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17

Wave Patterns in Spatial Games and the Evolution of Cooperation

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17.1 Introduction

Our understanding of the evolution of animal behavior has been greatly enhanced by the use of game theory (Maynard Smith 1982). Classical games assume that a given individual is equally likely to interact with any other member of the population and that the success of any individual depends on the frequency of all other strategies represented in the population. Yet natural environments possess a spatial dimension: individuals have limited mobility and interact locally with their neighbors. Only recently have attempts been made to incorporate this important property into the study of evolutionary games. Different approaches have been followed: numerical simulations of "games on grids" (Nowak and May 1992; Lindgren and Nordahl 1994; see Chapter 8); analytical study of correlation equations for games on lattices (Nakamaru *et al.* 1997; see Chapter 13); and analytical study of "replicator–diffusion" equations (e.g., Vickers 1989; Vickers *et al.* 1993; Ferrière and Michod 1995, 1996; see Chapter 22). In this chapter we restrict ourselves to the last of these methodologies and provide an introduction to its mathematical underpinnings and biological applications. Elements of a general theory of replicator–diffusion equations are expounded in detail in articles by Vickers (1989), Hutson and Vickers (1992), Vickers *et al.* (1993), and Cressman and Vickers (1997). We present an overview of these important results in Section 17.2. Sections 17.3 and 17.4 show how replicator–diffusion models can be used to study spatial versions of the iterated Prisoner's Dilemma game, a well-known metaphor for evolution toward cooperation between genetically unrelated individuals (Trivers 1971; Axelrod and Hamilton 1981; Maynard Smith 1982; Hofbauer and Sigmund 1998).

17.2 Invasion in Time- and Space-continuous Games

When considering the adaptive dynamics of long-term evolution, the crucial question is whether a mutant phenotype can invade resident phenotypes (Metz *et al.* 1992; Diekmann *et al.* 1996; Geritz *et al.* 1997; Dieckmann 1997). Obviously, the very nature of an invasion event requires individual mobility, while the game theoretical context requires interactions between individuals that share the same neighborhood. This creates the need for deriving invasibility criteria that explicitly account for spatial effects in the dynamics of mutant invasion. Much of the theory of invasion in time- and space-continuous games is relatively new. This section presents the basic ideas needed for subsequent applications and points to some unsolved questions.

Replicator–diffusion equations

Hereafter, the payoff matrix of a game is denoted by A. We set $A = \left[a_{ij}\right]$, where a_{ij} is the payoff to an individual who plays strategy i against an opponent who plays j. Let Q be a probability vector composed of q_i denoting the proportion of individuals who play strategy i. Taylor and Jonker (1978) have suggested incorporating continuous time into the dynamics of games using so-called replicator equations

$$\frac{dq_i}{dt} = q_i \left[(AQ)_i - Q^T AQ\right] \qquad (1 \le i \le k) \ , \tag{17.1}$$

where k is the number of strategies, $(AQ)_i$ denotes the ith coordinate of vector AQ, and the exponent T indicates vector transpose. This model stems from the idea that the growth rate of a strategy is equal to its absolute payoff $(AQ)_i$. Hence the abundance of strategy i is described by unlimited exponential growth, according to the equation $dn_i/dt = [(AQ)_i]n_i$. One can then write q_i as n_i divided by the total population density (i.e., the sum of the densities of all strategies) and use the latter equation to recover Equations (17.1). The replicator equation expresses the fact that the change in any strategy's frequency is determined by the population growth rate of that strategy compared with the average population growth rate, that is, the average payoff $Q^T AQ$. Equations (17.1) are important because there is a relationship between the stable equilibrium points of Equations (17.1) and the game's evolutionarily stable strategies, or ESSs (Zeeman 1980; Hofbauer and Sigmund 1998). [We recall that an ESS is a strategy that, when common in the population, cannot be invaded by any small group of individuals playing a different strategy; see, e.g., Maynard Smith (1982).]

The inclusion of continuous space is not so straightforward. If all individuals move at the same rate, we are on a well-worn trail (see Hadeler 1981). But it is quite reasonable to expect that the dispersal rate is affected by, or indeed part of, the strategy chosen. Using the standard diffusion approximation of a random walk (see Chapter 22), Vickers (1989) introduced the following "replicator–diffusion equations":

$$\frac{\partial n_i}{\partial t} = n_i \left(\frac{(AN)_i}{m} - \frac{N^T AN}{m^2} \right) + \mu_i \frac{\partial^2 n_i}{\partial x^2} \qquad (1 \le i \le s) \ , \qquad (17.2)$$

where each strategy is characterized by its own diffusion (or mobility) rate μ_i. Here, $n_i(x, t)$ is the density of the i-strategists at location x and time t and $m(x, t)$ is the total density at x and t ($m = n_1 + n_2 + \cdots + n_s$). For simplicity, we drop the x and t variables in the equations when there is no ambiguity.

Like the replicator equations, this model assumes that an individual playing strategy i and located at x at time t receives the a_{ij} payoff if it interacts with a neighbor playing strategy j, which occurs with a probability approximated by the frequency n_i/m of j-players at x and t. A bookkeeping of the payoff contributions to strategy i from all different j strategies yields the first part of the growth rate of strategy i [the bracketed term in Equations (17.2)]. In addition there is a regulatory, negative term that accounts for the fact that local densities stay bounded. This regulatory term takes the form of a discount precisely equal to the average payoff earned at location x at time t (which is calculated by summing over i the average payoff to strategy i weighted by its frequency n_i/m at location x and time t). It must be stressed that this discounting term is a very special one, chosen only for mathematical convenience. No particular physiological or behavioral mechanism is known that lets individuals adapt their per capita birth and death rates to local circumstances so as to keep the local population averages of these quantities exactly zero at all times. Cressman and his coworkers (see Cressman and Dash 1987; Cressman and Vickers 1997) have elaborated on this issue by assuming that an individual's fitness is composed of its payoff in the contest with other strategies together with a background fitness that is common to all strategies. Their approach has the merit of relating the spatial dynamics of the game to individual life-history traits, but it is hampered by very demanding mathematics (Cressman and Vickers 1997). In Section 17.3, we take advantage of the great mathematical tractability of replicator–diffusion equations (17.2) to explore invasion issues in the context of spatial games between cooperative and selfish players.

Hutson and Vickers (1995; see also Chapter 22) have used the background fitness model of local population regulations to address the same problem. In Section 17.4 we see that their results are consistent with those obtained through the analysis of the simpler replicator–diffusion equations.

Replicator–diffusion equations form a distinct class of reaction–diffusion models because of their specific reaction term. Equations (17.2) assume that space is one-dimensional and reduces to an "x-axis." The formalism, however, straightforwardly carries over to higher dimensions (see Chapter 22 for a detailed account of the rationale of reaction–diffusion models). If the spatial domain is bounded, impermeable boundary conditions are imposed.

Invasibility and evolutionary stability

A few mathematical results are available to investigate the invasibility or evolutionary stability of a strategy in a spatial game described by replicator–diffusion equations. They all relate the dynamics of the spatial model given by Equations (17.2) to its nonspatial counterpart, Equations (17.1). Here, we state the mathematical theorems in a self-contained manner to make them unambiguously applicable to any particular model that falls under their scope. The spatial iterated Prisoner's Dilemma (IPD) offers an opportunity to operate this machinery, as we will see in Section 17.3.

Vickers (1989) provided the first stability analysis of the replicator–diffusion equations. He found that an *interior* ESS is so stable that it precludes any spatial dependence:

Proposition 17.1 If matrix A has an interior ESS, that is, an ESS for the replicator equations [Equations (17.1)] given by a frequency vector Q with all nonzero coordinates, then this ESS is also stable in the spatial game governed by Equations (17.2) for all choices of the diffusion coefficients μ_i.

The situation becomes much more complicated if there is no interior ESS in the homogeneous game. Hutson and Vickers (1992) addressed the case where there are only two strategies and each pure strategy is an ESS. In the absence of spatial effects each ESS is, by definition, stable. The inclusion of diffusion creates the possibility of a traveling wave that in effect replaces one ESS with the other. To state Hutson and Vickers' main theorem, we first recast the payoff matrix A as

$$A = \begin{bmatrix} \alpha & 0 \\ 0 & \beta \end{bmatrix} \tag{17.3}$$

by setting $\alpha = a_{11} - a_{21}$ and $\beta = a_{22} - a_{12}$, an operation that does not affect the dynamics. To ensure that each pure strategy is an ESS, $\alpha > 0$ and $\beta > 0$. Hutson and Vickers (1992) investigated the invasion of a region dominated by one strategy – for example, for $x > 0$ strategy 1 is played by almost all individuals and for $x < 0$ strategy 2 is prevalent.

Proposition 17.2 Assume that A has the form (17.3) with $\alpha > 0$ and $\beta > 0$. There then exists a function F such that, if

$$\frac{\beta}{\alpha} > F\left(\frac{\mu_1}{\mu_2}\right) , \tag{17.4}$$

a traveling wave front with positive speed (i.e., moving from $x = -\infty$ to $x = \infty$ along the spatial axis) will connect the two homogeneous pure population equilibria. The function F is well approximated over the range 0.05–20 by $F(u) \approx u^{-0.61}$.

The following statements explain the importance of Proposition 17.2 for analyzing applications.

- Proposition 17.2 states that if inequality (17.4) is satisfied, then a traveling wave replaces a pure strategy-1 population with a pure strategy-2 population. If the inequality is reversed, the sign of the wave speed becomes negative and strategy 2 replaces strategy 1 in a traveling wave. There is virtually no room for coexistence, except perhaps in the atypical boundary case $\beta/\alpha = F(\mu_1/\mu_2)$. Thus, in a generic two-strategy game where both strategies are ESSs, a traveling wave necessarily exists and replaces one strategy with the other.
- If the payoffs α and β are not influenced by the mobility rates μ_1 and μ_2, condition (17.4) asserts that the dominating strategy must have large payoffs and small diffusion rates. (In the IPD, however, the payoffs do depend on the mobility rates.)
- There is strong numerical evidence to support the claim that the propagation of a traveling wave replacing strategy 1 with strategy 2 is strictly equivalent to the growth of a localized clump of individuals playing strategy 2 amid a "sea" of players using strategy 1. Accepting this conjecture, inequality (17.4) reads as a criterion of invasibility.

While Proposition 17.1 assumes that the replicator equation admits a stable solution corresponding to an interior (mixed) ESS, Proposition 17.2 addresses the case where the (ESS) equilibria associated with each pure strategy are the only ones. Vickers *et al.* (1993) have shed some light on the case where the replicator equation admits an internal stable equilibrium which is not an ESS. This is an interesting case because, in the spatial context, it may lead to the formation of patterns.

Let $\hat{Q}$ be an internal, stable solution to the replicator equation. Assuming that $\hat{Q}$ is not an ESS means that it is invadible, and the simplest situation here arises when $\hat{Q}$ can be invaded by a pure strategy (say, strategy 1). Vickers *et al.* (1993) proved the following theorem.

Proposition 17.3 If strategy 1 can invade $\hat{Q}$, that is, $a_{11} > (\hat{Q}^T A)_1$, then there exists a combination of mobility rates μ_i $(1 \leq i \leq k)$ such that $\hat{Q}$ is not spatially stable.

This statement is important in light of Turing's (1952) well-known idea that spatial patterns are often associated with equilibria which are stable in the nonspatial system (i.e., without diffusion) and unstable with respect to spatially heterogeneous perturbations. This phenomenon is the so-called Turing instability (see Chapter 22). In the framework of replicator–diffusion equations, Vickers *et al.* (1993) have raised three important points.

- A bifurcation analysis shows that this pattern-formation mechanism is operative in spatial games under the conditions of Proposition 17.3.
- There must be at least three pure strategies in the game for Proposition 17.3 to apply.
- A converse of Proposition 17.3 holds when there are exactly three strategies. If $\hat{Q}$ resists invasion by any pure strategy, then it is spatially stable and no spatial pattern can be produced.

Patterns arising from the Turing instability vary in space but are constant in time. Yet variations in space and time are essential features of the dynamics of ecological systems. Vickers *et al.* (1993) have provided a numerical example of a three-strategy game that exhibits another kind of instability (namely, a Hopf bifurcation) that results in spatial patterns which are periodic in time. It should be noted that a general theory of the bifurcations of the three-strategy game is still pending.

17.3 Invasion of *Tit For Tat* in Games with Time-limited Memory

In Chapter 8 of this volume, Nowak and Sigmund expound on the basics of the IPD game. Here, we refer to concepts and notations introduced by these authors. Investigating the relative invasibility of well-known strategies like the cooperative *Tit For Tat* (*TFT*) strategy and the selfish *Always Defect* (*AD*) strategy serves to demonstrate some of the mathematical techniques introduced in the previous section.

The spatial struggle of *Tit For Tat* and *Always Defect*

The IPD has proved tremendously fruitful as a paradigm for studying the evolution of cooperation. Game theorists originally identified the *TFT* strategy as the most robust and stable strategy in the IPD (Axelrod and Hamilton 1981). Subsequent theoretical developments (Nowak and Sigmund 1992, 1993) emphasized that the *TFT* strategy could be the first step toward cooperation in a world of unconditional defectors playing *AD*. To explain the emergence of cooperation, it is therefore crucial to understand how *TFT* can gain a foothold in a population dominated by *AD*.

A major problem concerning the nonspatial IPD is that it fails to convincingly settle this issue. Depending on the probability w of continuing the game, either *AD* is the only ESS, hence *TFT* has no chance to invade, or both *AD* and *TFT* are ESSs (which happens when w is sufficiently large), implying that *TFT* can invade an established *AD* population only if the *TFT* frequency exceeds a certain threshold. Because the nonspatial IPD assumes an infinite population, this result means that an initially finite group of *TFT* newcomers will never spread. It has long been claimed that small clusters of finite size should still have a chance of spreading, because cooperators within a cluster experience a high probability of interacting with each other. To weigh this claim, one might compare the average payoff earned by a *TFT* within the cluster with the *AD* payoff averaged over the whole population. In doing so, however, one would overlook *TFT*–*AD* interactions which locally influence the payoff to *AD* players in the vicinity of the cooperative focus – a local payoff likely to be of critical importance to determining the eventual fate of the *TFT* population. Numerical examples (Nowak and May 1992, 1993) based on cellular automata demonstrate that local interactions have a significant effect on the outcome of the game between cooperators and defectors. For this reason, there has been much interest in setting up versions of the IPD that specifically account for spatial dynamics and local contests.

A replicator–diffusion model

We now assume that *TFT* and *AD* players are free to move. We wish to describe the game using a replicator–diffusion equation. This amounts to writing down the payoff matrix A taking into account the organisms' mobility and other individual traits (mortality and interaction time). In the nonspatial game, the parameters are the payoffs S, P, R, T (see Chapter 8), and the probability w that two particular interacting individuals continue their interaction in the next round of the game. In the spatial version of the game, that probability w is influenced by the individuals' traits (including the mobility rates), and some work is required to make this relationship explicit.

Microscopic description of interactions. We first describe an individual-based model of the population. We assume that each individual in the population occupies a position in space that is a function of time. The population is distributed along a one-dimensional axis: it can be thought of as spread along a coastline or a river bank; or if the environment is really two-dimensional, variations in the strategy mix may occur in one direction only. For the purpose of defining local interactions, we regard space as being divided into discrete contiguous cells of length Δl so that each cell contains two individuals at any time. Interactions are initiated between two individuals located in the same cell. Thus Δl defines the "interaction length," which we assume to be constant across space. Each interaction lasts Δt units of time, which we define as the "interaction time" of the game. Interactions occur consecutively, without any "rest time" in between.

The payoffs S, P, R, and T determine the per capita reproductive rate. Thus if the payoff is S, for example, to each individual of a group of size n, then their numbers increase at a rate Sn in the absence of all other effects. We assume that interactions have no direct effect on individual mortality. Let us consider a *TFT* player within a given cell, and let p_T and p_D be the probabilities that the partner is a *TFT* or an *AD* player, respectively. Then the reproductive success of the nominal *TFT* player during the small time interval Δt is

- $R\Delta t$ if the co-player is a *TFT*, which occurs with probability p;
- $P\Delta t$ if the co-player is a defector already encountered on the previous interaction, which occurs with probability $p_D w$;
- $T\Delta t$ if the co-player is a defector not encountered on the previous interaction, which occurs with probability $p_D(1 - w)$.

Here w denotes the probability that the same two individuals located in a given cell at time t were also sharing a cell at time $t - \Delta t$.

From microscopic interactions to macroscopic dynamics. Mobility is modeled by a random walk, and we make the classical diffusion approximation. Thus we define mobility (or diffusion) rates for *TFT* and *AD* players, denoted by μ_T and μ_D, respectively. Then the derivation of w is straightforward (see Ferrière and Michod 1996, for details) and yields

$$w = \left[4\sqrt{\pi}\sqrt{(\mu_T + \mu_D)\Delta t}\right]^{-1} \times \iint_{u,v\in[-\Delta l/2,\Delta l/2]} \exp\left[-\frac{(u-v)^2}{4(\mu_T + \mu_D)\Delta t}\right] du\, dv \ . \tag{17.5}$$

For small cell length Δl, the following approximation holds [Equation (7) in Ferrière and Michod 1996]:

$$w \approx \frac{2}{\sqrt{\pi}} \frac{\Delta l}{\sqrt{\Delta t}} \frac{\mu_T \mu_D}{(\mu_T + \mu_D)^{5/2}} \ . \tag{17.6}$$

We derive a replicator–diffusion model of the population dynamics by letting Δl go to zero and rescaling time appropriately, such that $\Delta l/\sqrt{\Delta t}$ approaches a positive constant υ:

$$\frac{\Delta l}{\sqrt{\Delta t}} \to \upsilon \neq 0 \ . \tag{17.7}$$

Now we can define the densities of *TFT* and *AD* as continuous functions of space and time, denoted by $n_T(x,t)$ and $n_D(x,t)$. Let m be the total density $n_T + n_D$. We have $p_T = n_T/m$, $p_D = n_D/m$; thus, the *TFT* reproductive rate is

$$\frac{n_T}{m} R + \frac{n_D}{m} [wP + (1-w)S] \ . \tag{17.8}$$

Likewise, the *AD* reproductive rate is

$$\frac{n_D}{m} P + \frac{n_T}{m} [wP + (1-w)T] \ . \tag{17.9}$$

The payoff matrix of the replicator–diffusion game equations (17.2) follows readily:

$$A = \begin{bmatrix} R & wP + (1-w)S \\ wP + (1-w)T & P \end{bmatrix} , \tag{17.10}$$

with w given by

$$w = \frac{2\upsilon}{\sqrt{\pi}} \frac{\mu_T \mu_D}{(\mu_T + \mu_D)^{5/2}} \ . \tag{17.11}$$

Notice that for consistency with the assumption made above – that the interaction length is constant across space – the total density should vary very slowly in time and smoothly across space. Using numerical integration of Equation (17.2) with A given by Equations (17.10) and (17.11), we have found this requirement to be fulfilled when μ_T and μ_D were not vastly different.

A spatial version of Hamilton's rule

To analyze the replicator–diffusion model of the IPD by means of the theory developed in Section 17.2, we must first consider the nonspatial version of the system and investigate its equilibria. With this aim in view, it is convenient to introduce a cost–benefit parameterization of the IPD payoffs (Brown *et al.* 1982). Assume that a cooperator exhibits some behavior that benefits the fitness of its partner, the recipient, by an amount b which is larger than 0. The benefit is independent of the recipient's behavior. By providing its partner with the benefit b, the cooperator incurs a cost $-c$, $c > 0$. Again, this cost is independent of the recipient's behavior. If the effects on fitnesses are additive, with a baseline value taken to be 1, one obtains the following parameterization: $T = 1 + b$, $R = 1 + b - c$, $P = 1$, $S = 1 - c$.

Using this parameterization, we see that the replicator equation of the game admits two stable equilibria (corresponding to each pure strategy) whenever

$$w \geq \frac{c}{b} \ , \tag{17.12}$$

which is the condition found by Brown *et al.* (1982) for *TFT* and *AD* to simultaneously be ESSs in the standard, nonspatial game. Then Proposition 17.2 asserts that there exists a traveling wave replacing *AD* with *TFT* if

$$\frac{w}{1 + (1 - w)F(\mu_T/\mu_D)} > \frac{c}{b} \ . \tag{17.13}$$

This inequality provides a Hamilton rule (Hamilton 1964) for the increase of cooperation in a nonsocial, spatial environment. The left-hand side (hereafter denoted by H) generalizes the coefficient of reciprocation defined for the nonspatial IPD (Brown *et al.* 1982), which gives the probability that an individual's cooperative act is returned via reciprocation from other *TFT*. The right-hand side of the inequality is the cost–benefit ratio of cooperation. This spatial Hamilton rule can be further extended to include a cost to mobility (Ferrière and Michod 1996).

Inequality (17.13) defines a set of mobility rates μ_T and μ_D that cause an invasion of defectors *AD* by *TFT*: a traveling wave replaces *AD* with *TFT*. All other parameters being fixed, this set is delineated by the c/b isoclines drawn on the surface $H(\mu_T, \mu_D)$ (see Figure 17.1). [Notice that if a pair μ_T, μ_D satisfies inequality (17.13), then it automatically meets inequality (17.12).] We find that a range of mobility rates exists for which

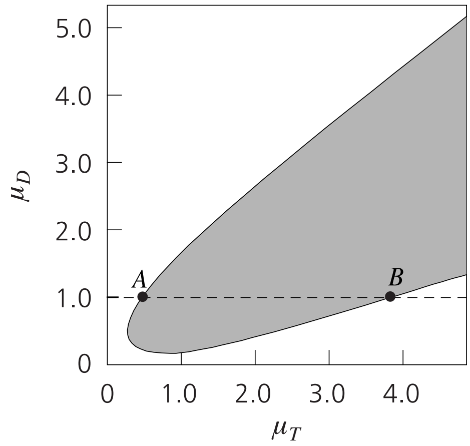

Figure 17.1 Mobility rates leading to an invasion of an established *AD* population by a wave of *TFT* players. The model assumes time-limited memory and is given by the system of replicator–diffusion equations (17.2). The payoff matrix A is specified by Equations (17.10) and (17.11) with $\upsilon = 1$. The shaded area contains all pairs of mobility rates μ_T, μ_D such that the coefficient of reciprocation $H(\mu_T, \mu_D)$ is larger than the cost–benefit ratio c/b (fixed at 0.22). For given defectors' mobility μ_D larger than a minimum value ($\approx$0.11) – for example, $\mu_D = 1.0$ (dashed line) – there is an interval (A, B) of μ_T mobility rates over which a *TFT* invading wave displaces a resident *AD* population.

TFT can invade provided that *AD* mobility exceeds a minimum threshold. In general, this range includes the mobility rate of resident defectors, μ_D, but it is skewed around μ_D so that *TFT* players may be much more mobile than defectors and yet successfully displace them.

As a consequence of the particular form taken by the function F in Equation (17.13) [$F(u) \approx u^{-0.61}$, see Proposition 17.2], a condition for the invasion by rare *AD*s of a *TFT* population is obtained by reversing inequality (17.13). (Note that the particular form of F is only an approximation. Dealing with the exact function would call for further investigation.) This condition determines the stability of *TFT* once established. It turns out that *TFT* is jeopardized by *AD* endowed with either high or very low mobility (see Figure 17.1). Also, *TFT* is immune to invasion for a much wider range of *AD* mobility rates when its own rate of mobility increases. Thus, by moving at higher rates, cooperators find more efficient protection against reinvasion by *AD*.

Why mobility can favor *Tit For Tat*

To answer this question and to give some intuitive understanding of the above results, Ferrière and Michod (1995) have developed an auxiliary model focusing on the stochastic motion of the players. Heuristically, the growth of an initially small cluster relies on two conditions: first, that the cluster can spread outward from the edge, and, second, that its core is not destroyed by *AD* intruders (Axelrod 1981; Eshel and Cavalli-Sforza 1982; Wilson *et al.* 1992). The first condition is ensured whenever *TFT*s can make safe moves toward the front of the invasion, that is, whenever *TFT* pioneers can avoid being suckered as they move outward. A *TFT* pioneering to the front of an invasion will not be suckered there if it can get assorted with another *TFT* also on a pioneering move or if it moves together with a known *AD* (in which case it will retaliate). The auxiliary model set up by Ferrière and Michod (1995) shows that both conditions are more likely to be met for high (but not too high) mobility in *TFT* and *AD*. Likewise, the second condition is met if a defector entering the core of a *TFT* cluster gets assorted there with another *AD* or if it undergoes retaliation by a *TFT* also moving back to the core. Again, the likelihood that either case will be realized is maximized at high *TFT* and *AD* mobility rates. To summarize, the following events are crucial for the emergence of *TFT* and are enhanced by significant mobility of the players: assortative meetings of *TFT*s at the front of an invasion or of *AD*s in the core of the cluster, and tracking of *AD*s by *TFT*s toward the front or toward the core.

17.4 Invasion of *Tit For Tat* in Games with Space-limited Memory

There are two important assumptions underlying the IPD replicator–diffusion equations investigated in the previous section. First, the memory is "space-extended" but "time-limited." That is, a player can recognize its opponent wherever they meet, but the player's memory is limited to the last round of the game. Second, the local density of each strategy is assumed to vary very slowly, in agreement with the assumption made in the microscopic description of the population that the spatial axis can be divided into contiguous cells of constant length, each cell containing two individuals. Hutson and Vickers (1995) have developed a different reaction–diffusion model of the spatial IPD where these assumptions have been modified or relaxed. In the Hutson–Vickers model, memory is not restricted to the last interaction but instead is space-limited: a player can remember any of its previous opponents provided that neither has moved out of the cell where they first met. Furthermore, a cell may now contain a variable number of players. The goal of this section is to present some important results drawn from their approach after examining structural differences between this model and the previous game-diffusion equations.

Model description

The Hutson–Vickers model is fully expounded in Chapter 22 (Section 22.2, A model for invasion of *Tit For Tat*). Here, we content ourselves with highlighting the specificities of this model.

- *Local interactions*. The spatial axis is still divided into contiguous cells of constant length l, but now each cell may contain many individuals. Opponents of any player in a given cell are drawn randomly within that cell.
- *Repeated interactions*. The Hutson–Vickers model relaxes the assumption that local population size varies on a slow time scale. Consequently, the probability w of players meeting is no longer a constant. In their model, Hutson and Vickers (1995) recast w into a dynamic "getting-to-know" function [denoted by $g(x, t)$] that gives the proportion of *AD* (or *TFT*) players within a cell that a typical *TFT* (or *AD*) player has already met. They further define $G = gn_T n_D$ as the number density of *TFT*–*AD* pairs within a cell that have already met.
- *Memory*. Memory is not limited to the last round. A *TFT* player recognizes an opponent on a second or subsequent occasion provided that neither has left the cell where the encounter occurred. This is in contrast with the game-diffusion model, where recognition may occur wherever the encounter takes place, but only on the next interaction.
- *Population regulation*. The per capita death rate is made density dependent. Therefore, it varies in space and time (but, as before, it is not influenced by the outcome of the game).

Main properties of the model

The analysis of the Hutson–Vickers model stems from ideas similar to those underlying Proposition 17.2. First, one has to determine the possible population equilibria assuming that player densities are spatially homogeneous. One may then turn to the effect of locally perturbing the stable equilibria, thereby mimicking the effect of an invasion attempt. When players have spatially homogeneous distributions, their densities and the getting-to-know function depend only on t. Then the model reduces to a system of ordinary differential equations [set $\partial^2 u/\partial x^2 = 0$ and $\partial^2 v/\partial x^2 = 0$ in Equations (22.17) and replace all partial derivatives with respect to t with ordinary derivatives in Equations (22.17) and (22.19) of Chapter 22]. Standard techniques of local stability analysis can now be used. The system turns out to have one of three simple structures:

1. There are stable equilibria with only *TFT*-players and only *AD*-players, and an unstable coexistence equilibrium.
2. There is a stable pure *AD* state and the only other equilibrium, that with just *TFT* players, is unstable.
3. In addition to the equilibria of structure (2), there are two coexistence states (one stable and one unstable) of *TFT* and *AD*.

The next step aims at determining whether a pure *TFT* state may evolve starting from initial conditions where *TFT* players are localized within an established *AD* population. This requires that the homogeneous *TFT* state must be stable, which actually happens with structure (1). Thus, we must deal with a situation similar to that handled by Proposition 17.2: two stable states and traveling waves that may "connect" them. However, the Hutson–Vickers model is not written as a system of replicator–diffusion equations (hence Proposition 17.2 does not apply), and a theoretical treatment presents rather formidable difficulties. A computational study suffices, however, to demonstrate the remarkable richness of the model's behavior. The most noteworthy point, as illustrated by the numerical example presented hereafter, is that large or small players' mobilities cannot be claimed to be unambiguously good or bad for the evolution of cooperation.

Existence of invading waves of *Tit For Tat*

In contrast with the case of replicator–diffusion models, no general theorem is available to guarantee the existence of traveling wave solutions to Hutson–Vickers equations. Yet numerical procedures do provide evidence that invasion dynamics develop wave patterns. As in Proposition 17.2, the sign of the wave speed determines whether the wave replaces *AD* with *TFT*, or *TFT* with *AD*. Figure 17.2 shows how for a specific set of parameter values the mobility rates influence the outcome of the game. To a certain extent, the results confirm those of the previous section. For small or large μ_T the cooperators are defeated, whereas for medium μ_T *TFT* successfully invades.

Hutson and Vickers (1995) gave the following interpretation of this result. Consider what happens as μ_T is reduced at points A and B in Figure 17.2. These points indicate stalemates, that is, traveling waves with zero speed. When μ_T is reduced, the wave front of the *TFT* players steepens so that density is reduced in the leading edge of the wave. The key factor is that at A the number of encounters between any given two players is determined by the death rate, whereas at B it is determined by mobility. At B, the getting-to-know function g and the number of *AD*–*TFT* pairs that

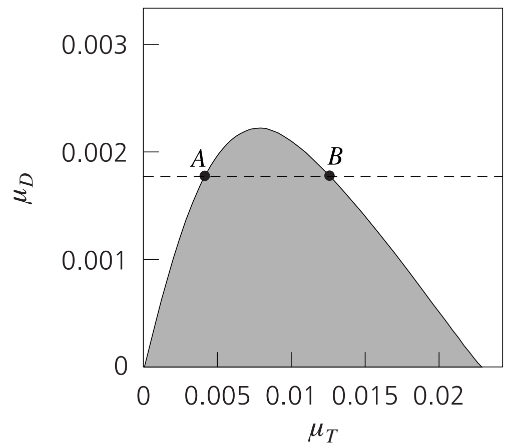

Figure 17.2 Mobility rates leading to an invasion of an established *AD* population by a wave of *TFT* players. The model assumes space-limited memory and can be written as a system of reaction–diffusion equations [see Chapter 22, Equations (22.17) and (22.19)]. The shaded area contains all pairs of mobility rates μ_T, μ_D for which there exists a traveling wave replacing *AD* with *TFT*. For given defectors' mobility μ_D smaller than a maximum value (≈0.0021) – for example, $\mu_D = 0.0018$ (dashed line) – there is an interval (A, B) of μ_T mobility rates over which invasion by *TFT* occurs. Model parameters: $\alpha = 1.3725$, $\beta = 0.9$, $\gamma = 1.45$, $\delta = 1$, $k = 4$, $b = 0 = d$, $\sigma = 1$, $\theta = 100(\mu_T + \mu_D)$.

have already met G increase significantly, causing the per capita birth rate in *TFT* to increase. Thus the *TFT* players have the advantage and a wave develops in which they advance. By contrast, at A there is little change in functions g and G so that the per capita birth rate of *TFT* is mainly influenced by the decrease in *TFT* density, which gives *AD* the advantage. The same type of argument suggests that reducing μ_D is always bad for *AD*, which is consistent with Figure 17.2 but contrasts with conclusions drawn from the replicator–diffusion model.

17.5 Concluding Comments

The importance of spatial structure for the IPD has long been realized (see, e.g., Axelrod 1984). Intuitively, individual mobility in the IPD is expected to raise an insurmountable obstacle to the spread of cooperation by allowing egoists to exploit cooperativeness and escape retaliation (Houston 1993). Dugatkin and Wilson (1991) and Enquist and Leimar (1993) addressed the issue, but their models had several limitations: only *AD* players were mobile; mobility was represented implicitly through some traveling cost; and only the question of the stability of *TFT* against *AD* was considered.

Reaction–diffusion models offer a natural framework to incorporate temporal and spatial effects in games. These models represent players that move in space in a random manner at a rate controlled by specific parameters. Their development is rooted in the Taylor–Jonker replicator equations (17.1). Players' mobility is included through the standard diffusion approximation of spatial motion, which yields second-order derivatives with respect to the spatial variable in Equations (17.2). We call the resulting system a "replicator–diffusion model." The reaction term can be modified further to allow for population limitation through density-dependent payoffs (Cressman and Dash 1987).

Once the reaction–diffusion model has been set up, one can address the central question in game theory: can an established population of one or several strategies be invaded by an initial spatially limited distribution of individuals playing an alternative strategy? Propositions 17.1 to 17.3 provide some insights into this problem in the context of replicator–diffusion models. The spatial dimension does not affect the stability of an internal strategy mix (i.e., all strategies are represented), which is an ESS in the standard game (Proposition 17.1). When there are only two strategies and both are ESSs in the nonspatial game, space dramatically alters the picture by allowing one strategy to displace the other (Proposition 17.2). Finally, in games with three (or more) strategies, spatial patterns (that is, spatially heterogeneous but temporally "frozen" distributions of coexisting strategies) develop when the replicator equation possesses a stable internal equilibrium that is not an ESS (Proposition 17.3). These results have been extended to spatial games including logistic population regulation (Cressman and Vickers 1997).

From the point of view of finding explicit, tractable invasibility criteria, two-strategy replicator–diffusion models are quite remarkable. If there is only one pure ESS in the standard game or if there is a mixed ESS, the stability property carries over nicely to the spatial game. A difficulty arises when both pure strategies are ESSs in the nonspatial game. In the spatial setting, the mathematical theory (Hutson and Vickers 1992) offers three statements that constitute the core of Proposition 17.2: one strategy invades and replaces the other (no coexistence); the invasion dynamics develop as a traveling front; there is a clear-cut invasibility criterion based on the sign of the speed of the traveling wave. On the basis of numerical simulations, the same invasibility rule proves to also apply to the more involved Hutson–Vickers model. Therefore, in these models it is the emergence of traveling waves that determines the evolutionary fate of individuals. The wave acts as a "vehicle" for population conflict (which mainly occurs around the fringe of the wave). In a sense, selection operates "at the level of the wave," although the wave itself is not a self-reproducing unit, just an expanding one. Obviously, the properties of waves are not in the definition of the system, instead they are derived from the individuals' behavioral and demographic traits. A similar phenomenon has been observed in individual-based models of host–parasitoid interactions where the formation of spiral waves determine the invasion success of mutant parasitoids (Boerlijst *et al.* 1993).

Other versions of the spatial IPD, designed as cellular automata, have recently been issued (Lindgren and Nordahl 1994; Nakamaru *et al.* 1997; see Chapter 13). Differences between these models and the reaction–diffusion approach lie in various (biological) assumptions about individual mobility and the effect of the game on individual life histories. The game pay-offs translate into a transmission rate (i.e., the probability of invading a neighboring site) in the model designed by Lindgren and Nordahl (1994), whereas they determine mortality rates in the framework by Nakamaru *et al.* (1997). The former model was analyzed though computer simulations; the latter received an analytical treatment by means of pair-approximation techniques (see Chapters 13 and 18). In both models, mobility is restricted to the dispersal of one offspring into a vacant neighboring site. Consequently, neither model allows connections to be drawn between the outcome of the game and different levels of individual mobility. Van Baalen and Rand (1998) have also developed a pair-approximation model of competition between altruists and non-altruists in a viscous population, in which they incorporated a rate of mobility (the same for both types of individuals). Although their system is not an iterated game, there is an interesting parallel between its behavior and that of the replicator–diffusion model. Again, invasion appears to be governed by a "spatially extended" Hamilton rule, where the coefficient of relatedness is recast into a coefficient of reciprocation depending on the birth, death, and mobility rates – much like the left-hand side of Equation (17.13). Also, the unit of selection becomes a "characteristic cluster" whose structure is described by a stable distribution of pairs of neighboring site occupancies, altruist–altruist, altruist–selfish, altruist–empty (a distribution that can be calculated from the model parameters). Van Baalen and Rand's model predicts that altruism can invade a selfish population background provided that the individual mobility rate is close to some optimum, intermediate value. As in the reaction–diffusion models, this ensures that the "scale of dispersal" is larger than the "scale of interaction." In other words, dispersal should be limited to guarantee a sufficient proportion of altruist–altruist pairings, but strong enough to ensure that altruists can "export" themselves and propagate through the environment.

The issue of invasion in spatial games arises from the study of a fascinating biological enigma – the origin and maintenance of cooperation – and yields profound mathematical challenges. The key relation between the existence of a traveling wave and invasion from a localized cluster is widely accepted on the basis of overwhelming numerical simulations; however, it has yet to be proved mathematically (see Chapter 22). The most urgent issue might be to further probe how the local mean-field description of spatial games based on reaction–diffusion models departs from the dynamics of the underlying discrete system of interacting individuals. Individual models cannot reach a sufficient level of generality, nor do they succeed at pointing out details at the individual level that are critical for understanding the macroscopic dynamics. Intermediate descriptions – for example, through moment or correlation equations (see Chapters 18 to 21) – have yet to be improved with respect to dealing with the initial stages of invasion processes, when the invading population is limited to a small area in space. In the meantime, we believe that the models of spatial games described in this chapter represent a significant improvement over previous mathematical attempts to describe the IPD and explain the evolution of cooperation.

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