlogl (1972) and Grassberger (1982).

(i) An occupied becomes vacant at a rate δ.

(ii) A vacant site becomes occupied at a rate equal to $k(k-1)/6$ where k is number of occupied neighbors.

Note that as in the contact process we have scaled time to make the maximum possible birth rate $= 1$.

    The critical value for survival of this process starting from a finite set $\delta_f = 0$. To see this note that if the initial configuration starts inside a rectangle it can never give birth outside of the rectangle and hence is doomed to die out whenever δ is positive. Somewhat surprisingly, the critical value for the existence of a stationary distribution $\delta_e > 0$. Bramson and Gray (1991) have shown

Theorem 6.1. *There is a $\delta_0 > 0$ so that if $\delta \leq \delta_0$ then the limit starting from all 1's is a nontrivial stationary distribution.*

    The numerical value of δ_0 produced in the proof of Theorem 6.1 is very small. To obtain quantitative estimates we can turn to simulation to conclude that $\delta_e \approx 0.1$. Or we can take a fast stirring limit and use Theorems 5.1 and 5.2 that with rapid stirring the system behaves like the following PDE.

$$(6.1) \qquad \frac{du}{dt} = \Delta u - \delta u + (1-u)u^2$$

As in the study of the predator-prey model, we begin with the mean field ODE.

$$(6.2) \qquad \frac{du}{dt} = -\delta u + (1-u)u^2$$

When $\delta > 1/4$, $-\delta + u(1-u) < 0$ for all $u \in (0,1)$ so 0 is a globally attracting fixed point. When $\delta \in (0, 1/4)$ the quadratic equation $\delta = u(1-u)$ has two

roots

$$0 < \rho_1 = \frac{1 - \sqrt{1 - 4\delta}}{2} < \rho_2 = \frac{1 + \sqrt{1 - 4\delta}}{2} < 1$$

This might suggest that as stirring becomes more rapid the critical value for a nontrivial equilibrium δ_e approaches 1/4. However, results of Noble (1992) and Durrett and Neuhauser (1994) show

Theorem 6.2. *As $\epsilon \to 0$, the critical value converges $\delta_e(\epsilon) \to 2/9$. Furthermore, if $\delta < 2/9$ then the equilibrium density $P(\xi_\infty^1(x) = 1) \to \rho_2$.*

To explain the value 2/9's we recall that in one dimension the limiting reaction diffusion equation has *traveling wave solutions*

$$(6.3) \qquad\qquad u(x,t) = w(x - ct)$$

that keep their shape but move at velocity c. This and the other PDE results we will quote for this example can be found in Fife and McLeod (1977).

Setting $f(u) = -\delta u + (1 - u)u^2$, since it will be clearer to do things for a general reaction term, it is easy to check that the recipe in (6.3) will lead to a solution of (6.1) if and only if

$$(6.4) \qquad\qquad -cw'(y) = w''(y) + f(w)$$

Suppose to fix an orientation of the wave that: w tends to ρ_2 as $y \to -\infty$ and $w \to 0$ as $y \to \infty$. Multiplying by $w'(y)$ and integrating we have

$$(6.5) \qquad \begin{aligned} -c \int w'(y)^2 \, dy &= \int w''(y)w'(y) \, dy + \int f(w(y))w'(y) \, dy \\ &= 0 - \int_0^{\rho_2} f(z) \, dz \end{aligned}$$

Here to get the 0 we observed that the antiderivative of $w''w'$ is $(w')^2/2$ which vanishes at infinity, and in the second integral we have changed variables $z = w(y)$, and reversed the order of the limits.

(6.5) does not allow us to compute the value of c but since $\int w'(y)^2 \, dy > 0$ it does tell us that the sign of c is the same as that of $\int_0^{\rho_2} f(z) \, dz$. A little calculus now confirms that the speed is positive for $\delta < 2/9$ and negative for $\delta > 2/9$. To check this easily, note that when $\delta = 2/9$ the three roots of the cubic are 0, 1/3, and 2/3, so symmetry dictates that the positive and negative areas must cancel and the speed is 0.

Sketch of the proof of Theorem 6.2. To prove that if $\delta < 2/9$ coexistence occurs for rapid stirring it suffices to check ($\star$) in Section 5 and apply Theorem 5.3. This can be done easily with the help of results in Fife and McLeod (1977), and was done Noble's (1992) Ph.D. thesis.

The other direction is a little more tricky since one must show that if $\delta > 2/9$ and stirring is rapid, the 1's die out, not just that their density in equilibrium is close to 0. Durrett and Neuhauser (1994) do this by using the PDE result to drive the density of 1's to a low level and then use auxiliary arguments to check that the 1's will then die out. □

Up to this point we have concentrated only on the critical value for a nontrivial equilibrium. From the proof of Theorem 6.2 one gets easily that

Theorem 6.3. As $\epsilon \to 0$, the critical value for survival from a finite set, $\delta_f(\epsilon) \to 2/9$.

It is known in general that $\delta_f \geq \delta_e$. This may sound obvious but it is difficult to prove. See Bezuidenhout and Gray (1994). Once there is stirring at a positive rate $\delta_f > 0$. In fact we

Conjecture. If the stirring rate $\nu > 0$ then $\delta_f = \delta_e$.

Remark. The techniques described above have been used by Durrett and Swindle (1994) to prove results for a catalytic surface. Keeping to biological models, we will continue with

Example 6.2. Colicin. The inspiration for this model came from Chao (1979) and Chao and Levin (1981). Bacteria may produce toxic substances, known collectively as bacteriocins, that kill or inhibit the growth of competing bacteria of different genotypes. In general, bacteria that are capable of producing such chemicals are immune to their action. The colicins, the most extensively studied class of bacteriocins, are produced by the bacterium *Escherica coli* and other members of the family Enterobacteriaceae. For more about the biology, and an alternative approach to the modeling, see Frank (1994).

To model the competition we will use a spatial model with three states: $0 = $ vacant, $1 = $ occupied by a colicin producer, $2 = $ occupied by a colicin

sensitive bacterium. If we let f_i be the fraction of the four nearest neighbors in state i, we can formulate the transition rates as follows:

birth	rate	death	rate
$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$0 \to 2$	$\beta_2 f_2$	$2 \to 0$	$\delta_2 + \gamma f_1$

In words, each type is born at empty sites at a rate proportional to the fraction of neighbors of that type. The colicin producing strain dies at a constant rate δ_1, while the colicin sensitive strain experiences deaths at rate δ_2 plus γ times the fraction of colicin producing neighbors.

To see what behavior to expect from the spatial model, we begin by writing down the mean field ODE. Let u_1 be the density of colicin-producing and let u_2 be the density of the ordinary, colicin-sensitive bacteria. Assuming that all sites are independent we have

(6.6)
$$\begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1 (1 - u_1 - u_2) - \delta_1 u_1 \\ \frac{du_2}{dt} &= \beta_2 u_2 (1 - u_1 - u_2) - \delta_2 u_2 - \gamma u_1 u_2 \end{aligned}$$

The system (6.6) has locally stable boundary equilibria at

$$(1 - \delta_1/\beta_1, 0) \quad \text{and} \quad (0, 1 - \delta_2/\beta_2)$$

provided

(6.7)
$$\delta_i < \beta_i \qquad \frac{\delta_2}{\beta_2} < \frac{\delta_1}{\beta_1} < \frac{\delta_2 + \gamma}{\beta_2 + \gamma}$$

There is moreover an interior saddle point $(\bar{u}_1, \bar{u}_2)$ in this case. See Figure 6.1 for a picture of what happens when $\delta_1 = \delta_2 = 1$, $\beta_1 = 3$, $\beta_2 = 4$ and $\gamma = 3$. The interpretation of the inequalities in order from left to right is

(i) the birth rate exceeds the death rate so either type can maintain a population in isolation from the other;

(ii) there is a cost to colicin production, reflected in a lower carrying capacity in isolation

(iii) the competitive benefit of colicin production is sufficiently large so that an established colicin-producing community can repel invasion by the wild type.

The implication of this analysis is that colicin production is an evolutionarily stable strategy, but so is nonproduction. In the dynamical system pictured in Figure 6.1, if the density of the colicin sensitive bacteria is near the equilibrium value then the colicin producing bacteria cannot invade. That is, if they are introduced at a low level then their density will shrink to 0. On the other hand, if the colicin producers are introduced at a large enough level, their density will increase to 1 and the density of the colicin sensitive strain will approach 0. In words, selection will only favor genotypes when they are common, rare species cannot invade, and genetic diversity will not be maintained. This situation is "disruptive frequency dependent selection" (see B.R. Levin (1988), Thoday (1959–64)).

The last paragraph identifies the colicin system as belonging to Case 2, so we expect that there is one stronger type that is the winner starting from generic initial conditions, i.e., configurations in which there are infinitely many sites in each of the possible states. In the case of colicin, it is not natural to introduce rapid stirring and even if we did we would not know how to analyze the PDE's that result. Thus we turn to the computer to confirm our theoretical predictions.

Computer simulations. Figure 6.2 shows the density of colicin producers and colicin sensitive bacteria in a simulation of the spatial model with parameters: $\delta_1 = \delta_2 = 1$, $\beta_1 = 3$, $\beta_2 = 4$ and $\gamma = 3$. Here the lattice is 100×100 and to avoid edge effects we have used *periodic boundary conditions.* That is, sites on the bottom row are neighbors of those on the top row; sites on the left edge are neighbors of those on the right edge. We start at time 0 from *product measure.* That is, the states of the sites at time 0 are assigned independently, i.e., by making repeated calls to a random number generator. We started the simulation with colicin producers (1's) at density 0.01 and the colicin sensitive strain (2's) at density 0.50; but as the graph shows, the colicin producers gradually increase to their equilibrium level while the density of colicin sensitive bacteria drops to 0. The colicin producers first establish themselves in clumps that grow linearly in radius and take over the system.

The victory of the colicin producers in the last example is due to the fact that the colicin induced death rate $\gamma = 3$ is large enough to compensate for the fact that the colicin producing strain has birth rate $\beta_1 = 3$ versus $\beta_2 = 4$ for the colicin sensitive strain. If we reduce γ to 1 the situation reverses

and the colicin sensitive strain is victorious even when it starts from a low density. For values of γ between 1 and 3 coexistence might be possible but this does not occur: there is a critical value γ_c so that 2's take over when $\gamma < \gamma_c$, while 1's take over when $\gamma > \gamma_c$.

More generally if we fix $\delta_1 = \delta_2 = 1$, $\beta_2 = 4$, and vary β_1 and γ then we get the phase diagram drawn in Figure 6.3. The figure is a free-hand sketch that emphasizes the generic qualitative properties but is not exact. For each fixed value of β_1 there is a critical value $\gamma_c(\beta_1)$ so that 2's take over when $\gamma < \gamma_c(\beta_1)$ while 1's take over when $\gamma > \gamma_c(\beta_1)$. When $\beta_1 = 4 = \beta_2$, $\gamma_c(\beta_1) = 0$. Decreasing β_1 increases $\gamma_c(\beta_1)$ until it reaches ∞ at a point we have labeled β_c. β_c, which is ≈ 1.65 for the neighborhood $\mathcal{N}_0$, is the minimum value of the birth rate needed for a single strain to survive in the absence of the other. When there is a single strain the model reduces to the basic contact process, see Durrett and Levin (1994a).

Example 6.3. A Three Species Colicin System. In the two examples above, the ODE and the spatial model sometimes disagreed on who would win the competition, but both approaches agreed that one type would always competitively exclude the other. We will now describe a system in which three species coexist in the spatial model, but in the ODE there is always only one winner.

To describe the system in words, we assume 1's and 2's both produce colicin, to which they are immune, and to which 3 is sensitive. The rates for this system are:

birth	rate	death	rate
$0 \to 1$	$\beta_1 f_1$	$1 \to 0$	δ_1
$0 \to 2$	$\beta_2 f_2$	$2 \to 0$	δ_2
$0 \to 3$	$\beta_3 f_3$	$3 \to 0$	$\delta_3 + \gamma_1 f_1 + \gamma_2 f_2$

Here, f_i is the fraction of the four nearest neighbors in state i. In our concrete example we will set all the $\delta_i = 1$ and

$$\beta_1 = 3 \quad \beta_2 = 3.2 \quad \beta_3 = 4 \quad \gamma_1 = 3 \quad \gamma_2 = 0.5$$

Here we imagine that species 1 produces more colicin than 2 does but has the lowest birth rate. The parameters are chosen so that 1's win against 3's while 3's win against 2's. When only 1's and 2's are present the system

reduces to the multitype contact process studied in Neuhauser (1992). Since $\beta_2 > \beta_1$, the 2's win against the 1's in this case.

If we write u_i for the fraction of sites in state i then the mean field ODE is:

(6.8)
$$\begin{aligned}
\frac{du_1}{dt} &= \beta_1 u_1 u_0 - \delta_1 u_1 \\
\frac{du_2}{dt} &= \beta_2 u_2 u_0 - \delta_2 u_2 \\
\frac{du_3}{dt} &= \beta_3 u_3 u_0 - u_3(\delta_3 + \gamma_1 u_1 + \gamma_2 u_2)
\end{aligned}$$

If we insert the values for the concrete example then the picture in Figure 6.4 results. In the $u_1 u_2$ plane all trajectories starting with u_1 and u_2 positive are attracted to $(0, \hat{u}_2, 0)$ where $\hat{u}_i = (\beta_i - \delta_i)/\beta_i$. In the three dimensional ODE there is a surface which connects the two separatrices in the $u_1 u_3$ and $u_2 u_3$ planes, so that above the surface trajectories converge to $(0, 0, \hat{u}_3)$ while those below converge to $(0, \hat{u}_2, 0)$. These conclusions are true whenever $\beta_1 < \beta_2$ and equilibria exist in the interior of the $u_1 u_3$ and $u_2 u_3$ planes. (Conditions for this can be derived from (6.7).)

In contrast to the behavior of the ODE, the spatial model shows coexistence, at least for a long time. See Figure 6.5 for a simulation of the process on a 200×200 grid with periodic boundary conditions. Here we started in an initial product measure in which the states $i = 1, 2, 3$ each have density $1/3$ and plotted the observed density of the three species every one thousand units of time out to time 50,000. The densities fluctuate but none of them seems in danger of hitting 0.

7. Case 3. Periodic Orbits

Our first example was introduced by Silvertown et al. (1992) to investigate the competitive interaction of five grass species. We have given it a new name to place it in context in the theory of interacting particle systems.

Example 7.1. The Multitype Biased Voter Model. Each site will always be occupied by exactly one of the species $1, 2, \ldots, K$. The process is described by declaring that:

(i) An individual of species i produces new offspring of its type at rate β_i.

(ii) An offspring of type i produced at x is sent to y with probability $q_i(x, y) = \varphi_i(|y - x|)$ where $|y - x|$ is the distance from x to y. To avoid unnecessary

complications, we will suppose that $\varphi_i(1) > 0$ and that there is an $R < \infty$ so that $\varphi_i(r) = 0$ when the distance $r > R$. In other words, there is a finite dispersal range, but nearest neighbors are always accessible.

(iii) If site y is occupied by type j, and type i disperses to that site, a successful invasion occurs (i.e., the state of y changes from j to i) with probability p_{ij}; if invasion does not occur, the site y is unchanged.

To explain the name we note that if there are only two types then the model reduces to the biased voter model introduced by Williams and Bjerknes (1972) and studied by Griffeath (1978) and Bramson and Griffeath (1980), (1981). For a summary of their results see Chapter 3 of Durrett (1988).

If we were to ignore space and assume that the states of the sites in the grid are always independent, then the fraction of sites occupied by species i, u_i, would satisfy

(7.1)
$$\frac{du_i}{dt} = \sum_j u_i u_j \{\beta_i p_{ij} - \beta_j p_{ij}\}$$

In the model (and of course also in the ODE) only the value of $\lambda_{ij} = \beta_i p_{ij}$ is important, so we can describe the concrete example investigated by Silvertown et al (1992) by giving the matrix λ_{ij}.

i	$j \rightarrow$	1	2	3	4	5
1	Agrostis	0	0.09	0.32	0.23	0.37
2	Holcus	0.08	0	0.16	0.06	0.09
3	Poa	0.06	0.06	0	0.44	0.11
4	Lolium	0.02	0.06	0.05	0	0.03
5	Cynosurus	0.02	0.03	0.05	0.03	0

Simulations of this process from a randomly chosen initial state were not very interesting to watch. "Three of the five species went extinct very rapidly. The two survivors *Agrostis* and *Holcus* were the same as the species that survived the longest in the aggregated models." To explain why this occurs, we say that species i *dominates* species j and we write $i \geq j$ if $a_{ij} = \lambda_{ij} - \lambda_{ji} \geq 0$. When the difference is > 0, we say i *strictly dominates* j and write $i > j$. In the concrete case given above, *Agrostis* strictly dominates all other species but beats *Holcus* by only 0.01, so it should not be surprising that *Agrostis* takes over the system with *Holcus* offering the most resistance. Indeed, Durrett and Levin (1997) have shown

Theorem 7.1. *Assume that the dispersal distribution φ_i does not depend on i and that type 1 is strictly dominant over type i for $2 \le i \le K$. If we let A_t^1 denote the event that type 1 is still alive at time t then $P(A_t^1, \xi_t(x) \ne 1) \to 0$ as $t \to \infty$.*

This result says simply that if all species disperse equally, a competitive dominant type will almost certainly outcompete all others. To explain the mathematical statement, note that if we start with infinitely many sites in state 1 then $P(A_t^1) = 1$ for all $t > 0$ and the theorem implies that type 1 comes to dominate at every site. If we only start with finitely many 1's then bad luck in the early stages can wipe out all the 1's. Our result says that if this does not happen then the 1's will take over the system.

The outcome in Theorem 7.1 is the one we should expect. It is also the one predicted in the mean field case by the ordinary differential equations, (7.1). To see this for the ODE, note that the domination condition implies that all the $a_{1i} > 0$, so $u_1(t)$ is increasing. Being increasing and bounded by 1, $\lim_{t \to \infty} u_1(t)$ exists; but this is only possible if $du_1/dt \to 0$, which implies $\sum_{i>1} u_i(t) \to 0$.

Cyclic Biased Voter Model. In view of the discussion just completed, the simplest system that can have interesting behavior is a three-species systems with a competitive loop: $1 < 2 < 3 < 1$. This may at first appear to be a rather special and esoteric situation, but its generality becomes clearer when it is recognized that late successional species (the competitive dominants) typically would be replaced by early successional species following a disturbance. Thus, if, for example, species 1, 2, and 3 are respectively grass, bushes, trees, or some other representation of the successional cycle, the ordering $1 < 2 < 3 < 1$ makes sense in terms of competitive replacement. Bramson and Griffeath (1989) have considered this system with $n \ge 3$ competitors in one dimension. Griffeath alone (1988) and with his co-workers Fisch and Gravner (1991a, 1991b) has studied related cellular automata. Tainaka (1993, 1995) has considered a variation on the model in which 1's mutate into 3's with the paradoxical result that this enhances the density of 1's.

In our situation, if we suppose $1 < 2 < 3 < 1$ and let

$$\beta_1 = \lambda_{13} \qquad \beta_2 = \lambda_{21} \qquad \beta_3 = \lambda_{32};$$

then the system (7.1) can be written as

(7.2)
$$\begin{aligned}
\frac{du_1}{dt} &= u_1(\beta_1 u_3 - \beta_2 u_2) \\
\frac{du_2}{dt} &= u_2(\beta_2 u_1 - \beta_3 u_3) \\
\frac{du_3}{dt} &= u_3(\beta_3 u_2 - \beta_1 u_1)
\end{aligned}$$

If for example we take $\beta_1 = 0.3$, $\beta_2 = 0.7$, and $\beta_3 = 1.0$ then the ODE behaves as indicated in Figure 7.1. There is a family of periodic orbits around the fixed point $(0.5, 0.15, 0.35)$.

To show that in general we get pictures similar to the concrete example, we begin by dividing each equation by the product of the betas that appear in it to conclude that any fixed point ρ has

$$\frac{\rho_3}{\beta_2} = \frac{\rho_2}{\beta_1} = \frac{\rho_1}{\beta_3}$$

Recalling that the equilibrium densities must sum to one, we conclude that

$$\rho_1 = \frac{\beta_3}{\beta_1 + \beta_2 + \beta_3} \qquad \rho_2 = \frac{\beta_1}{\beta_1 + \beta_2 + \beta_3} \qquad \rho_3 = \frac{\beta_2}{\beta_1 + \beta_2 + \beta_3}$$

To see that there is a family of periodic orbits surrounding the fixed point we write $H(u) = \sum_i \rho_i \log u_i$ and note that

$$\begin{aligned}
\frac{\partial H}{\partial t} &= \sum_i \frac{\rho_i}{u_i} \frac{du_i}{dt} \\
&= c\left(\frac{u_3}{\beta_2} - \frac{u_2}{\beta_1}\right) + c\left(\frac{u_1}{\beta_3} - \frac{u_3}{\beta_2}\right) + c\left(\frac{u_2}{\beta_1} - \frac{u_1}{\beta_3}\right) = 0,
\end{aligned}$$

where $c = \beta_1\beta_2\beta_3/(\beta_1 + \beta_2 + \beta_3)$. Thus H is constant along solutions of the ODE.

The situation described above is similar to that of May and Leonard (1975) and Gilpin (1975) who considered a system in which there were invariant sets of the form $\sum_i \log u_i = K$. Gilpin (1975) observed that the "system is neutrally stable on the plane $u_1 + u_2 + u_3 = 1$, therefore stochastic effects (environmental noise) will cause it to decay to a single species system." This conclusion does not apply to the stochastic spatial model. Well separated regions oscillate out of phase, and the result is a stable equilibrium density for each of the three types.

Figure 7.2 gives the percentage of sites occupied by species 1 for the first 500 units of time when we look at the system in windows of size 30×30

or 120 × 120, or average over the whole 480 × 480 system (which again has periodic boundary conditions). Note that in the smallest viewing window, the densities fluctuate wildly; but when the averages are taken over the largest length scale, the oscillations are confined to the initial period when the system is converging to equilibrium.

Between the two extremes mentioned in the last paragraph is a moderate length scale that physicists would call the correlation length. This is the "most interesting" scale on which to view the system. Densities computed in boxes with sides of the correlation length vary smoothly in time, but undergo substantial changes. As we mentioned earlier, Rand and Wilson (1995), and Keeling et al. (1997) have considered the problem of precisely defining this length scale in terms of the variance of box averages. Pascual and Levin (1998) have recently taken a different approach by identifying the length scale at which to aggregate to achieve a maximum amount of determinism in the evolution of the local densities.

Example 7.2. Hawks-Doves. Our next model is a spatial version of Maynard Smith's (1982) evolutionary games. Our formulation follows Brown and Hansell (1987). Others have studied this system using cellular automata: Nowak and May (1992), (1993), Hubermann and Glance (1993), Nowak, Bonhoeffer, and May (1994), and May (1994), (1995).

In our model (and most of the others that have been considered), there are two types of individuals, called Hawks and Doves, whose interaction is described by a game matrix. The three examples we will be interested in are given by:

#1	H	D		#2	H	D		#3	H	D
H	.4	.8		H	.7	.4		H	−.6	.9
D	.6	.3		D	.4	.8		D	−.9	.7

Finally we list the general case, which serves to define notation we will use

	H	D
H	a	b
D	c	d

To explain the general game matrix we note that 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 $ap+b(1-p)$.

We interpret $ap + b(1 - p)$, which may be positive or negative (see e.g., game #3), as the net birth rate of hawks in this situation.

Once we have decided on a game matrix then following Brown and Hansell (1987), we can let $\eta_t(x)$ and $\zeta_t(x)$ be the number of hawks and doves at x at time t and formulate the dynamics as follows:

(i) *migration*. Each individual changes its spatial location at rate ν 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 $x + (1,0)$, $x - (1,0)$, $x + (0,1)$, $x - (0,1)$ 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 $\mathcal{N} = \{z \in \mathbf{Z}^2 : |z_1|, |z_2| \leq 2\}$ be a 5×5 square centered at (0,0). Let

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

be the number of hawks and doves in the interaction neighborhood of x at time t, and let

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

be 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 $cp_t(x) + d(1 - p_t(x))$.

If we assume that all sites remain independent then we arrive at the following mean field ODE for the densities of hawks (u) and doves (v):

$$(7.3) \qquad \begin{aligned} \frac{du}{dt} &= u\left\{a\frac{u}{u+v} + b\frac{v}{u+v} - \kappa(u+v)\right\} \\ \frac{dv}{dt} &= v\left\{c\frac{u}{u+v} + d\frac{v}{u+v} - \kappa(u+v)\right\} \end{aligned}$$

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 since $u/(u + v) + v/(u + v) = 1$.

The Hawks and Doves model quite naturally divides itself into three cases, which were our original motivation for formulating the three cases announced in the introduction. To motivate the division into cases, we change variables

$p = u/(u + v)$, $s = u + v$ in the dynamical system to get

(7.4)
$$\frac{dp}{dt} = (a - b - c + d)p(1 - p)(p - p_0)$$
$$\frac{ds}{dt} = s\{\alpha p^2 + \beta p + \gamma\} - \kappa s^2$$

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, $a \geq c$ and $b \geq d$, then $p_0 \geq 1$ or $p_0 \leq 0$ (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

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

When $p_0 \in (0, 1)$, it may be (Case 1) an attracting or (Case 2) a repelling fixed point. Matrices #1 and #2 above are examples of Case 1 and Case 2 respectively. Since we have discussed these situations at length, we turn now to the case in which $p_0 = 1$, i.e., the hawk strategy always dominates the dove strategy. If $a > 0$ the system is boring since the hawks will take over the world. However if $a < 0$ and $d > 0$, as in matrix #3, things are quite interesting.

This case is often called Prisoner's Dilemma after the two person non-zero sum game in which two individuals have a choice to cooperate (C) or defect (D). The payoffs to the first and second player for their actions are given as follows:

	C	D
C	(R, R)	(S, T)
D	(T, S)	(P, P)

Here $T > R > P > S$ so the defector strategy dominates cooperation, but double defection leads to less happiness than cooperation of each player. See Luce and Raiffa (1957) or Owen (1968).

It is easy to see that in Case 3, the ODE dies out. Figure 7.3 gives a picture of the ODE for matrix #3. From the picture it should be clear that the fraction of individuals that are hawks increases in time. This observation leads easily to:

Theorem 7.2. *If the initial condition for the dynamical system has $u(0) > 0$ then $(u(t), v(t)) \to (0,0)$.*

Proof. From (7.4) it follows that $p(t) = u(t)/(u(t) + v(t))$ converges to 1 as $t \to \infty$. Once $p(t)$ gets close enough to 1, both growth rates are negative and the populations decay to 0 exponentially fast. □

In contrast, the hawks and doves coexist in the our stochastic spatial model. 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 7.4 gives a graph of the density of hawks and doves vs. time for a simulation on a 50×50 grid, while Figure 7.5 shows the same statistics for a 150×150 grid. As the system size increases 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.

Example 7.3. Epidemics with regrowth of susceptibles. In this model the states are $0 =$ susceptible, $1 =$ infected, and $2 =$ removed. Writing f_i for the fraction of the four nearest neighbors in state i we can write the rates as

$$0 \to 1 \quad \beta_1 f_1 \qquad 1 \to 2 \quad \delta \qquad 2 \to 0 \quad \alpha$$

Durrett and Neuhauser (1991) have shown that if the epidemic without regrowth (i.e., when $\alpha = 0$) does not die out, then whenever $\alpha > 0$ there is a nontrivial translation invariant stationary distribution.

If α is small and we make the correspondence: infecteds = Hawks, suceptibles = Doves, and removed = vacant, then the behavior of the model (when viewed in windows of size $1/\alpha$) is much like the Hawks-Doves system.

(i) Epidemics sweep through the system wiping out most susceptibles,

(ii) When susceptibles are scarce, the epidemic becomes subcritical and the density of infecteds then drops to a low level.

(iii) When infecteds are scarce, susceptibles increase. When the density of susceptibles is large enough, one of the few surviving infecteds starts another epidemic.

For simulation results on this phenomenon, see Durrett (1995c). The conference proceedings, Mollison (1995), in which that paper appears is an excellent source for information on all sorts of epidemic models.

Example 7.4. WATOR. The name is short for WAter TORus, a system considered in A.K. Dewdney's Computer Recreations column in Scientific American in December 1984. Each site can be in state 0 = vacant, 1 = occupied by a prey (fish), or 2 = occupied by a predator (shark). The original model was defined in discrete time, but we reformulate it in continuous time as follows:

(i) Fish are born at vacant sites at rate β_1 times the fraction of neighbors occupied by fish.

(ii) Each shark at rate 1 inspects q neighboring sites, chosen without replacement from the neighbor set. It moves to the first fish it finds and eats it. A shark that has just eaten gives birth with probability β_2. A shark that finds no fish dies with probability δ.

(iii) There is *stirring* (also called *swimming*) at rate ν: for each pair of nearest neighbor sites x and y we exchange the values at x and at y at rate ν.

The stirring mechanism automatically preserves the restriction of at most one individual per site and has the mathematical advantage that the trajectory of any single particle is just a continuous time random walk. Of course, if one watches the movements of two particles there is a (very small) correlation

between their locations due to the occasional stirring steps that affect both particles at the same time.

Letting $u_i(t)$ be the fraction of sites in state i at time t, and computing the rate of change by supposing that adjacent sites are always independent we see that the mean field ODE in this case is:

$$(7.4) \qquad \begin{aligned} du_1/dt &= \beta_1 u_1(1 - u_1 - u_2) - u_2\{1 - (1 - u_1)^q\} \\ du_2/dt &= \beta_2 u_2\{1 - (1 - u_1)^q\} - \delta u_2(1 - u_1)^q \end{aligned}$$

Here, the first term on the right represents the birth of fish onto vacant sites. To explain the second and third terms, we note that $u_2\{1 - (1 - u_1)^q\}$ gives the fraction of sites occupied by sharks times the probability a given shark will find at least one fish when it inspects q neighbors, so β_2 times this gives the rate at which new sharks are produced. For similar reasons the fourth term represents the sharks who find no fish to eat, got a bad coin flip, and were told to die.

To begin to understand the ODE we note that in the absence of fish, sharks can't breed and their density drops to 0. Conversely, in the absence of sharks, fish don't die and will fill up the space. The last two results give the direction of motion of the ODE on two sides of the right triangle that we use for the possible states of the system: $\Gamma = \{(u_1, u_2) : u_1, u_2 \geq 0, u_1 + u_2 \leq 1\}$.

Since fish do not die in the absence of sharks, there is a boundary equilibrium at $(1,0)$. Considering the second equation in (7.4) and setting $u_1 = 1 - \epsilon_1$ and $u_2 = \epsilon_2$ where the ϵ_i are small shows that $(1,0)$ is always a saddle point. This behavior suggests the presence of a fixed point $(\bar{u}_1, \bar{u}_2)$ with both components positive, a fact which can easily be confirmed by algebraic manipulation. To do this neatly, and to pave the way for later calculations, we will first rewrite the system in (7.4) as

$$(7.5) \qquad \begin{aligned} du_1/dt &= A(u_1) - u_2 B(u_1) \\ du_2/dt &= u_2 C(u_1) \end{aligned}$$

where $A(u_1) = \beta_1 u_1(1 - u_1)$,

$$B(u_1) = \beta_1 u_1 + \{1 - (1 - u_1)^q\}$$

and $C(u_1) = \beta_2 - (\beta_2 + \delta)(1 - u_1)^q$. In order for $du_2/dt = 0$ we must have

$$(7.6) \qquad C(\bar{u}_1) = 0 \qquad \text{or} \qquad \bar{u}_1 = 1 - \left(\frac{\beta_2}{\beta_2 + \delta}\right)^{1/q}$$

Having found $\bar{u}_1$ we can now set $du_1/dt = 0$ to find

$$(7.7) \qquad\qquad \bar{u}_2 = A(\bar{u}_1)/B(\bar{u}_1)$$

To investigate the nature of the fixed point at $(\bar{u}_1, \bar{u}_2)$ we let $v_i = u_i - \bar{u}_i$ be the displacement from it in the ith component. Assuming the v_i are small and using (7.6) and (7.7) we arrive at the linearized equation

$$(7.8) \qquad\qquad \begin{aligned} dv_1/dt &= Fv_1 + Gv_2 \\ dv_2/dt &= Hv_1 \end{aligned}$$

where $F = A'(\bar{u}_1) - \bar{u}_2 B'(\bar{u}_1)$, $G = -B(\bar{u}_1)$, and $H = u_2 C'(\bar{u}_1)$. This ODE is analyzed in the Appendix of Durrett and Levin (1998) with the following result.

Theorem 7.4. *The interior fixed point is always locally attracting when $q \leq 3$. Conversely, if $q > 3$ and the values of β_2 and δ are held constant, decreasing β_1 leads to a Hopf bifurcation that produces a limit cycle.*

Figure 7.5 gives a picture of a case of the ODE with a limit cycle: $\beta_1 = 1/3$ $\beta_2 = 0.1$, $\delta = 1$, and $q = 4$.

To make connections between our model and reaction diffusion equations, we use Theorems 5.1 and 5.2 to conclude that if we let the stirring rate $\nu \to \infty$ and consider our process on a scaled version of the square lattice in which the spacing between sites is reduced to $\nu^{-1/2}$ then the densities of fish and sharks converge to the solution of the partial differential equation:

$$(7.9) \qquad\qquad \begin{aligned} \partial u_1/\partial t &= \Delta u_1 + g_1(u_1, u_2) \\ \partial u_2/\partial t &= \Delta u_2 + g_2(u_1, u_2) \end{aligned}$$

where the g_i are the right-hand sides of the equations in (7.4).

The next result, proved in Durrett and Levin (1998), says that sharks and fish coexist in the reaction-diffusion equation.

Theorem 7.5. *Suppose that the initial conditions $u_i(x, 0)$ are continuous, always in the set Γ of sensible values, and each u_i is not identically 0. Then there are positive constants ρ, ϵ_1 and ϵ_2 so that for large t, $u_i(x, t) \geq \epsilon_i$ whenever $|x| \leq \rho t$.*

In words, the densities stay bounded away from zero on a linearly growing set. Using methods of Durrett (1993), and Durrett and Neuhauser (1994), it is not hard to convert Theorem 2 into a conclusion about the particle system. See also Sections 4 and 8 of Durrett (1995), or the more recent work of Shah (1997).

Theorem 7.6. *When the stirring rate is large there is coexistence, i.e., there is a stationary distribution for the particle system that concentrates on configurations with infinitely many sites in each of the possible states.*

Simulations. The last result proves the existence of the stationary distribution but does not yield much information about its spatial structure. To understand that, we turn to simulation. Immediately, however, we run into the difficulty that while fast stirring is convenient for making connections with reaction-diffusion equations, it is painful to implement on the computer, since most of the computational effort is spent moving the particles around.

   To find a variant of the WATOR model that we can more easily simulate, we note that at any moment when a fish or shark at x inspects its neighbors, it sees a set of sites that have been subject to stirring at rate ν since the previous time site x decided to try to change. Since the flip rates stay constant as $\nu \to \infty$ this time is of order 1, and the neighbors will move a distance of order $\nu^{1/2}$. With this mind, we will replace stirring by choose our neighbors at random (with replacement) from a square of radius $r = \nu^{1/2}$ centered at the point of interest.

   Figures 7.7 and 7.8 show results of computer simulations when $r = 5$, i.e., neighbors are chosen at random from an 11×11 square centered at the point. Note that densities oscillate wildly when measured in a 50×50 window but are much smoother in time in a 200×200 window.

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