THE EVOLUTION OF COOPERATION IN SPATIALLY HETEROGENEOUS POPULATIONS

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Abstract.—A challenging problem in sociobiology is to understand the emergence of cooperation in a nonsocial world. Recent models of the iterated Prisoner's Dilemma (IPD) game conclude that population mixing due to individual mobility limits cooperation; however, these models represent space only implicitly. Here we develop a dynamical IPD model where temporal and spatial variations in the population are explicitly considered. Our model accounts for the stochastic motion of individuals and the inherent nonrandomness of local interactions. By deriving a spatial version of Hamilton's rule, we find that a threshold level of mobility in selfish always-defect (AD) players is required to beget invasion by social "tit for tat" (TFT) players. Furthermore, the level of mobility of successful TFT newcomers must be approximately equal to or somewhat higher than that of resident defectors. Significant mobility promotes the assortment of TFT pioneers on the front of invasion and of AD intruders in the core of a cooperative cluster. It also maximizes the likelihood of TFT retaliation. Once this first step whereby TFT takes over AD is completed, more generous and perhaps more suspicious strategies may outperform and displace TFT. We derive the conditions under which this continued evolution of more robust cooperative strategies occurs.

One of the most difficult problems of sociobiology is to understand the emergence of cooperation in a nonsocial world. For this purpose, the iterated Prisoner's Dilemma (IPD) game has proved to be a fruitful tool of investigation. In a well-known computer tournament that simulated an IPD, the simple strategy "tit for tat" (TFT) did outstandingly well (Axelrod 1980). The TFT strategy, which initiates a partnership by cooperating and next imitates its partner's behavior, has become a leading paradigm for cooperative behavior based on reciprocation between unrelated individuals. Further analytical work (Boyd and Lorberbaum 1987) and new computer tournaments (Nowak and Sigmund 1992, 1993) have shown that TFT plays a pivotal role in an evolution of cooperation. In a scenario where the unconditionally defective strategy "always defect" (AD) is initially common, the emergence of TFT must be the first step toward sociality. Once established, TFT paves the way for more robust forms of reciprocal altruism, represented by strategies like "generous tit for tat" (GTFT) that are prone, with a certain probability, to forgive a defective act. In order to explain the emergence of any form of cooperative behavior, it is therefore crucial to understand how TFT can gain a foothold in a world of egoists and how it can effec-

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tively serve as a stepping stone for the establishment of more generous strategies.

The first problem is that a world of AD players can always resist invasion by any cooperative strategy if the newcomers (mutants, immigrants) arrive one at a time. Axelrod and Hamilton (1981) argued that newcomers must arrive in small clusters to have a chance of spreading. By comparing the fitness of a TFT player within a cluster to the average fitness of defectors over the whole population, Axelrod (1981) even suggested that invasion of AD players by TFT clusters should be very easy. There is one basic problem with this approach, however, when cast in an explicit spatial framework. Because the payoff to defectors is averaged over the whole population, it does not reflect the local payoff to AD players in the vicinity of the TFT cluster. Even if TFT is initially rare in the population, the proportion of interactions between AD and TFT cannot be seen as a negligible second-order term in the payoff balance of the game when it is computed locally, in the vicinity of the cluster—and one can expect this local balance to be of critical importance to determining whether the cluster will grow and spread out or collapse.

There is a second, more basic problem with the IPD paradigm as typically implemented in studies of cooperation, and that is that the basic biological issues are treated as a priori constants. For example, a central issue in determining the outcome of the game is the probability of continuing the game with the same partner, $w$. Basic individual features like survival and mobility influence $w$ but are commonly ignored (Houston 1993). In our work $w$ emerges from these more basic individual features and the dynamics of interactions in time and space.

Attempts to remedy these problems have been recently initiated. Under the assumptions of random interactions, Dugatkin and Wilson (1991) and Enquist and Leimar (1993) have considered a version of the IPD between sedentary TFT and mobile AD players. They have shown that when a selfish organism is free to terminate an interaction by moving to a new location, one may expect the evolution of “roving” or “free-rider” defectors, which are very efficient at exploiting and devastating clusters of naive cooperators.

In a preliminary study, we introduced a model involving nonrandom interactions, mortality, and potential mobility in both TFT and AD (Ferriere and Michod 1995). Our goal in the present article is to further develop a general model of the IPD game that, while being as simple as possible, accounts for both spatial and temporal effects that arise from the local, nonrandom nature of interactions, the mobility of players, and basic aspects of their life cycle (rate of mortality, rate of interaction). We apply this model to the evolution of TFT and AD to address whether a small, finite cluster of mobile TFT individuals can spread from rarity in an infinite population of mobile AD individuals. Then we consider the stability of TFT, once established, against reinvasion by AD, as well as against a wide class of strategies (the so-called stochastic strategies, including GTFT) whose probability to cooperate depends on the opponent’s previous move (Nowak 1990).
THE SPATIAL ITERATED PRISONER'S DILEMMA

In this section we develop a dynamical model of the IPD between two types of players (labeled 1 and 2), which combines both temporal and spatial effects on the game. The main assumption is that the total population density of contestants is large and does not fluctuate dramatically in time and space. We are concerned primarily with strategies that are specified by the outcome of the previous round, but the model can be easily extended.

**Basic Features of the IPD**

In the IPD game, players have two options, cooperate or defect. If both players cooperate, both obtain $R$ fitness units (the “reward payoff”); if both defect, each receives $P$ (the “punishment payoff”); if one player cooperates and the other defects, the cooperator gets $S$ (the “sucker’s payoff”) while the defector gets $T$ (the “temptation payoff”). The payoff values are ranked $T > R > P > S$ and $2R > T + S$. An additive cost-benefit parameterization of these payoffs will be useful (Brown et al. 1982). Assume that a cooperator exhibits some behavior that benefits the fitness of his partner, the recipient, by $b > 0$. 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. An act of defection is assumed to bestow no benefit to the partner and to incur no cost to the actor. The total effect on fitness of a given interaction is assumed to be the sum of the appropriate terms; the increments to fitness are added to a baseline fitness taken to be one. With this parameterization, the payoff $T$ results from receiving $b$ from the cooperator but incurring no cost: $T = 1 + b$. Similarly, one gets $R = 1 + b - c$, $P = 1$, $S = 1 - c$.

**The Population**

Each individual occupies a position in space that is a function of time. For simplicity, we consider a one-dimensional spatial axis, $X$, so the population lies on a line, or at least any spatial variation is in one direction only. Let $n_1(x, t)$ and $n_2(x, t)$ (in short, $n_1$ and $n_2$) denote the densities of types 1 and 2 at location $x$ and time $t$. As is commonly assumed in the theory of spatial population dynamics (Fife 1979), we assume that these densities are smooth functions of $x$. The vector $n$ has components $n_1$ and $n_2$. The total population density at $x$ and $t$ is $N = n_1 + n_2$. We assume that the carrying capacity $K$ has been attained, for any $x$ and $t$ (but, of course, the strategy mix may change). As one strategy spreads through the population, there may be a small, temporary change in population density, without significant consequences on the conclusions of our model (Hutson and Vickers 1992; Ferriere and Michod 1995).

**Individual Mobility**

Individuals move along the axis in a stochastic manner. We consider random motion in space as represented by a standard diffusion approximation (e.g., Crank 1975). Individual mobility is quantified by a single parameter $\mu$, the so-called mobility rate. The probability that a certain distance is moved in the time $\Delta t$ by
an individual with mobility $\mu$ has the Gaussian distribution with mean zero and variance $2\mu \Delta t$.

In the most general situation, we assume that a moving individual incurs a cost of mobility, denoted by $\gamma$, and this cost may be a function of $\mu$, and thus it may vary across strategies.

*The Life Cycle*

The life cycle is characterized by the instantaneous death rate $d$ and by the rate of interaction $\tau$. The death rate is the same for all strategists and is not affected by the game. Its main effect is on $w$, the probability of repeated interactions. Every $\tau$ time units, two neighboring players engage in a new round of the game, and their fitness is increased or decreased in terms of reproductive success, according to the outcome of the round. Thus, $\tau$ determines the timing of reproduction of an individual along its life span.

*Local Interactions*

In the IPD, where strategies are specified by the outcome of the previous round, a critical parameter is the probability $w$ that a player interacts twice consecutively with the same partner (Axelrod and Hamilton 1981; Brown et al. 1982). To model local interactions between players, we regard space as subdivided into discrete contiguous cells, defined in such a way that each cell contains two players at any given time. Every $\tau$ units of time, the two players in each cell interact. They play the game again on the next interaction if they both survive and both end up in the same cell on the next interaction. This happens with probability $w$—an emergent variable that is a complicated nonlinear function of the mobility rates, death rate, interaction time, and environment carrying capacity (see the appendix). This $w$ is analogous to $w$ in the standard IPD, the probability of continuing the game (Axelrod and Hamilton 1981). But the critical difference is that the original $w$ is an exogenous parameter imposed on the players (whatever their behavior or life cycle), in contrast to the derived, endogenous $w$ in our model.

*Temporal and Spatial Variation in Strategy Densities*

Temporal and spatial changes in strategy densities are modeled by a reaction-diffusion system that stems from the idea that the growth rate of a strategy depends on how well individuals perform relative to the local average payoff (a view rooted in Fisher 1930 and elaborated in Vickers 1989). Thus the equations involve a term representing population growth as determined by the outcome of the game and a diffusion term that accounts for mobility:

\[
\begin{align*}
\frac{\partial n_1}{\partial t} &= n_1(\Phi_1 - \Phi) + \mu_1 \frac{\partial^2 n_1}{\partial x^2} \\
\frac{\partial n_2}{\partial t} &= n_2(\Phi_2 - \Phi) + \mu_2 \frac{\partial^2 n_2}{\partial x^2},
\end{align*}
\]

(1)

where $\Phi_1 = \Phi_1(x, t)$ and $\Phi_2 = \Phi_2(x, t)$ are the local payoff per unit time to type
1 and type 2 and $\Phi$ stands for $\Phi(x, t)$, the average payoff per unit time of the local population at $x$ and $t$,

$$
\Phi = \frac{n_1}{N} \Phi_1 + \frac{n_2}{N} \Phi_2. \quad (2)
$$

For linear games (such as IPD) there is a matrix $A = [a_{ij}]_{1 \leq i, j \leq 2}$, the so-called payoff matrix, such that the fitness terms in equations (1) and (2) become

$$
\Phi_i = \frac{(An)_i}{N}, \quad i = 1, 2 \quad (3a)
$$

and

$$
\Phi = \frac{\langle n, An \rangle}{N^2}. \quad (3b)
$$

The $a_{ij}$'s are the payoffs per unit time to a type $i$ player against a type $j$ opponent ($i, j = 1, 2$). The notation $(An)_1$ refers to the first component of the vector $An$ (respectively, the second component for $(An)_2$); $\langle n, An \rangle$ denotes the scalar product of the two vectors. The matrix $A$ is entirely determined when the strategies 1 and 2 are specified. It will depend on the basic payoff of a single round of the IPD, as well as the other parameters of the game (probability of repeated interactions $w$, death rate $d$, interaction time $\tau$, carrying capacity $K$, and any other variable involved in the definition of the strategies). A priori, $A$ may vary in time and space. However, we will see that in games putting TFT in opposition to AD or to stochastic strategies, $A$ is actually constant.

**Spatial Dominance and Invasion**

Providing a rigorous mathematical definition of invasion in spatial population models can be difficult. The usual concept of evolutionarily stable strategy (ESS) applies to spatially homogeneous populations, if newcomers (mutants, immigrants) arrive in small frequency and are uniformly distributed across space. Invasion in more realistic situations—such as a spatially heterogeneous population in which a finite number of potential invaders are initially localized in a small cluster—is more complicated. Vickers (1989) showed that if the payoff matrix $A$ is independent of space and time and there is exactly one ESS, this ESS is still stable when spatial heterogeneity is considered. However, if $A$ defines a two-strategy game in which each pure strategy is an ESS, "spatial dominance" of one ESS by the other may occur (Hutson and Vickers 1992; see also Vickers et al. 1993). Spatial dominance means that a traveling wave propagates in the population, which in effect replaces one ESS by the other. From a biological viewpoint, spatial dominance means that an initially small cluster of invaders will grow and eventually take over the resident strategy.

In practice, the exploration of spatial dominance begins with the study of the spatially homogeneous system (the standard replicator equation; see Taylor and Jonker 1978), obtained by setting $\frac{\partial^2 n_i}{\partial x^2} = \frac{\partial^2 n_2}{\partial x^2} = 0$ in system (1). The equilibrium solutions to this system are $(0, 1)$ and $(1, 0)$. Whenever $a_{11} > a_{21}$ and
\[ a_{22} > a_{12}, \] both equilibria are asymptotically stable, which entails that both strategies would be ESSs in the spatially homogeneous game. In a spatially heterogeneous population, these equilibria may be connected by a traveling wave: spatial dominance then occurs. Hutson and Vickers (1992) provide the mathematical conditions for the existence of a traveling wave replacing type 2 by type 1. If
\[ \frac{a_{11} - a_{21}}{a_{22} - a_{12}} > \theta(\mu_1/\mu_2), \]
where \( \theta(\mu_1/\mu_2) \), a complicated integral function, is well approximated by \( (\mu_1/\mu_2)^{0.61} \), then type 1 dominates type 2. Reversing inequality (4) provides the condition for type 2 to dominate type 1. Thus, spatial dominance makes the two types exclusive (except in the degenerated case of equality in inequality [4]). In addition, when type 1 is dominant, if it is less mobile than type 2, the density of type 2, \( n_2(x, t) \), is a monotonic function of \( x \) at any time \( t \) is large enough ("monotone dominance"). In contrast, if type 1 is more mobile than type 2, \( n_2(x, t) \) becomes a unimodal function of \( x \) for any large \( t \) ("unimodal dominance"), displaying a unique maximum in the region of overlap between strategies 1 and 2 (a region that we call the "fringe" of the traveling wave). See figure 1.

**INITIAL INCREASE OF TFT VERSUS AD IN THE SPATIAL IPD**

An individual playing TFT invariably cooperates when its partner is perceived as a stranger; when interacting with an individual recognized from a previous interaction, a TFT behaves as did its partner in their previous encounter. The payoff matrix \( A \) for a spatial IPD opposing TFT and AD is calculated in the appendix, where type 1 is TFT (abbreviated as subscript T) and type 2 is AD (subscript D). Using the cost-benefit (\( c/b \)) parameterization of the payoffs \( T, R, P, \) and \( S \) introduced above, the conditions \( a_{11} > a_{21} \) and \( a_{22} > a_{12} \) reduce to
\[ w > c/b. \]
Fig. 2.—The combinations (μ_T and μ_D) of TFT and AD mobilities for spatial invasion by TFT of a resident AD population. The cost of mobility is constant. A, Equidistant contours of the surface defined by the coefficient of reciprocation \( H \) in inequality (6) for \( K = 0.25 \), \( \tau = 1 \) and \( d = 0 \). Ca. 0.0065 apart. For example, with \( c/b = 0.21 \), mobility combinations within the bold contour allow TFT to invade AD, and arrows point to the range \([μ_T^{min}, μ_T^{max}]\) of invading TFT mobilities when \( μ_D = 1 \). B, Slice at \( μ_D = 1 \). The range \([μ_T^{min}, μ_T^{max}]\) of mobility rates for which TFT can invade corresponds to the portion of the curve located above the level fixed by the cost-benefit ratio (straight horizontal line).

Under condition (5), TFT spatially dominates AD when (see inequality [4])

\[
\frac{w}{1 + (1 - w) \theta (μ_T/μ_D)} > \frac{c}{b},
\]

(6)

where \( w \) is as given in the appendix.

Inequality (6) provides a Hamilton’s rule (Hamilton 1964; Michod and Hamilton 1980) 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 standard IPD (Brown et al. 1982), which gives the probability that an individual’s cooperative act is returned via reciprocation from other TFTs. The right-hand side of inequality (6) is the cost-benefit ratio of cooperation. The spatial Hamilton’s rule in inequality (6) can further be extended to encompass the case of a cost to mobility dependent on mobility rates (see the appendix).

Combinations of \( μ_T \) and \( μ_D \) that permit the spatial dominance by TFT of a resident AD population can be calculated from inequality (6). For a given carrying capacity \( K \) and interaction time \( τ \), and assuming that the death rate \( d \) is zero (which corresponds to a situation where an individual is engaged in infinitely many interactions during its lifetime), if values of \( μ_T \) and \( μ_D \) are contained in the isocline of the coefficient of reciprocation \( (H) \) at the level of the cost-benefit ratio \( c/b \), then TFT can invade AD (fig. 2).

An unexpected result is that AD mobility must exceed a minimum threshold for TFT to get a chance of invading the population (fig. 2A). In other words, a background of sufficiently mobile defectors is needed for the emergence of cooperation. Under this condition, there exists a range of mobility rates for which
TFT can invade (fig. 2B). Except if the $c/b$ ratio nearly reaches the maximum value permitting invasion, the mobility of TFT, $\mu_T$, can be slightly smaller than, equal to, or a lot larger than that of resident defectors $\mu_D$ (e.g., $c/b = 0.21$, the bold isocline in fig. 2A). If $c/b$ is very close to the maximum value permitting invasion, then $\mu_T$ must be larger than $\mu_D$ (e.g., along the isocline inside the bold lines in fig. 2A; note that the dotted line $\mu_T = \mu_D$ lies outside of this isocline). In this case, the invading range shifts to the right of the resident $\mu_D$ value.

The effect of total population density, assessed by the carrying capacity $K$, can be discussed analytically. If $K$ is increased by a factor $\kappa > 1$, a straightforward change of variable shows that $w$ computed with this new carrying capacity is equal to $w$ computed for $K$ and new mobility rates $\kappa^2 \mu_T$ and $\kappa^2 \mu_D$. Thus a higher density (larger $K$) results in a isotropic squeeze toward the origin (with rate $1/\kappa^2$) of the surface whose contours are pictured in figure 2A. We therefore expect the biological facts to be left unchanged, since with higher density less mobility is required to achieve a certain number of encounters over a given period of time. Furthermore, the peak of the surface in question is unaltered. Thus the maximum cost-benefit ratio tolerated by the species for mobility rates begetting TFT invasion to exist does not depend on the total population density.

We now examine how changes in $d$ and $\tau$ affect the range of mobility rates $\mu_T$, allowing invasion by TFT (defined by inequality [6]). This can be done analytically by making use of an approximate expression of $w$ derived in the appendix, which is valid for large $K$ and mobilities that are not too small:

$$w = \psi \frac{\mu_1 \mu_2}{(\mu_1 + \mu_2)^{5/2}}, \quad (7a)$$

with

$$\psi = \frac{4}{K \sqrt{\pi}} \frac{e^{-d\tau}}{\sqrt{\tau}}. \quad (7b)$$

By substituting equation (7a) into inequality (6), we obtain an approximate but tractable condition for TFT to dominate AD in terms of $\psi$ and the mobility rates. Figure 3A shows how the critical values of $c/b$ vary as a function of $\psi$. Increasing $\psi$ results in a wider range of TFT mobility rates causing invasion; indeed, the minimum mobility for invasion decreases, and the maximum mobility increases. This pattern is generic and unaffected by changes in the value of $\mu_D$. From equation (7b), it is apparent that an increase in $\psi$ occurs when either $d$ or $\tau$ is decreased (fig. 3B). Thus, decreased mortality or interaction time will broaden the range of those mobility rates that allow TFT to spatially dominate AD. Furthermore, a decrease $-\Delta d$ in mortality along with an increase $+\Delta \tau$ in the interaction time can benefit TFT, allowing for invasion for both lower and larger mobility rates, provided that

$$\frac{\Delta d}{d} > \alpha \frac{\Delta \tau}{\tau}, \quad (8)$$
with $\alpha = 1 + 1/(2d\tau)$. (This is because the change caused in $\psi$ can be written as $\Delta \psi = \psi[\tau \Delta d - (d + 1/(2\tau)) \Delta \tau].$)

Finally, when the cost of mobility $\gamma$ depends on the mobility rate (but remains lower than the cost $c$ of a cooperative act), the maximum rate of mobility $\mu_T$ begetting invasion (for given $\mu_D$) decreases. Yet unexpectedly the minimum mobility rate required for successful invasion by TFT may be raised, and this happens when the cost-benefit ratio $c/b$ of cooperation is high. These statements are mathematically substantiated in the appendix.

**WHY DOES MOBILITY HELP TFT INVADE AD?**

For the TFT strategy to prosper, there needs to be a high proportion of TFT-TFT pairings. Various mechanisms have been envisioned that increase the frequency of TFT-TFT pairings (Eshel and Cavalli-Sforza 1982; Feldman and Thomas 1987). A common expectation is that high mobility leads to random mixing, which should act against assortative encounters among TFT players and therefore make it more difficult for the TFT players to invade. Our results, however, run counter to this expectation. We argue that mobility helps the TFT invasion process in spatially heterogeneous populations, because it increases the likelihood of assortative encounters between moving TFT players that travel into the front of invasion and moving AD players that intrude the core of the cluster, and the chance of retaliation by a TFT player against a moving AD player.

The successful invasion of a finite cluster of TFT players in an infinite population of AD players requires pioneering moves toward the inhospitable surrounding area occupied only by AD players at the front of invasion. This is the very essence of an effective spatial expansion. Therefore, of primary importance are TFT pairings in this region between individuals that come from the core of
the cluster, and mobility appears to increase the likelihood of such assortments of TFT players that are on a pioneering move. High (but not extreme) mobility maximizes the probability that two individuals move out of the core of the cluster and end up paired together on the front of invasion.

In order to spread, TFT players must primarily avoid being suckered. They may succeed in doing so, not only by playing themselves, but also by retaliating. When retaliating, a TFT player will not perform worse than an AD individual playing itself. Therefore, even if retaliation does not entail an increase in TFT relative fitness, it prevents AD from doing better. Furthermore, retaliation does help the invasion process for two reasons. The first reason is that as an AD player undergoes retaliation, this individual is no longer available to interact with and sucker a naive TFT player. This is especially valuable for the well-being of TFT when it applies to AD players that intrude the core of the TFT cluster: as they remain tied up with known TFT players, such AD players end up neutralized and incapable of exploiting naive TFT players. Second, retaliation coupled with a move toward the front of invasion replays the Trojan horse metaphor: a TFT player is taken onto the front of invasion where AD players are still thriving, without facing the threat of getting paired there with an AD stranger. Again, we claim that significant, yet not extremely high, mobility increases the likelihood of retaliation against a moving defector.

The explanations are based on a very simple auxiliary model of stochastic motion. This is designed to capture the key features of the players’ diffusion process while ignoring the effects of the game on the growth of the two strategies. Indeed, our goal in setting up this model was to enable us to examine the sole effects of mobility on the invasion process on a microscopic scale (that of pairwise interactions), without resorting to numerical simulations of the full-model dynamics.

The line occupied by the population is subdivided into discrete, contiguous cells. An individual may move from one cell to another, with a certain probability. If \( p \) denotes the probability of staying in place, let us assume that the probability of moving \( n \) cells to the left or to the right is obtained by discounting \( p \) by a factor \( q^n \). For the series \( \{ p, pq, pq^2, pq^3, \ldots \} \) to be a probability distribution, it must sum up to one, which imposes \( p = 1 - q \). As shown in figure 4A for \( q = 0.1 \) and \( q = 0.6 \), this probability distribution is a space-discrete analogue to the Gaussian distribution of distances moved that is involved in our full model. The variance of the latter was merely proportional to the diffusion rate \( \mu \); here, the variance is still an increasing function of \( q \); thus, the parameter \( q \) can also be regarded as a measure of individual mobility. Here the variance of the distance moved is equal to \( 2 \sum_{k=1}^{\infty} k^2 pq^k \), which, after some algebra, reduces to \( 2q(1 + q)/(1 - q) \).

Let us consider a localized cluster of TFT individuals with motion probability \( q \), spread over \( C \) contiguous cells. In agreement with our full model, each cell contains two individuals. We first consider the cumulative probability \( Q \) that a TFT player located in the cluster moves out and ends up paired on the front of invasion with another TFT player also coming from the cluster. The probability \( Q \), computed in the appendix, is shown in figure 4B (lower curve) as a function
of the motion probability $q$. This is a unimodal function, maximized at large values of $q$, which reaches higher values as $C$ is increased. For example, with $C = 20$, the maximum ($= 0.20$) is obtained with $q = 0.92$.

We wish to compare this probability $Q$ of moving outside the cluster and getting paired with another individual from the cluster with that, denoted by $Q'$, of moving outward and not getting assorted. The ratio $Q/Q'$ will tell us how more likely an individual is to make a successful pioneering move, instead of being suckered when settling down on the front of invasion. If $Q''$ stands for the probability that a TFT player picked at random in the cluster stays therein, $Q$, $Q'$ and $Q''$ are straightforwardly related: $Q' = 1 - Q - Q''$. Figure 4B portrays $Q'$ and $Q''$ as functions of $q$, for $C = 5$. Like $Q$, the ratio $Q'/Q'$, displayed in figure 4C, attains its maximum value for a high motion probability $q$. This maximum also increases as the size of cluster, $C$, increases. In conclusion, given a cluster size, an individual sees its chance of making a successful pioneering move maximized by moving at a substantial rate. Even more mobility will be helpful as the invasion progresses (increasing cluster size).

We now turn to the effect of mobility on the likelihood of retaliation between moving players. Consider two individuals (a TFT and an AD) initially located in the same cell but characterized by different motion probabilities $q_1$ and $q_2$. In the appendix, we calculate the probability $Q_{\text{retal}}$ that they move away, making a jump of at least $M$ cells, say, to the right, but remain paired together (fig. 5A). Figure 5B displays contours of the surface defined by $Q_{\text{retal}}$ as a function of $q_1$ and $q_2$, when $M = 1$. It shows that $Q_{\text{retal}}$ is maximized at high values of $q_1$ and $q_2$ (also, the larger $M$, the more peaked the surface). Thus, a TFT player has a better chance of keeping track of and retaliating against a moving AD player if both the AD player and its own motion probabilities are high.

Coming back to our full model, a final remark concerns the influence of mobility on the specific pattern of dominance (monotonous or unimodal). For a given AD mobility, a low mobility in TFT creates unimodal dominance by AD: the TFT
Fig. 5.—A, Tracking: two individuals characterized by different motion probabilities and initially located in the same cell make a move of at least $M$ cells and end up paired together again. B, Contours of the surface defined by $Q_{\text{real}}(q_1, q_2)$ for $M = 1$ (eq. [A23]).
distribution is humped over the fringe of the traveling wave, which creates a rich, easy-to-access diet of naive cooperators that AD players entering the cluster can feed on. As TFT mobility increases, TFT becomes dominant, and, as long as $\mu_T$ remains lower than $\mu_D$, dominance is monotonous. When $\mu_T$ exceeds $\mu_D$, dominance becomes unimodal again, with an accumulation of AD players over the fringe. This AD aggregation is dramatized as $\mu_T$ keeps increasing, and that produces a "wall" of defectors in the fringe much harder for TFT players to beat.

STABILITY OF TFT

It has been suggested (Boyd and Lorberbaum 1987; Nowak and Sigmund 1992, 1993) that understanding how TFT can gain a foothold in a population of AD is crucial to explaining the origin of cooperation in the IPD game. A different issue is the maintenance of cooperation: once established, will TFT be able to persist when facing the threat of new strategies entering the population? Reinvasion by AD is a particular aspect of this problem. More generally, Nowak (1990) proposed to consider a restricted, yet widely scattered array of strategies for the IPD, the so-called stochastic strategies, as test opponents to probe the stability of TFT when common.

In stochastic strategies, the decision to cooperate or defect in each round depends stochastically on the outcome of the previous round. This is meant to apply to biological situations where decisions are uncertain and subject to errors of judgment (or imperfect memory). A stochastic strategy is characterized by a pair of parameters $(s, g)$ where $s$ is the probability of cooperating on the first round and, on subsequent rounds, of cooperating if the partner cooperated on the previous round and $g$ is the probability of cooperating if the partner defected on the previous round. The parameter $g$ has been termed a measure of "generosity" (Nowak 1990). For instance, TFT is $(1, 0)$ and AD is $(0, 0)$. Running computer simulations of the standard nonspatial IPD, Nowak and Sigmund (1992) showed that TFT was invariably superseded by GTFT $(s = 1, g > 0)$, provided that other specific stochastic strategies were present in the population at low frequency. This is because a new strategy like GTFT is typically neutral when playing TFT and requires a third strategy with specific properties to gain an advantage over TFT. Our point here is that spatial heterogeneity can also drive the evolutionary process from TFT toward more robust forms of cooperation, but without requiring such additional, rare strategies.

So as to substantiate our statement, we shall first derive the analytical condition for TFT to dominate a stochastic strategy in the spatial IPD. Because the more general problem of a struggle between any two stochastic strategies is not harder, we will offer a solution to this general case. Let us consider two stochastic strategies $(s_1, g_1)$ and $(s_2, g_2)$, with mobility rates $\mu_1$ and $\mu_2$, respectively. We want to compute the expected payoff per interaction, $e_{ij}$, to strategy $i$ when interacting with strategy $j (i, j = 1, 2)$. We denote by $E = (R, S, T, P)^*$ the vector of payoffs for a single round of the IPD and by $w_{ij}$ the probability that an $i$ player meets twice consecutively with the same $j$ partner. We also need to
introduce the Markovian matrix (see the appendix) $Z_{ij}$ given by

$$Z_{ij} = \begin{pmatrix} s_is_j & g_is_j & s_ig_j & g_ig_j \\ s_i(1 - s_j) & g_i(1 - s_j) & s_i(1 - g_j) & g_i(1 - g_j) \\ (1 - s_i)s_j & (1 - g_i)s_j & (1 - s_i)g_j & (1 - g_i)g_j \\ (1 - s_i)(1 - s_j) & (1 - g_i)(1 - s_j) & (1 - s_i)(1 - g_j) & (1 - g_i)(1 - g_j) \end{pmatrix}.$$  \hspace{1cm} (9)

Then the expected payoff $e_{ij}$, derived in the appendix, is

$$e_{ij} = (1 - w_{ij}) \langle ((\mathcal{S} - w_{ij}Z_{ij})^{-1} \pi_{ij}, E \rangle$$  \hspace{1cm} (10)

(where $\mathcal{S}$ stands for the identity matrix), and the condition for spatial dominance of strategy $j$ by strategy $i$ is similar to inequality (4):

$$(e_{ij} - e_{ji})/(e_{jj} - e_{ij}) > \delta(\mu_i/\mu_j).$$  \hspace{1cm} (11)

Numerical computations using equation (10) and inequality (11) show the following results. First, in spatially homogeneous populations, there exist values of the mobility rates that make TFT stable against any stochastic strategy, all other parameters being kept fixed (if TFT is type 1 and the stochastic strategy is type 2, this reads $e_{11} > e_{21}$). However, spatial heterogeneity makes it possible for generous, but somewhat "suspicious," strategies to dominate TFT. This is demonstrated in figure 6. The set of stochastic strategies is covered by the whole square, with TFT being located in the lower right corner. Values of mobility rates for TFT and any alternative strategy were selected so that TFT could resist invasion by any stochastic strategy in a homogeneous population, that is, if newcomer stochastic players were uniformly spread over the whole population. Yet if the stochastic players arrive in a small cluster, thereby creating spatial heterogeneity, any stochastic strategy picked in the shaded area will be able to invade TFT. Thus, spatial heterogeneity by itself can allow a suspicious-generous cooperative strategy to displace TFT, without requiring that other stochastic strategies be present in the population. In a forthcoming paper, we will report on a more detailed study that makes use of the criterion of spatial invasion derived above to investigate the evolutionary dynamics through the entire space of stochastic strategies.

The particular case of reinvasion by AD individuals can be discussed in a more straightforward fashion. Simply by reversing inequality (6) one obtains the condition for invasion by rare AD individuals of a TFT population. Indeed, the concept of spatial dominance entails that any potential invader is either successful and completely replaces the resident type or is completely unearthed from the population—stable coexistence of the two strategies is excluded (Hutson and Vickers 1992). Figure 2A shows that TFT is jeopardized by AD endowed with either high or very low mobility but not by defectors with mobility near its own. Also, TFT is immune to invasion for a much wider range of AD mobility rates as the TFT rate of mobility is raised. Thus, by moving at the highest possible rate, cooperators will find the most efficient protection against reinvasion by AD.
Fig. 6.—Tit for tat vs. stochastic strategies. A stochastic strategy is represented by a point in the \((s, g)\) plane, where \(1 - s\) measures the degree of suspiciousness of the strategy and \(g\) its degree of generosity. The TFT strategy is at \((1, 0)\), in the lower right corner of the panel. The shaded area shows the set of stochastic strategies able to dominate TFT in a spatially heterogeneous population. Simulations were run using the approximate value of \(\omega\) (eq. [7a]) with \(\Psi = 3.0\) and mobilities equal to 0.5 for all strategies; basic payoffs \(T, R, P,\) and \(S\) were assigned traditional values of 5, 3, 1, and 0, respectively.

DISCUSSION

General Comments

In the IPD game studied here, the assumption of random interactions is relaxed, and spatial and temporal effects resulting from individual mobility (possibly entailing a cost) and mortality are explicitly incorporated. This is in contrast with previous studies of nonspatial IPD games that assume that a player repeatedly meets with a single opponent or a set of opponents drawn at random from the population. When the spatial dimension of a population is taken into account, which means that we keep track of the exact locations of organisms, meetings must be nonrandom, and it is natural to regard interactions as taking place be-
between near neighbors. Individual mobility and mortality affect the outcome of the game by influencing the likelihood that interactants meet again.

By considering unconditional strategies far simpler than TFT, previous work (Nowak and May 1992, 1993; Wilson et al. 1992) had already illustrated the importance of nonrandom, local interactions to the outcome of evolutionary conflicts. Nowak and May (1992) studied an iterated two-strategy game between players who either always cooperate or always defect when interacting in a two-dimensional spatial array. While standard ESS theory, ignoring the spatial dimension, would predict that defectors should win the game, cellular automata simulations uncover the effect of local interactions with near neighbors by showing that "cooperate" and "defect" may both persist indefinitely (along chaotically changing spatial patterns). Wilson et al. (1992) also considered local interactions between altruistic and nonaltruistic phenotypes in a two-dimensional array. Although Wilson et al.'s approach is not based on game theory, the altruistic and nonaltruistic types they considered resemble TFT and AD more than they resemble unconditional strategies. Like TFT and AD under condition (5), each of the phenotypes considered in Wilson et al. (1992) has the highest fitness when it is in the majority, but populations composed entirely of altruists are more fit than populations composed entirely of nonaltruists. Like in the standard IPD, in a single panmictic population such altruists could not take over unless they surmounted a substantial frequency threshold. However, Wilson et al.'s simulations showed that a small, localized cluster of altruists could invade. In fact, the cluster was not vulnerable to invasion by nonaltruists, and it could spread outward from the edges. Our results confirm Wilson et al.'s numerical experiments.

In their approach to spatial effects in evolutionary games, Nowak and May (1992) and Wilson et al. (1992) focused on local interactions in which mobility was very restricted in nature. Diffusion was limited to offspring, and an offspring could take only one step from its birth site. Furthermore, generations were discrete. Thus, the possibility of successive rounds was ignored. In the theory of Vickers (1989), Futson and Vickers (1992), and Vickers et al. (1993), on the other hand, multiple interactions were allowed for, and diffusion was described in a quantitative, more flexible fashion, but, unlike Nowak and May's (1992) and Wilson et al.'s (1992) models, the payoffs of the game were not made dependent on the structure of local interactions. Our primary goal here was to develop a mathematical approach to the IPD that combined the effects of players' mobility with those of complex local interactions in spatial two-strategy games.

Our model makes four key assumptions: the game affects individual reproductive success, not the individual survivorship (hence we assume a constant intrinsic death rate \(d\)); a small interaction time \(\tau\); a large carrying capacity \(K\); and a total population density staying near \(K\). Under these assumptions, we found a range of TFT mobility rates begetting spatial invasion in a resident AD population, so long as the AD players are sufficiently mobile. Changing the environment carrying capacity \(K\) has no effect on this range. Increasing either the death rate or the interaction time (while keeping the other parameter constant) makes matters more difficult for TFT, as it shrinks the range of TFT mobility rates that allow invasion. A higher instantaneous death rate not compensated by a shorter delay between encounters has a negative
effect on the likelihood of repeated encounters in the game, thus on the chance that a TFT player retaliates against a known AD player. However, we also found that a decrease in mortality along with an increase in the interaction time can benefit TFT, permitting invasion for both lower and larger mobility rates (see inequality [8]). The consequence is the same if the mortality rate increases and the interaction time decreases. Both of these results make sense, in light of our auxiliary model of stochastic motion. Less mortality and more time between interactions may allow for more numerous and longer TFT pioneering moves toward the front of invasion. Successful assortments between these “long-distance” pioneers is enhanced by more mobility. Indeed, the probability that two players get assorted is maximized at a larger rate of mobility as the number of cells moved prior to assortment increases (i.e., $m$ increases in eq. [A18]). On the other hand, reducing mortality may give suckered TFT players a better chance to retaliate. Raising the interaction time, however, can be detrimental to this respect, because this amounts to leaving more time to a defector for moving away from its TFT victim. Yet this effect is buffered when mobility rates are reduced ($Q_{\text{retal}}$ defined in the appendix increases with mobilities), and this may explain why less mobility also allows TFT to invade as $d$ is decreased and $\tau$ is raised.

Although our model is limited to two-strategy games, the two strategies involved result in a variety of effects, depending on the local spatial setting in which they occur. For example, in the TFT versus AD spatial struggle, consider a suckered TFT player that gets a chance of retaliating against an AD player. If the AD player is moving to the core of the cluster, the retaliating TFT player ties up the intruder and prevents him from exploiting a naive TFT player in the cluster—in so doing, the TFT player has neutralized a defector on a move that puts the cluster at risk. Retaliation against an AD player that moves to the front of invasion is also valuable for the progress of the whole invasion wave, for it allows the retaliating TFT player to make a safe move to the front, protected by its partnership with a known AD player. Thus a variety of effects emerge whereby individuals playing a given strategy serve the invasion progress in different manners, depending on their location in space and their motion. This heterogeneity primarily results from the stochastic nature of mobility, which allows players to make moves of different lengths. Two individuals playing the same strategy but starting from different locations can nonetheless get assorted in critical regions of the traveling wave. Spatial heterogeneity of behaviors in two-strategy games further allows for the evolution of more robust cooperative strategies. Without mobility, additional strategies that are maintained (e.g., by mutation) as rare variants may operate to “catalyze” the evolution of such strategies once TFT has taken over AD (Boyd and Lorberbaum 1987; Nowak and Sigmund 1992, 1993). When mobility is explicitly represented, it turns out that the spatial heterogeneity of behaviors can make up for the lack of multiple strategies: among mobile players in a two-strategy game, no extra strategy may be required for the replacement of TFT by stochastic strategies like GTFT.

**Comparison with Other Models of Cooperation between Mobile Organisms**

The fact that players’ mobility and life cycle may have a dramatic impact on the outcome of a game between TFT (or a variant thereof) and AD was suggested
by Dugatkin and Wilson (1991) and Enquist and Leimar (1993). Yet those models have several limitations: only AD players are mobile; mobility is represented implicitly through some traveling cost, and not explicitly in terms of a diffusion process; finally, only the question of the stability of TFT against AD is addressed, not that of the initial increase of TFT.

Dugatkin and Wilson’s model (termed below the “DW model”) assumes a population made up with an infinite number of patches, each of given constant size. The TFT strategy is the resident strategy in that population. The TFT individuals are assumed to be sessile, whereas defectors can move from one individual to another within a patch, as well as from one patch to another. There is an interpatch travel time during which no payoff can be achieved, resulting in a cost to mobility. The DW model can make the classical assumption of ESS theory that encounters are random, because it assumes that there are infinitely many patches, that patches are small enough for individuals within a patch to meet each other many times, and that the patches visited by a defector are randomly sampled from the global population. Dugatkin and Wilson’s conclusions indicate that if the travel time between patches is not prohibitive, AD individuals should take advantage of moving from patch to patch in search of naive TFT individuals. Thus, one can expect the evolution of “roving” defectors, characterized by an optimal stay time within a patch.

The DW model considers the moves of defectors between many possible clusters (patches), but it does not represent those occurring within a patch, where a defector may flip from one TFT individual to another. Our model is fundamentally different from the DW model, because we primarily deal with a single cluster or patch (TFT-pure, or possibly mixing TFTs and ADs) settled in a uniform ocean of defectors. Thus, intercluster mobility is irrelevant to our case. Instead, our model emphasis is on intrACLuster mobility. This difference between the models is critical, because intrACLuster mobility sets up the dynamics of encounters within and around the fringe of the traveling wave, and this appears to determine the outcome of the invasion process.

Enquist and Leimar (1993) have also studied the stability of cooperation once it is established. The cooperative strategy they consider consists in cooperating on the first round; if the partner reply is defection, the cooperator interrupts the interaction and the defector must move away in search of another cooperating individual to exploit. Once two players start interacting, Enquist and Leimar say that a “coalition” has been formed. The average duration of a coalition between two cooperators is referred to as the “coalition time.” In our framework, the coalition time of TFT is determined by the interaction time \( \tau \), mortality rate \( d \), and mobility rate \( \mu_T \). Increasing \( \mu_T \) would decrease the coalition time. Also, Enquist and Leimar define the “search time” as the mean time taken for a defector to find a cooperator to interact with. The search time of Enquist and Leimar has no straightforward equivalent in our model, but we can interpret our model in this way. For an AD player the search time would be equal to the time spent being paired consecutively with other AD players and unable to sucker TFT players. In a population in which AD is rare (this being Enquist and Leimar’s assumption), this search time is approximately equal to the time spent while paired with the same AD player. Using notations from our auxiliary model, the
search time for a defector would thus be $Q_{\text{pair}} \tau + Q_{\text{pair}}^2 \tau + \ldots = \tau Q_{\text{pair}}/(1 - Q_{\text{pair}})$, where $Q_{\text{pair}}$ denotes the probability that two individuals with motion probabilities $q$, moving or not, meet again on the next interaction: $Q_{\text{pair}} = (1 - q)^2 \times \{1 + (1/2)[q^2/(1 - q^2)]\}$. This search time decreases as the motion probability increases. Enquist and Leimar conclude that a longer search time for defectors and a longer coalition time for cooperators favor cooperation. In our model, maximum search time and maximum coalition time are achieved for zero mobility in both AD and TFT. In this respect, our results are at odds with Enquist and Leimar’s. However, in our approach, mobilities not only influence cooperators’ coalition time and defectors’ search time but also affect the likelihood of TFT pairings on the front of invasion, that of AD assortments in the core of the cluster, and that of TFT individuals keeping track of AD individuals. The bottom line is that maximizing those three quantities, which require mobilities to exceed critical minima, is more important in determining the success of a spatial invasion of TFT than minimizing the coalition time and the search time.

Most recently, Hutson and Vickers (1995) have investigated a spatial version of the IPD similar to ours. While we aimed at developing a model tractable by purely analytical means, Hutson and Vickers’s approach is mainly numerical. Our spatial version of Hamilton’s rule (inequality [6]) was grounded on the assumption that the population has reached or stays near the environment’s carrying capacity $K$. The model designed by Hutson and Vickers does not resort to this approximation but, rather, can be written as a more complicated set of differential equations that no longer belongs to the class of “replicator-diffusion” systems. Computer simulations confirm the possibility of invasion by TFT and further uncover that of the long-term stable coexistence of TFT and AD.

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APPENDIX

Probability of Repeated Interactions

For the purpose of defining local interactions between players, it is convenient to regard space as subdivided into discrete contiguous cells of size $L$ such that, each cell contains on average two individuals at any time (hence $L = 2/K$). This representation is possible through the assumption that the total population has attained the environment carrying capacity $K$ (constant and uniform over space) and may fluctuate only mildly around it. Two interacting individuals will play each other again on the next round if, after time $\tau$ has elapsed, they end up in a same cell again.

Given that a type 1 player located at $x$, at time $t$ interacts with a type 2 located at $y$, at time $t$, we are looking for the probability that the type 1 meets with the same type 2 on
its next interaction (at time $t + \tau$). This probability is equal to the probability that type 2
survives over the time interval $[t, t + \tau]$ times the probability that, assuming it does
survive, it stands in the cell occupied by type 1 at $t + \tau$. The former is $e^{-d\tau}$. The latter
can be written as the conditional probability

$$\tilde{w} = \text{Prob}(y_{t+\tau} \in [(X_{t+\tau})^*L, (X_{t+\tau})^* + 1)L] | y_t \in [(X_t)^*L, (X_t)^* + 1)L),$$

(A1)

where $[z]$ denotes the integer part of $z$, and $X = x/L$. (Here we have assumed, without
loss of generality, that the origin of the spatial axis coincides with a boundary point of
one of the cells.) We first recondition $\tilde{w}$ (for handling conditional probabilities, see Chung
1979) with respect to $x_{t+\tau}$. By introducing the Gaussian distribution of the diffusion
process, we get

$$\tilde{w} = \int_{\xi \in \mathbb{R}} \text{Prob}(y_{t+\tau} \in [(X_{t+\tau})^*L, (X_{t+\tau})^* + 1)L] | y_t = \xi \times e^{-\frac{\xi^2}{4\tau \mu_1}} \frac{2}{\sqrt{\pi \tau \mu_1}} d\xi.$$  (A2)

The possible initial positions $y_t$ are equally likely over $[(X_t)^*L, (X_t)^* + 1)L]$; thus

$$\tilde{w} = \int_{\alpha = [X_t]L}^{([X_t]+1)L} \int_{\xi \in \mathbb{R}} \text{Prob}(y_{t+\tau} \in [(X_{t+\tau})^*L, (X_{t+\tau})^* + 1)L] | y_t = \alpha \times e^{-\frac{\xi^2}{4\tau \mu_1}} \frac{2}{\sqrt{\pi \tau \mu_1}} d\xi d\alpha,$$

and  $x_{t+\tau} = x_t + \xi \times e^{-\frac{(v-u)^2}{4\tau \mu_2}} \frac{2}{\sqrt{\pi \tau \mu_2}} d\xi dv,$

(A3)

as we make use, once again, of the Gaussian distribution that defines the mobility rates.
The approximation $[X_t + \xi/L] = [X_t] + \xi/L$ has minor effects as long as $\mu_1$ and $\mu_2$ are
not too close to zero and/or $K$ is large enough, so that the Gaussian functions involved in
the above integral are not too peaked and/or the intervals of integration are short enough.
This approximation together with the changes of variable $u := u - [X_t]L$ and $v := v - [X_t]L - \xi$ finally yields

$$\tilde{w} = e^{-\frac{(v-u)^2}{4\tau \mu_2}} \frac{2}{\sqrt{\pi \tau \mu_2}} d\xi d\alpha,$$

(A4)

from which we get

$$w = \frac{Ke^{-d\tau}}{8\pi \sqrt{\mu_1 \mu_2}} \int_{\alpha \in \mathbb{R}} \int_{(u,v) \in [-1/K, 1/K]^2} e^{-\frac{1}{4\tau \mu_1} \frac{(\xi-u)^2}{4\mu_1} + \frac{(\xi-v)^2}{4\mu_2}} d\xi d\alpha d\xi d\alpha,$$

(A5)

ASYMPTOTIC DEVELOPMENT OF $w$ FOR LARGE $K$

Let us set $\epsilon = 1/K$. We seek an asymptotic development of

$$w = \frac{e^{-d\tau}}{8\pi \epsilon \sqrt{\mu_1 \mu_2}} \int_{\alpha \in \mathbb{R}} \int_{(u,v) \in [-\epsilon, \epsilon]^2} e^{-\frac{1}{4\tau \mu_1} \frac{(\xi-u)^2}{4\mu_1} + \frac{(\xi-v)^2}{4\mu_2}} d\xi d\alpha d\xi d\alpha,$$

(A6)

for small $\epsilon$. Let us set $\sigma_1 = \sqrt{2\tau \mu_1}$, $\sigma_2 = \sqrt{2\tau \mu_2}$, and $\delta = 1/(1/\sigma_1^2 + 1/\sigma_2^2)$. Then we have
\[ w = \frac{e^{-\sigma^2 t}}{2\pi} \int_{\xi \in \mathbb{R}} d\xi \left( \frac{1}{\sqrt{2\pi \sigma_1}} \int_{\mu = -\epsilon}^{\epsilon} e^{-\frac{(\mu - \xi)^2}{2\sigma_1^2}} du \right) \left( \frac{1}{\sqrt{2\pi \sigma_2}} \int_{\nu = -\epsilon}^{\epsilon} e^{-\frac{(\nu - \xi)^2}{2\sigma_2^2}} dv \right). \]  
(A7)

We will denote the terms between parentheses by \( F_1(\xi) \) and \( F_2(\xi) \), respectively. Thus we have

\[ w = \frac{e^{-\sigma^2 t}}{2\epsilon} \int_{\xi \in \mathbb{R}} F_1(\xi) F_2(\xi) d\xi. \]  
(A8)

A straightforward change of variables gives

\[ F_i(\xi) = \frac{1}{\sqrt{2\pi}} \int_{\eta_i^{(\xi+\epsilon)}}^{\eta_i^{(\xi-\epsilon)}} e^{-\frac{1}{2}\xi^2} d\eta \quad (i = 1, 2). \]  
(A9)

We now expand the integrand in \( \epsilon \) around \( \epsilon = 0 \) and integrate. The leading-order term is the width of the interval (i.e., \( 2\epsilon/\sigma_i \)) times the function value at the midpoint, \( \exp(-\xi^2/2\sigma_i^2) \). Higher-order terms in \( \epsilon \) also have the same exponential prefactor, so they can be safely integrated over \( \xi \) and the result will be of higher order in \( \epsilon \). Then we find

\[ F_i(\xi) = \frac{1}{\sqrt{2\pi}} \frac{2\epsilon}{\sigma_i} e^{-\xi^2/2\sigma_i^2} \quad (i = 1, 2). \]  
(A10)

Substituting into equation (A8) gives

\[ w = \frac{e^{-\sigma^2 t}}{\pi} \frac{\epsilon}{\sigma_1 \sigma_2} \int_{\xi \in \mathbb{R}} e^{-\sigma_2 \xi^2} d\xi, \]  
(A11)

which yields

\[ w = \frac{\epsilon e^{-\sigma^2 t}}{\sigma_1 \sigma_2 \sqrt{\pi \sigma_2}}. \]  
(A12)

Equation (7) ensues. Notice that the requirement \( w \leq 1 \) does impose a restriction on the domain of validity of this approximation, namely, that \( \mu_1 \) and \( \mu_2 \) not be too small—an assumption we already had to put forward when we calculated the exact expression (A5) of \( w \).

**PAYOFF MATRIX FOR TFT VERSUS AD IN THE SPATIAL IPD**

In order to calculate \( \Phi_T \) in equation (1), let us consider a TFT player located at \( x \) at time \( t \). To this location corresponds a discrete cell in which only two individuals are standing. The TFT individual interacts with the other player that is present in the same cell and that is located at \( y \) at this moment. With probability \( n_T(y, t)/N(y, t) \), the other partner plays TFT too; with probability \( n_D(y, t)/N(y, t) \), it plays AD. Under the assumptions that the densities \( n_T \) and \( n_D \) vary smoothly over space and that the length of a cell \( L \) is small enough (large \( K \)), we have the first-order approximations \( n_T(y, t)/N(y, t) \approx n_T(x, t)/N(x, t) \) and \( n_D(y, t)/N(y, t) \approx n_D(x, t)/N(x, t) \). If, in effect, the partner is a TFT, the first TFT player will receive a payoff of \( R \) over the time period \( t \). Yet this payoff has to be discounted by the cost of mobility, \( \gamma \), defined per interaction. Should the partner be an AD, the payoff earned by the TFT player will be \( P - \gamma \) if the interactant is recognized from the previous encounter (TFT player retaliates). This happens with probability \( w \). With probability \( 1 - w \), the TFT player interacts with a stranger and gets the sucker’s payoff \( S - \gamma \). A payoff is earned if the player survives over the interaction time, which happens with probability \( e^{-\sigma^2 t} \). Overall, the payoff per unit time obtained by the TFT player is given by

\[ \Phi_T = \frac{n_T}{N} \beta(R - \gamma) + \frac{n_D}{N} \beta[w(P - \gamma) + (1 - w)(S - \gamma)], \]  
(A13a)
where $\beta = e^{-d_t/\tau}$. Likewise, we have

$$
\Phi_D = \frac{n_D}{N} \beta (P - \gamma) + \frac{n_T}{N} \beta [w (P - \gamma) + (1 - w)(T - \gamma)].
$$

(A13b)

Deriving $\Phi$ is then straightforward. Payoff matrix entries follow readily:

$$
a_{11} = \beta R, \quad (A14a)
$$

$$
a_{12} = \beta [w (P - \gamma) + (1 - w)(S - \gamma)], \quad (A14b)
$$

$$
a_{21} = \beta [w (P - \gamma) + (1 - w)(T - \gamma)], \quad (A14c)
$$

and

$$
a_{22} = \beta P. \quad (A14d)
$$

COST OF MOBILITY DEPENDENT ON THE MOBILITY RATE

Our nominal case assumes a cost of mobility independent of the mobility rate. Let us consider a fixed value of defectors' mobility $\mu_D$. Then the range of $\mu_T$ begetting invasion is an interval, denoted by $[\mu_T^{\text{min}}, \mu_T^{\text{max}}]$, which corresponds to the portion of the curve defined by the left-hand side of inequality (6) that lies above the constant level $c/b$ (fig. A1). Now let us assume that the cost of mobility does depend on the mobility rate. Using the cost-benefit parameterization of the payoffs $T$, $R$, $P$, and $S$ introduced above, the conditions $a_{11} > a_{21}$ and $a_{22} > a_{12}$ read

$$
-\frac{c}{b} (1 - w) < \frac{\Delta \gamma}{b} < -\frac{c}{b} + w.
$$

(A15)

When condition (A15) is met, TFT can dominate AD according to inequality (4). This happens when

$$
\frac{w}{1 + (1 - w) \delta (\mu_T/\mu_D)} > \frac{c}{b} + \frac{\Delta \gamma}{b} + \frac{1 + \delta (\mu_T/\mu_D)}{1 + (1 - w) \delta (\mu_T/\mu_D)}.
$$

(A16)

The value $\Delta \gamma$ stands for the difference of the costs paid for moving at rates $\mu_T$ and $\mu_D$:

$$
\Delta \gamma = \gamma(\mu_T) - \gamma(\mu_D).
$$

(A17)

We keep on considering a given value of $\mu_D$. It must be noticed that $\Delta \gamma$ is an increasing function of $\mu_T$, null at $\mu_T = \mu_D$. We first show that condition (A15) is matched for any value of $\mu_T$ belonging to $[\mu_T^{\text{min}}, \mu_T^{\text{max}}]$, provided that the cost of mobility $\gamma(\mu)$ does not increase too rapidly with $\mu$. Let us first address the case of values of $\mu_T$ smaller than $\mu_D$. Then the left-hand side of equation (A15) is satisfied if $\Delta \gamma$ remains small enough; to be precise, we request that $\Delta \gamma$ takes on a value larger than $-c$ at $\mu_T = 0$; that is, $\gamma(\mu_D) < c$. The right-hand side will hold true for any $\mu_T$ such that $w > c/b$. As we increase $\mu_T$ such that we just pass the resident defectors' mobility $\mu_D$, $\Delta \gamma/b$ becomes positive and the left-hand inequality involved in condition (A15) is automatically matched. If at $\mu_T = \mu_D$, $w$ is still $\geq c/b$, and if $\gamma(\mu_T)$ increases slowly enough as $\mu_T$ increases, then the right-hand inequality will be satisfied as well. Finally, we have $w > c/b$ for any $\mu_T$ in $[\mu_T^{\text{min}}, \mu_T^{\text{max}}]$, because the denominator of the left-hand side of inequality (A16) is greater than one.

Next we discuss the effect of a mobility-dependent cost of mobility on inequality (A16). The right-hand side of inequality (A16) is an increasing function of the mobility rate $\mu_T$ that is represented by the thin curve in figure A1. Here, inequality (A16) is satisfied when the thick curve is above the thin one. Geometrically, $[\mu_T^{\text{min}}, \mu_T^{\text{max}}]$ is shifted to the left when $\mu_D$ lies in $[\mu_D^{\text{min}}, \mu_D^{\text{max}}]$ (fig. A1, panel A), whereas $[\mu_T^{\text{min}}, \mu_T^{\text{max}}]$ is narrower when $\mu_D$ is smaller than $\mu_D^{\text{min}}$ (fig. A1, panel B). In the latter case, if the cost of mobility increases rapidly, there may be no mobility rate satisfying condition (A16); then the thin line would be above the thick curve in figure A1, panel B.
Fig. A1.—Effect of making the cost of mobility dependent on the mobility rate. Thick curve (a), schematic graph of the cost of reciprocation $H$ given by the left-hand side of inequality (A16). Thin curve (b), schematic graph of the generalized cost-benefit ratio given by the right-hand side of eq. (A21). Horizontal line, $c/b$ level. The interval $[\mu_T^{\text{min}}, \mu_T^{\text{max}}]$ contains $\mu_T$ values that permit invasion by cooperators when the cost of mobility is independent of the mobility rate ($\Delta \gamma = 0$). The interval $[\tilde{\mu}_T^{\text{min}}, \tilde{\mu}_T^{\text{max}}]$ is the range of $\mu_T$ for which condition (A21) is satisfied, when the cost of mobility does depend on the mobility rate. A, $\mu_D$ lies in $[\mu_T^{\text{min}}, \mu_T^{\text{max}}]$. B, $\mu_D$ is smaller than $\mu_T^{\text{min}}$. 
DERIVATION OF $Q$, $Q'$, $Q''$, AND $Q_{retal}$

We take the right edge of the cluster as the origin along the axis. From this origin, the cells on the left that define the cluster are numbered $1, 2, \ldots, C$. The value $C$ defines the size of the cluster, in number of cells. The cells on the right (right part of the front of invasion) are generically indexed by $m$ ($m = 1, 2, \ldots$). The probability that a TFT player located in cell $i$ within the cluster gets paired in cell $m$ on the right front with a partner from the cluster is

$$
\frac{1}{2} (1 - q) q^{m+i-1} \left[ (1 - q) q^{m} + \ldots + \frac{1}{2} (1 - q) q^{m+i-1} + \ldots + (1 - q) q^{m+C-1} \right]
$$

(A18)

$$
= \frac{1}{2} (1 - q) q^{m+i-1} q^{m} \left[ 1 - q^{C} - \frac{1}{2} (1 - q) q^{l-1} \right].
$$

The probability that an individual located in cell $i$ within the cluster gets paired in cell $m$ on the right front with a player from the cluster, too, is obtained by summing these terms for $m = 1, 2, \ldots$. Then the cumulative probability $Q$ follows by taking the average over $i$ varying from 1 to $C$ and using the symmetry of the front of invasion (which extends on the left and on the right of the cluster). We obtain

$$
Q = \frac{1}{C} \frac{q^2}{1-q^2} \left( 1-q^C \right) \left[ 1 - q^{C} - \frac{1}{2} \frac{(1-q)(1+q^C)}{1+q} \right].
$$

(A19)

To get the expression of $Q'$, we notice that the probability that an individual located in cell $i$ within the cluster remains inside is

$$
\frac{1}{2} (1 - q) q^{l-1} + \ldots + \frac{1}{2} (1 - q) q + (1 - q) + \frac{1}{2} (1 - q) q
$$

(A20)

$$
+ \ldots + \frac{1}{2} (1 - q) q^{C-1} = 1 - \frac{1}{2} (q^{l} + q^{C-l+1}).
$$

By averaging these terms over $i$ running from 1 to $C$ we get

$$
Q'' = 1 - \frac{1}{C} \frac{q}{1-q}(1-q^C).
$$

(A21)

Finally, by definition of $Q_{retal}$ we have:

$$
Q_{retal} = \left[ \frac{1}{2} (1-q_1) q_1^M \right] \left[ \frac{1}{2} (1-q_2) q_2^M \right]
$$

(A22)

$$
+ \left[ \frac{1}{2} (1-q_1) q_1^{M+1} \right] \left[ \frac{1}{2} (1-q_2) q_2^{M+1} \right] + \ldots,
$$

which recasts into

$$
Q_{retal} = \frac{1}{4} (1-q_1)(1-q_2) \frac{(q_1 q_2)^M}{1-q_1 q_2}.
$$

(A23)

PAYOFF MATRIX FOR TFT VERSUS STOCHASTIC STRATEGIES IN THE SPATIAL IPD

In a game involving two stochastic strategies, the behavior of each player on a given round is determined by the whole history of past encounters between these two players. We keep on assuming that player’s memory is limited to the last round of the game. Let us recall the notations introduced in the main text: $E = (R, S, T, P)^*$ is the vector of payoffs for a single round of the IPD, and $w_{ij}$ is the probability that an $i$ player meets twice consecutively with the same $j$ partner. If the two players have not met in the
previous interaction (which happens with probability $1 - w_{ij}$), the payoff to $i$ is $R$ if both
$i$ and $j$ cooperate (a situation we call the “CC state’’); $S$ if $i$ cooperates while $j$ defects
(CD state); $T$ if $i$ defects whereas $j$ cooperates (DC state); $P$ if both individuals defect (DD
state). Furthermore, the probability of the CC state is $p_ip_j$; that of CD is $p_i(1 - p_j)$; DC,
$(1 - p_i)p_j$; DD, $(1 - p_i)(1 - p_j)$. Now, if the two players have met in the previous
interaction but not in the other one before (probability $[1 - w_{ij}]w_{ij}$), the probabilities of
the states CC, CD, DC, and DD can be obtained by regarding the successive interactions
of the two players as a Markov chain on the state space CC, CD, DC, and DD (see Nowak
1990). In the previous interaction, the probabilities of each state were exactly the simple
ones explicated above; we denote them by $\pi_{ij}^0$, $\pi_{ij}^1$, $\pi_{ij}^T$, $\pi_{ij}^P$. Thus, the probabilities that
we are now looking for are merely given by the components of $\mathcal{T}_{ij}\pi_{ij}$, where $\pi_{ij}$ is the
vector ($\pi_{ij}^0$, $\pi_{ij}^1$, $\pi_{ij}^T$, $\pi_{ij}^P$) and $\mathcal{T}_{ij}$ designates the transition matrix of the Markov process
(Nowak 1990), given by equation (9). More generally, the probability that the two players
met exactly $k$ times consecutively prior to the current round is $(1 - w_{ij})w_{ij}^k$, and the probabilities of the state CC, CD, DC, and DD on the current play are given by the
components of the vector $\mathcal{T}_{ij}^k\pi_{ij}$. Finally, the expected payoff $e_{ij}$ is

$$e_{ij} = (1 - w_{ij})\langle \pi_{ij}, E \rangle + (1 - w_{ij})w_{ij}\langle \mathcal{T}_{ij}\pi_{ij}, E \rangle + (1 - w_{ij})w_{ij}^2\langle \mathcal{T}_{ij}^2\pi_{ij}, E \rangle + \ldots,$$

(A24)

which yields equation (10).

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