Working Paper

The Evolution of Cooperation in Spatially Heterogeneous Populations

Régis Ferrière and Richard E. Michod

WP-96-29
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THE EVOLUTION OF COOPERATION IN SPATIALLY HETEROGENEOUS POPULATIONS

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TIT-FOR-TAT IN A SPATIAL GAME

ABSTRACT

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. The outcome of this game is basically determined by the probability $\underline{w}$ of repeated interactions between players. Traditional models of the IPD game neglect factors that are likely to influence $\underline{w}$, including spatial mobility of players and their rate of mortality. More sophisticated models that involve changing partners because of movement and death conclude that population mixing due to individual mobility limits cooperation. However these models represent space only implicitly, without keeping track of the exact positions of organisms. Here we develop a dynamical model of the IPD where temporal and spatial variations in the population are explicitly considered. This model accounts for the stochastic motion of individuals and the non-randomness of local interactions; it makes the probability of repeated interactions dependent upon the player's behavior and life cycle; and it allows investigation on the outcome of the game of basic traits of the life-cycle (death rate, interaction time) and environment (carrying capacity). The model is first used to derive a spatial version of the Hamilton's rule for the increase of cooperation, represented by individuals playing tit-for-tat (TFT) and initially organized in a small cluster, against unconditional defection (always-defect strategy, AD). We find that a threshold level of mobility in AD players is required to beget invasion by TFT. Furthermore, the level of mobility in successful TFT newcomers must be approximately equal or somewhat higher than that of resident defectors. Substantial 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. If players are able to adjust their mobility rate, TFT individuals arriving in a cluster will benefit from increasing their own as the cluster spreads out. 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. For a second cooperative strategy to invade and replace TFT in spatially homogeneous populations, a third strategy—with characteristics specific to those of the potential invader—must be present or else invasion will not occur. However, in spatially heterogeneous populations this strategic heterogeneity is not required to pass through TFT on the way to more robust forms of cooperation.

INTRODUCTION

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). TFT, 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 towards sociality. Once established, TFT paves the way for more robust forms of reciprocal altruism, represented by strategies like "generous tit-for-tat" (GTFT) 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 effectively serve as a stepping stone for the establishment of more generous strategies.

The first problem is that a world of ADs 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 by clusters of TFT 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 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 TFTs and mobile ADs. 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, very efficient at exploiting and devastating clusters of naive cooperators.

In a preliminary study, we introduced a model involving non-random interactions, mortality and potential mobility in both TFT and AD (Ferriere and Michod 1995). Our goal in the present paper is to further develop a general model of the IPD game which, while being as simple as possible, accounts for both spatial and temporal effects that arise from the local, non-random, 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 TFTs can spread from rarity in an infinite population of mobile ADs. Then we consider the stability of TFT, once established, against re-invasion 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 as 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 primarily concerned 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 which 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 which 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 μ; the so-called mobility rate. The probability that a certain distance is moved in the time Δt by an individual with mobility μ has the Gaussian distribution with mean 0 and variance $2\mu\Delta t$.

In the most general situation, we assume that a moving individual incurs a cost of mobility, denoted by γ and this cost may be a function of μ, 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 τ. 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 τ 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, τ determines the timing of reproduction of an individual along its lifespan.

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 & 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 τ 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 which is a complicated nonlinear function of the mobility rates, death rate, interaction time and environment carrying capacity (see Appendix). This *w* is analogous to *w* in the standard IPD, the probability of continuing the game (Axelrod & 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, endogeneous *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 which stems from the idea that the growth rate of a strategy depends upon how well individuals perform relative to the local average payoff (a view rooted in Fisher (1930) and elaborated by Vickers (1989)). Thus the equations involve a term representing population growth as determined by the outcome of the game, and a diffusion term which accounts for mobility:

$$\begin{cases} \dfrac{\partial n_1}{\partial t} = n_1\left(\Phi_1 - \overline{\Phi}\right) + \mu_1 \dfrac{\partial^2 n_1}{\partial x^2} \\ \dfrac{\partial n_2}{\partial t} = n_2\left(\Phi_2 - \overline{\Phi}\right) + \mu_2 \dfrac{\partial^2 n_2}{\partial x^2} \end{cases}, \tag{1}$$

where $\underline{\Phi_1 \equiv \Phi_1(x,t)}$ and $\underline{\Phi_2 \equiv \Phi_2(x,t)}$ are the local payoff per unit time to type-1 and type-2, and $\underline{\overline{\Phi}}$ stands for $\underline{\overline{\Phi}(x,t)}$, the average payoff per unit time of the *local* population at *x* and *t*,

$$\overline{\Phi} = \frac{n_1}{N}\Phi_1 + \frac{n_2}{N}\Phi_2 . \tag{2}$$

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

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

$$\overline{\Phi} = \frac{\langle \mathbf{n}, \mathbf{An} \rangle}{N^2} \tag{3b}$$

The $\underline{a_{ij}}$'s are the payoffs per unit time to a type-*i* player against a type-*j* opponent (*i*, *j* = 1, 2). The notation $(\mathbf{An})_1$ refers to the first component of the vector $\mathbf{An}$ (respectively the second component for $(\mathbf{An})_2$). $\langle \ , \ \rangle$ denotes the scalar product of two vectors. The matrix $\mathbf{A}$ is entirely determined when the strategies 1 and 2 are specified. It will depend upon 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 $\underline{\tau}$, carrying capacity *K*, and any other variable involved in the definition of the strategies). A priori, $\mathbf{A}$ may vary in time and space. However, we will see that in games opposing *TFT* to *AD* or to stochastic strategies, $\mathbf{A}$ is actually constant.

Spatial dominance and invasion.-- Providing a rigorous mathematical definition of invasion in spatial population models can be difficult. The usual ESS concept of evolutionary stability 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 $\mathbf{A}$ is independent of space and time and there is exactly one ESS, this ESS is still stable when spatial heterogeneity is considered. However, if $\mathbf{A}$ defines a two-strategy game in which each pure strategy is an ESS, "spatial dominance" of one ESS by the other may occur (Hutson & Vickers 1992; see also Vicker 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 $\partial^2 n_1/\partial x^2 = \partial^2 n_2/\partial x^2 = 0$ in (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

$$(a_{11} - a_{21})/(a_{22} - a_{12}) > \vartheta(\mu_1/\mu_2) \qquad (4)$$

where $\vartheta(\mu_1/\mu_2)$, 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 (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 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* VS. *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 on their previous encounter. The payoff matrix A for a spatial IPD opposing *TFT* and *AD* is calculated in the Appendix. There type-1 is *TFT* (abbreviated in "T") and type-2 is *AD* ("D"). Using the cost-benefit parameterization of the payoffs *T*, *R*, *P*, *S* introduced above, the conditions $a_{11} > a_{21}$ and $a_{22} > a_{12}$ reduce to

$$w > c/b . \tag{5}$$

Under condition (5), *TFT* spatially dominates *AD* when (cf. equation (4))

$$\frac{w}{1 + (1-w)\,\vartheta(\mu_T/\mu_D)} > \frac{c}{b}. \tag{6}$$

where *w* is given in the Appendix.

Equation (6) provides a Hamilton's rule (Hamilton 1964, Michod and Hamilton 1980) for the increase of cooperation in a non-social, 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 *TFT*s. The right-hand side of (6) is the cost-benefit ratio of cooperation. The spatial Hamilton's rule (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 (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, μ_T, can be slightly smaller, equal or a lot larger than that of resident defectors μ_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 μ_T must be larger than μ_D (e.g. along the isocline inside the bold one in fig. 2A; note that the dotted line $\mu_T = \mu_D$ lies out of this isocline). In this case, the invading range shifts to the right of the resident μ_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 towards 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 upon the total population density.

We now examine how changes in d and τ affect the range of mobility rates μ_T allowing invasion by TFT (defined by equation 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:

$$w \approx \psi \frac{\mu_1\mu_2}{(\mu_1 + \mu_2)^{5/2}} \tag{7a}$$

with

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

By reporting equation (7a) into (6), we obtain an approximate but tractable condition for TFT to dominate AD in terms of ψ and the mobility rates. Figure 3A shows how the critical values of c/b varies as a function of ψ. Increasing ψ 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 μ_D. From equation (7b), it is apparent that an increase in ψ occurs when either d or τ is decreased (fig. 3B). Thus, decreased mortality or interaction time will increase the range of mobility rates allowing 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

$$\frac{\Delta d}{d} > E\frac{\Delta\tau}{\tau} \tag{8}$$

with $E = 1 + 1/(2d\tau)$.[i]

Finally, when the cost of mobility γ depends on the mobility rate (but remains lower than the cost c of a cooperative act), the maximum rate of mobility μ_T begetting invasion (for given μ_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.

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[i] This is because the change caused in ψ writes $\Delta\psi = \psi\left[\tau\Delta d - \left(d + 1/(2\tau)\right)\Delta\tau\right]$.

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 which 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 TFTs, and therefore make it more difficult for TFT 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 (i) the likelihood of assortative encounters between moving TFTs that travel into the front of invasion, and moving ADs that intrude the core of the cluster; and (ii) the chance of retaliation by a TFT against a moving AD.

The successful invasion of a finite cluster of TFT in an infinite population of AD requires pioneering moves towards the inhospitable surrounding area occupied only by AD 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 TFTs which 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 must primarily avoid being suckered. It may succeed in doing so, not only by playing itself, but also by retaliating. When retaliating, a TFT will not perform worse than an AD 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. Firstly, because as an AD undergoes retaliation, this individual is no longer available to interact with and sucker a naive TFT. This is especially valuable for the well-being of TFT when it applies to ADs that intrude the core of the TFT cluster: as they remain tied up with known *TFTs*, such *ADs* end up neutralized and incapable of exploiting naive *TFTs*. Second, retaliation coupled with a move towards the front of invasion replays the Trojan horse metaphor: a *TFT* is taken onto the front of invasion where *ADs* are still thriving, without facing the threat of getting paired there with a stranger *AD*. 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—and unavoidably parameter-dependent—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 1, which imposes $p = 1 - q$. As shown in figure 4*A* for $q = 0.1$ and $q = 0.6$, this probability distribution is a space-discrete analog 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 μ; here, the variance is still an increasing function of q, thus the parameter q can also be regarded as a measure of individual mobility.[ii]

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

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[ii] 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 $2q(1+q)/(1-q)$.

individuals. We first consider the cumulative probability *Q* that a *TFT* located in the cluster moves out and end up paired on the front of invasion with another *TFT* also coming from the cluster. *Q*, computed in the Appendix, is shown on figure *B* (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 outward 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* picked at random in the cluster stays therein, *Q*, *Q’* and *Q’”* are straightforwardly related: $Q' = 1-Q-Q''$. Figure 4*B* portrays *Q’* and *Q”* as functions of *q*, for $C = 5$. Like *Q*, the ratio Q/Q', displayed in figure 4*C*, 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_{retal} that they move away, making a jump of at least *M* cells, say, to the right, but remain paired together (fig. 5*A*). Figure 5*B* displays contours of the surface defined by Q_{retal} as a function of q_1 and q_2, when $M = 1$. It shows that Q_{retal} is maximized at high values of q_1 and q_2 (also, the larger *M*, the more peaked the surface). Thus, a *TFT* has a better chance of keeping track of and retaliating against a moving AD if both the AD's 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 given AD mobility, a low mobility in TFT creates unimodal dominance by AD: the TFT distribution is humped over the fringe of the traveling wave, which creates a rich, easy-to-access diet of naive cooperators that ADs entering the cluster can feed on. As TFT mobility increases, TFT becomes dominant and, as long as μ_T remains lower than μ_D, dominance is monotonous. When μ_T exceeds μ_D, dominance becomes unimodal again, with an accumulation of ADs over the fringe. This AD aggregation is dramatized as μ_T keeps on increasing, and that produces a "wall" of defectors in the fringe much harder to beat for TFT.

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? Re-invasion 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; *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 non-spatial IPD, Nowak and Sigmund (1992) showed that *TFT* was invariably superseded by *GTFT* $\underline{(s = 1, g > 0)}$, 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 towards 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 fro 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 $\underline{(p_1, q_1)}$ and $\underline{(p_2, q_2)}$, with mobility rates $\underline{\mu_1}$ and $\underline{\mu_2}$ 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 $\mathbf{E} = \underline{(R, S, T, P)^*}$ the vector of payoffs for a single round of the *IPD*, and by $\underline{w_{ij}}$ the probability that a *i*-player meets twice consecutively with the same *j*-partner. We also need introduce the Markovian matrix (see the Appendix) $\underline{\mathfrak{X}_{ij}}$ given by

$$\mathfrak{X}_{ij} = \begin{pmatrix} p_i p_j & q_i p_j & p_i q_j & q_i q_j \\ p_i(1-p_j) & q_i(1-p_j) & p_i(1-q_j) & q_i(1-q_j) \\ (1-p_i)p_j & (1-q_i)p_j & (1-p_i)q_j & (1-q_i)q_j \\ (1-p_i)(1-p_j) & (1-q_i)(1-p_j) & (1-p_i)(1-q_j) & (1-q_i)(1-q_j) \end{pmatrix}. \tag{9}$$

Then the expected payoff $\underline{e_{ij}}$ is

$$e_{ij} = (1-w_{ij})\langle\, (\mathfrak{I} - w_{ij}\mathfrak{X}_{ij})^{-1}\pi_{ij}\,,\ \mathbf{E}\,\rangle \tag{10}$$

(where $\mathfrak{I}$ stands for the identity matrix), and the condition for spatial dominance of strategy *j* by strategy *i* is similar to equation (4):

$$\left(e_{ii} - e_{ji}\right)/\left(e_{jj} - e_{ij}\right) > \vartheta\left(\mu_i/\mu_j\right). \tag{11}$$

Numerical computations using (10) and (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 $\underline{e_{11} > e_{21}}$). 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 (Ferriere and Michod, manuscript in preparation), 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 re-invasion by AD can be discussed more straightforwardly. Simply by reversing inequality (6) one obtains the condition for invasion by rare ADs 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 TFT's rate of mobility is raised.

Thus, by moving at the highest possible rate, cooperators will find the most efficient protection against re-invasion by AD.

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 non-spatial IPD games which 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 non-random and it is natural to regard interactions as taking place 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 non-random, 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 non-altruistic phenotypes in a two-dimensional array. Although Wilson et al.'s approach is not based on game theory, the altruistic and non-altruistic 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 non-altruists. 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, localised cluster of altruists could invade. In fact, the cluster was not vulnerable to invasion by non-altruists while 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), Hutson 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 upon 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: (i) the game affects individual reproductive success, not the individual survivorship (hence we assume a constant intrinsic death rate d), (ii) a small interaction time τ, (iii) a large carrying capacity K, and (iv) a total population density staying near K. Under these assumptions, we found a range of TFT mobility rates begetting spatial invasion in a resident population of ADs, so long as AD is 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 TFT retaliates against a known AD. 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 Eq. (8)). The consequence is the same if the mortality rate increases and the interactions 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 equation (A18)). On the other hand, reducing mortality may give suckered TFTs a better chance to retaliate. Raising the interaction time, however, can be detrimental to this respect, because this amounts to leave more time to a defector for moving away from its TFT victim. Yet this effect is buffered when mobility rates are reduced (Q_{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 τ is raised.

Although our model is limited to two-strategy games, the two strategies involved result in a variety of effects, depending upon the local spatial setting in which they occur. For example, in the TFT-AD spatial struggle, consider a suckered TFT which gets a chance of retaliating against an AD. If the AD is moving to the core of the cluster, the retaliating TFT ties up the intruder and prevents him from exploiting a naive TFT in the cluster—in so doing, the TFT has neutralized a defector on a move that puts the cluster at risk. Retaliation against an AD that moves to the front of invasion is also valuable for the progress of the whole invasion wave, for it allows the retaliating TFT to make a safe move to the front, protected by its partnership with a known AD. 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 maintain (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 severe 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. *TFT* is the resident strategy in that population. *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 inter-patch 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 (i) that there are infinitely many patches, (ii) that patches are small enough for individuals within a patch to meet each other many times and (iii) 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*s should take advantage of moving from patch to patch in search of naive *TFT*s. 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* 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 *TFT*s and *AD*s) settled in a uniform ocean of defectors. Thus inter-cluster mobility is irrelevant to our case. Instead, our model emphasis is on intra-cluster mobility. This difference between the models is critical, because intra-cluster 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 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 τ, mortality rate d and mobility rate μ_T. Increasing μ_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* the search time would be equal to the time spent being paired consecutively with other *AD* players and unable to sucker *TFT*s. 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 remaining paired with the same *AD*. Using notations from our auxiliary model, the search time for a defector would thus be $Q_{pair}\tau + Q_{pair}^2\tau + \ldots = \tau Q_{pair}/(1-Q_{pair})$, where Q_{pair} denotes the probability that two individuals with motion probabilities q, moving or not, meet again on the next interaction: $Q_{pair} = (1-q)^2\{1+(1/2)[q^2/(1-q^2)]\}$. 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 TFTs keeping track of ADs. The bottom line is that maximizing those three quantities, which require mobilities to exceed critical minima, is more important at 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 Vicker's approach is mainly numerical. Our spatial version of Hamilton's rule (Eq. (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 Vicker does not resort to this assumption, but, in return, writes as a more complicated set of differential equations which 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, approximately, each cell contains 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 τ has elapsed, they end up in a same cell again.

Given that a type-1 player located at x_t at time t interacts with a type-2 located at y_t 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 the 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

$$\tilde{w} = \mathrm{Prob}\left(y_{t+\tau} \in \left[\,[X_{t+\tau}]L\,,\,([X_{t+\tau}]+1)L\,\right] \,\middle|\, y_t \in \left[\,[X_t]L\,,\,([X_t]+1)L\,\right]\right) \quad \text{(A1)}$$

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 re-condition $\tilde{w}$ (for handling conditional probabilities, see Chung 1979) with respect to $x_{t+\tau}$. By introducing the Gaussian distribution of the diffusion process, we get

$$\tilde{w} = \int_{\xi \in R} \mathrm{Prob}\left(y_{t+\tau} \in \left[\,[X_{t+\tau}]L\,,\,([X_{t+\tau}]+1)L\,\right] \,\middle|\, y_t \in \left[\,[X_t]L\,,\,([X_t]+1)L\,\right] \text{ and } x_{t+\tau} = x_t + \xi\right) \times \frac{e^{-\frac{\xi^2}{4\tau\mu_1}}}{2\sqrt{\pi\tau\mu_1}}\, d\xi$$

(A2)

The possible initial positions $\underline{y_t}$ are equally likely over $\underline{\big[\,[X_t]L\,,\,([X_t]+1)L\,\big]}$, thus

$$\tilde{w} = \int_{u=[X_t]L}^{([X_t]+1)L} \int_{\xi\in R} \operatorname{Prob}\Big(y_{t+\tau} \in \big[\,[X_{t+\tau}]L\,,\,([X_{t+\tau}]+1)L\,\big] \;\Big|\; y_t = u \text{ and } x_{t+\tau} = x_t + \xi\Big)$$

$$\times \frac{e^{-\frac{\xi^2}{4\tau\mu_1}}}{2\sqrt{\pi\tau\mu_1}}\, d\xi\, \frac{du}{L}$$

$$= \int_{v=[X_t+\xi/L]L}^{([X_t+\xi/L]+1)L} \int_{u=[X_t]L}^{([X_t]+1)L} \int_{\xi\in R} \frac{e^{-\frac{(v-u)^2}{4\tau\mu_2}}}{2\sqrt{\pi\tau\mu_2}} \frac{e^{-\frac{\xi^2}{4\tau\mu_1}}}{2\sqrt{\pi\tau\mu_1}}\, d\xi\, \frac{du}{L}\, dv$$

(A3)

as we make use, once again, of the Gaussian distribution which defines the mobility rates. The approximation $\underline{[X_t+\xi/L] \approx [X_t]+\xi/L}$ has minor effects as long as $\underline{\mu_1}$ and $\underline{\mu_2}$ are not too close to zero and/or $\underline{K}$ 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 $\underline{u := u - [X_t]L}$ and $\underline{v := v - [X_t]L - \xi}$ finally yield

$$\tilde{w} = \frac{1}{4\pi\tau L\sqrt{\mu_1\mu_2}} \iiint_{\substack{\xi\in R\\ (u,v)\in[0,L]^2}} e^{-\frac{(v+\xi-u)^2}{4\tau\mu_2}}\, e^{-\frac{\xi^2}{4\tau\mu_1}}\, d\xi\, du\, dv, \tag{A4}$$

from which we get

$$w = \frac{Ke^{-d\tau}}{8\pi\tau\sqrt{\mu_1\mu_2}} \iiint_{\substack{\xi\in R\\ (u,v)\in[-1/K,1/K]^2}} e^{-\frac{1}{\tau}\left[\frac{(\xi-u)^2}{4\mu_1}+\frac{(\xi-v)^2}{4\mu_2}\right]}\, du\, dv\, d\xi\,. \tag{A5}$$

Asymptotic development of w for large K

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

$$w = \frac{e^{-d\tau}}{8\pi\tau\varepsilon\sqrt{\mu_1\mu_2}} \iiint_{\substack{\xi\in R\\(u,v)\in[-\varepsilon,\varepsilon]^2}} e^{-\frac{1}{\tau}\left[\frac{(\xi-u)^2}{4\mu_1}+\frac{(\xi-v)^2}{4\mu_2}\right]}\,du\,dv\,d\xi \qquad \text{(A6)}$$

greek pi

greek delt.

for small ε. Let us set $\sigma_1 = \sqrt{2\tau\mu_1}$, $\sigma_2 = \sqrt{2\tau\mu_2}$ and $\delta = \frac{1}{2}\left(\frac{1}{\sigma_1^2}+\frac{1}{\sigma_2^2}\right)$. Then we have

$$w = \frac{e^{-d\tau}}{2\varepsilon}\int_{\xi\in R} d\xi \left(\frac{1}{\sqrt{2\pi}\sigma_1}\int_{u=-\varepsilon}^{\varepsilon} e^{-\frac{(u-\xi)^2}{2\sigma_1^2}}\,du\right)\left(\frac{1}{\sqrt{2\pi}\sigma_2}\int_{v=-\varepsilon}^{\varepsilon} e^{-\frac{(u-\xi)^2}{2\sigma_2^2}}\,dv\right). \qquad \text{(A7)}$$

greek pi

greek pi

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

$$w = \frac{e^{-d\tau}}{2\varepsilon}\int_{\xi\in R} F_1(\xi)F_2(\xi)\,d\xi\,. \qquad \text{(A8)}$$

A straightforward change of variables gives

$$F_i(\xi) = \frac{1}{\sqrt{2\pi}}\int_{\frac{1}{\sigma_i}(\xi-\varepsilon)}^{\frac{1}{\sigma_i}(\xi+\varepsilon)} e^{-\frac{1}{2}z^2}\,dz \qquad (i = 1,\ 2). \qquad \text{(A9)}$$

greek pi

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

$$F_i(\xi) = \frac{1}{\sqrt{2\pi}}\frac{2\varepsilon}{\sigma_i}e^{-\xi^2/2\sigma_i^2} \qquad (i = 1,\ 2). \qquad \text{(A10)}$$

rek pi

Substituting into (A8) gives

$$w = \frac{e^{-d\tau}}{\pi}\frac{\varepsilon}{\sigma_1\sigma_2}\int_{\xi\in R} e^{-d\xi^2}\,d\xi \qquad \text{(A11)}$$

ek pi

which yields

$$w = \frac{\varepsilon e^{-d\tau}}{\sigma_1\sigma_2\sqrt{\pi}\sqrt{\delta}}. \qquad \text{(A12)}$$

greek pi

greek delta

Equation (7) ensues. Notice that the requirement $w \leq 1$ does impose a restriction on the domain of validity of this approximation, namely that μ_1 and μ_2 be not too small -- an assumption we already had to put forward when we calculated the exact expression (A5) of w.

Payoff matrix for TFT vs. AD in the spatial IPD

In order to calculate Φ_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 who is present in the same cell and who 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 τ. Yet this payoff has to be discounted by the cost of mobility, γ, defined per interaction. Should the partner be an AD, the payoff earned by the TFT will be $P-\gamma$ if the interactant is recognized from the previous encounter (TFT retaliates). This happens with probability w. With probability $1-w$, the TFT 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 $e^{-d\tau}$. Overall, the payoff per unit time obtained by the TFT player is given by

$$\Phi_T = \frac{n_T}{N}\beta(R-\gamma)+\frac{n_D}{N}\beta\left[w(P-\gamma)+(1-w)(S-\gamma)\right]. \qquad \text{(A13a)}$$

where $\beta = e^{-d\tau}/\tau$. Likewise, we have

$$\Phi_D = \frac{n_D}{N}\beta(P-\gamma)+\frac{n_T}{N}\beta\left[w(P-\gamma)+(1-w)(T-\gamma)\right] \qquad \text{(A13b)}$$

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

$$a_{11} = \beta R \tag{A14a}$$

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

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

$$a_{22} = \beta P. \tag{A14d}$$

Cost of Mobility Dependent upon 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 μ_D. Then the range of μ_T begetting invasion is an interval, denoted by $\left[\mu_T^{\min}, \mu_T^{\max}\right]$, which corresponds to the portion of the curve defined by the left-hand side of equation (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 parametrization of the payoffs T, R, P, S introduced above, the conditions $a_{11} > a_{21}$ and $a_{22} > a_{12}$ read

$$-\frac{c}{b}(1-w) < \frac{\Delta\gamma}{b} < -\frac{c}{b} + w. \tag{A15}$$

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

greek thet.

$$\frac{w}{1 + (1-w)\,\vartheta(\mu_T/\mu_D)} > \frac{c}{b} + \frac{\Delta\gamma}{b}\,\frac{1 + \vartheta(\mu_T/\mu_D)}{1 + (1-w)\,\vartheta(\mu_T/\mu_D)} \tag{A16}$$

greek theta

greek theta

$\Delta\gamma$ stands for the difference of the costs paid for moving at rates μ_T and μ_D:

$$\Delta\gamma = \gamma(\mu_T) - \gamma(\mu_D). \tag{A17}$$

We keep on considering a given value of μ_D. It must be noticed that $\Delta\gamma$ is an increasing function of μ_T, null at $\mu_T = \mu_D$. We first show that condition (A15) is matched for any value of μ_T belonging to $\left[\mu_T^{\min}, \mu_T^{\max}\right]$, provided that the cost of mobility $\gamma(\mu)$ does not increase too rapidly with μ. Let us first address the case of values of μ_T smaller than

μ_D. Then the left-hand side of (A20) is satisfied if $\Delta\gamma$ remains small enough; precisely we request that $\Delta\gamma$ takes on a value larger than $-c$ at $\mu_T = 0$, i.e., $\gamma(\mu_D) < c$. The right-hand side will hold true for any μ_T such that $w > c/b$. As we increase μ_T such that we just pass the resident defectors mobility μ_D, $\Delta\gamma/b$ becomes positive and the left-hand inequality involved in (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 μ_T increases, then the right-hand inequality will be satisfied as well. Finally, we have $w > c/b$ for any μ_T in $\left[\mu_T^{\min}, \mu_T^{\max}\right]$, because the denominator of the left-hand side of (A16) is greater than 1.

Next we discuss the effect of a mobility-dependent cost of mobility on inequality (A16). The right hand-side of (A16) is an increasing function of the mobility rate μ_T that is represented by the thin curve in fig. A1. Here, the inequality (A16) is satisfied when the thick curve is above the thin one. Geometrically, $\left[\tilde{\mu}_T^{\min}, \tilde{\mu}_T^{\max}\right]$ is shifted to the left when μ_D lies in $\left[\mu_T^{\min}, \mu_T^{\max}\right]$ (fig. A1, panel A), whereas $\left[\tilde{\mu}_T^{\min}, \tilde{\mu}_T^{\max}\right]$ is narrower when μ_D is smaller than $\mu_T^{\min}$ (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 fig. A1, panel B.

Derivation of Q, Q', Q'', 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, ..., C. 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, ...). The probability that a TFT located in cell i within the cluster, gets paired in cell m on the right front with a partner from the cluster is

$$\begin{aligned}&\frac{1}{2}(1-q)q^{m+i-1}\left[(1-q)q^{m}+\ldots+\frac{1}{2}(1-q)q^{m+i-1}+\ldots+(1-q)q^{m+C-1}\right]\\&=\frac{1}{2}(1-q)q^{m+i-1}q^{m}\left[1-q^{C}-\frac{1}{2}(1-q)q^{i-1}\right]\end{aligned} \qquad \text{(A18)}$$

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, ... 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

$$Q = \frac{1}{C}\frac{q^2}{1-q^2}\left(1-q^C\right)\left[1-q^C-\frac{1}{2}\frac{(1-q)\left(1+q^C\right)}{1+q}\right] \qquad \text{(A19)}$$

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

$$\begin{aligned}&\frac{1}{2}(1-q)q^{i-1}+\ldots+\frac{1}{2}(1-q)q+(1-q)+\frac{1}{2}(1-q)q+\ldots+\frac{1}{2}(1-q)q^{C-1}\\ &= 1-\frac{1}{2}\left(q^i+q^{C-i+1}\right)\end{aligned} \qquad \text{(A20)}$$

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

$$Q'' = 1-\frac{1}{C}\frac{q}{1-q}\left(1-q^C\right) \qquad \text{(A21)}$$

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

$$Q_{\mathrm{retal}} = \left[\frac{1}{2}(1-q_1)q_1^{M}\right]\left[\frac{1}{2}(1-q_2)q_2^{M}\right]+\left[\frac{1}{2}(1-q_1)q_1^{M+1}\right]\left[\frac{1}{2}(1-q_2)q_2^{M+1}\right]+\ldots \qquad \text{(A22)}$$

which recasts into

$$Q_{\mathrm{retal}} = \frac{1}{4}(1-q_1)(1-q_2)\frac{(q_1q_2)^M}{1-q_1q_2}. \qquad \text{(A23)}$$

Payoff matrix for TFT vs. 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: $\mathbf{E} = (R,S,T,P)^*$ is the vector of payoffs for a single round of the *IPD*, and w_{ij} is the probability that a *i*-player meets twice consecutively with the same *j*-partner. If the two players have not met on 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 $p_i p_j$; 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 on the previous interaction, but not on 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, DD (see Nowak 1990). On the previous interaction, the probabilities of each state were exactly the simple ones explicated above; we denote them by π_{ij}^{R}, π_{ij}^{S}, π_{ij}^{T}, π_{ij}^{P}. Thus, the probabilities that we are now looking for are merely given by the components of $\boldsymbol{\mathcal{T}}_{ij}\boldsymbol{\pi}_{ij}$, where $\boldsymbol{\pi}_{ij}$ is the vector $\left(\pi_{ij}^{R}, \pi_{ij}^{S}, \pi_{ij}^{T}, \pi_{ij}^{P}\right)^{*}$ and $\boldsymbol{\mathcal{T}}_{ij}$ 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, DD on the current play are given by the components of the vector $\boldsymbol{\mathcal{T}}_{ij}^{k}\boldsymbol{\pi}_{ij}$. Finally, the expected payoff e_{ij} is

$$e_{ij} = (1-w_{ij})\langle \pi_{ij}, \mathbf{E} \rangle + (1-w_{ij})w_{ij}\langle \boldsymbol{\mathcal{T}}_{ij}\pi_{ij}, \mathbf{E} \rangle + (1-w_{ij})w_{ij}^{2}\langle \boldsymbol{\mathcal{T}}_{ij}^{2}\pi_{ij}, \mathbf{E} \rangle + \dots \qquad \text{(A24)}$$

which yields equation (10).

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FIGURE LEGENDS

Figure 1.-- Travelling waves of invasion by tit-for-tat (TFT) of a population of always-defect (AD). A TFT invading wave develops when condition (4) (see text) is satisfied. The figures schematically portray snapshots of the distributions (density) of TFT and AD along the spatial axis x. Horizontal arrows indicate the way of progression of the TFT population. "Core" = region of pure TFT. "Fringe" = region of overlap between TFT and AD. "Front" = region of pure AD. A, the mobility rate μ_T of TFT is lower than that, μ_D, of AD: the travelling wave is monotone; B, $\mu_T > \mu_D$: the travelling wave is unimodal, the AD density reaches a maximum value in the fringe.

Figure 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 equation (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 $\left[\mu_T^{\min}, \mu_T^{\max}\right]$ of invading TFT mobilities when $\mu_D = 1$. B, Slice at $\mu_D = 1$. The range $\left[\mu_T^{\min}, \mu_T^{\max}\right]$ 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.)

Figure 3.-- *A*, Coefficient of reciprocation as approximated by equation (7a), graphed as a function of μ_T, for $\mu_D = 1$ and different values of ψ. For a given cost-benefit ratio (here exemplified by the horizontal line at $c/b = 0.1$), the range of *TFT* mobility rates begetting invasion is defined like in figure 2*B*; it appears to be widened as ψ is increased. *B*, Contour plot of ψ, (equation (7b) with $K = 4/\sqrt{\pi}$), as a function of the mortality rate d and the interaction time τ.

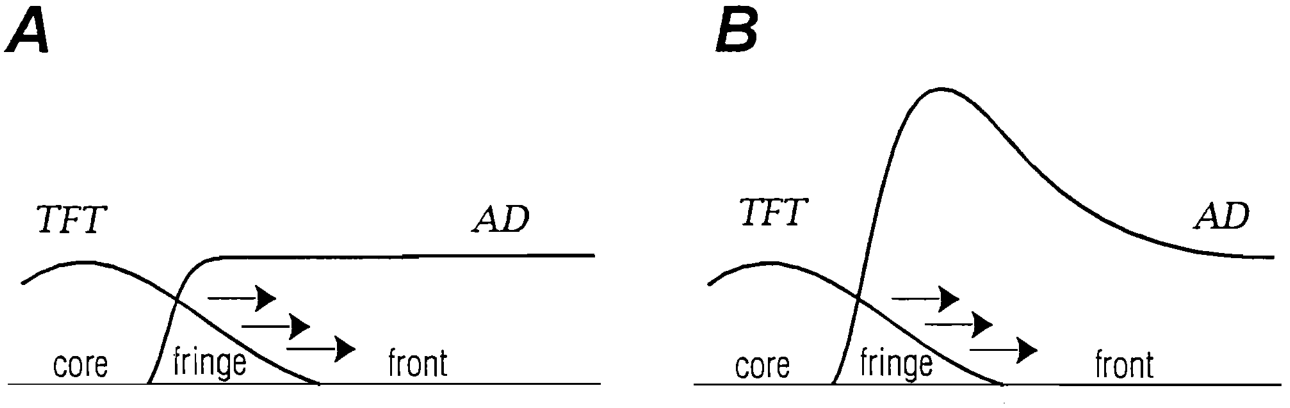
Figure 4.-- *A*, Probability distribution of moves amplitude in the auxiliary model of stochastic motion, for q (motion probability) equal to 0.1 and 0.6. *B*, Cumulative probabilities *Q*, *Q'* and *Q"* as functions of q, for $C = 5$ (Eqq. (A19) and (A21)). *Q* = probability that a *TFT* picked at random in the cluster will move out and get assorted with another *TFT* from the cluster. *Q'* = probability that a *TFT* picked at random in the cluster will move out *but will not* get assorted with another *TFT* from the cluster. *Q"* = probability that a *TFT* picked at random in the cluster will not move out of the cluster. *C*, Ratio Q/Q' for different cluster sizes: C = 5, 10, 20, 50.

Figure 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 $Q_{retal}(q_1, q_2)$ for $M = 1$ (equation (A23)).

Figure 6.-- *TFT* versus 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. *TFT* is at $(1,0)$, in the lower right corner of the panel. 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 w (equation (7a)) with $\psi = 3.0$, and mobilities equal to 0.5 for all strategies; basic payoffs *T*, *R*, *P*, *S* were assigned traditional values 5, 3, 1, 0, respectively.

Figure A1.-- Effect of making the cost of mobility dependent upon the mobility rate. Thick curve (*a*): schematic graph of the cost of reciprocation H given by the left-hand side of equation (A16). Thin curve (*b*): schematic graph of the generalized cost-benefit ratio given by the right-hand side of equation (A21). Horizontal line: c/b -level. The interval $\left[\mu_T^{min}, \mu_T^{max}\right]$ contains μ_T values that permit invasion by cooperators when the cost of mobility is independent of the mobility rate ($\Delta\gamma \equiv 0$). The interval $\left[\tilde{\mu}_T^{min}, \tilde{\mu}_T^{max}\right]$ is the range of μ_T for which condition (A21) is satisfied, when the cost of mobility does depend on the mobility rate. *A*, μ_D lies in $\left[\mu_T^{min}, \mu_T^{max}\right]$. *B*, μ_D is smaller than μ_T^{min}.

Figure 1



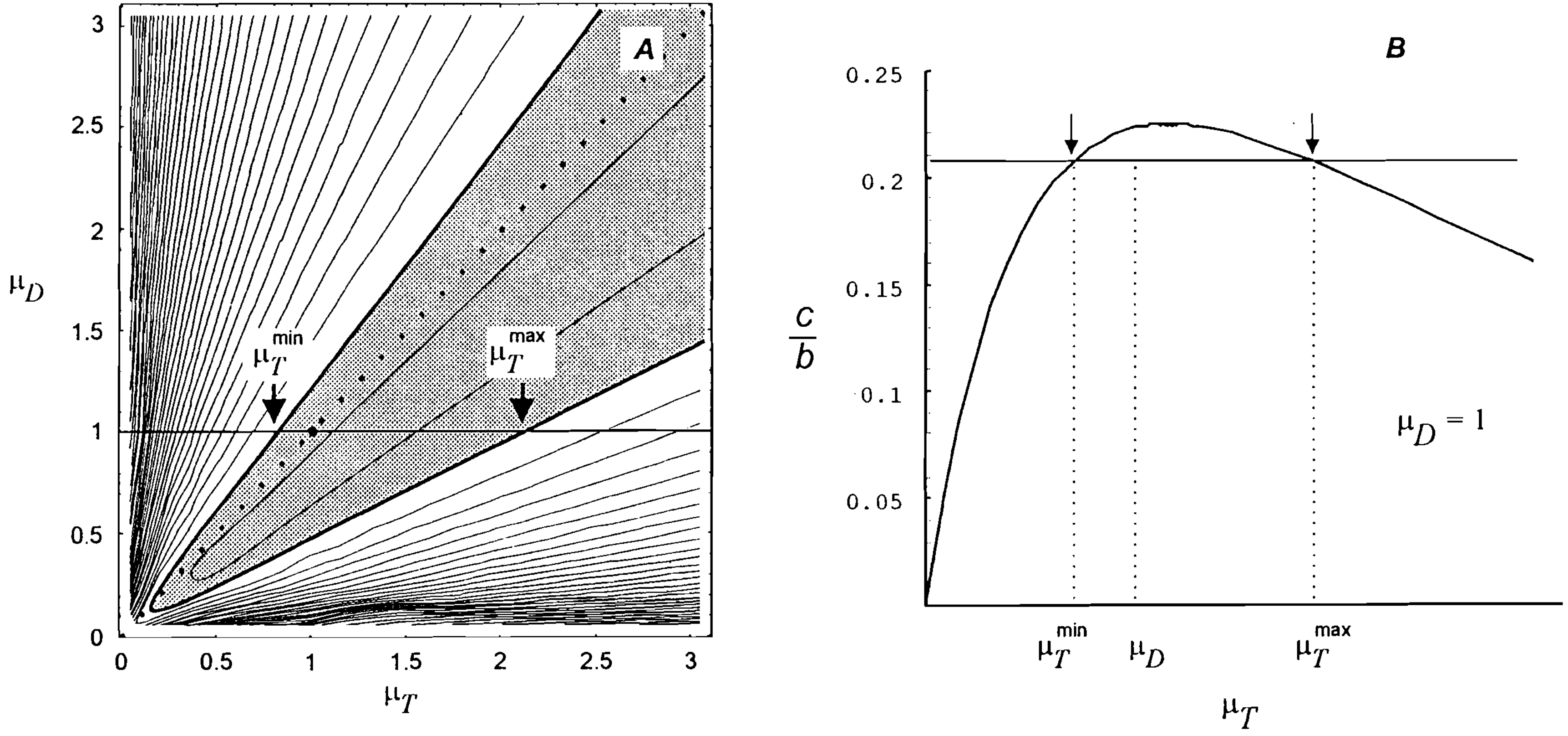

A
μ_D
μ_T
$\mu_T^{\min}$
$\mu_T^{\max}$
0
0.5
1
1.5
2
2.5
3
B
$\frac{c}{b}$
0.25
0.2
0.15
0.1
0.05
$\mu_D = 1$
$\mu_T^{\min}$
μ_D
$\mu_T^{\max}$
μ_T

Figure 2

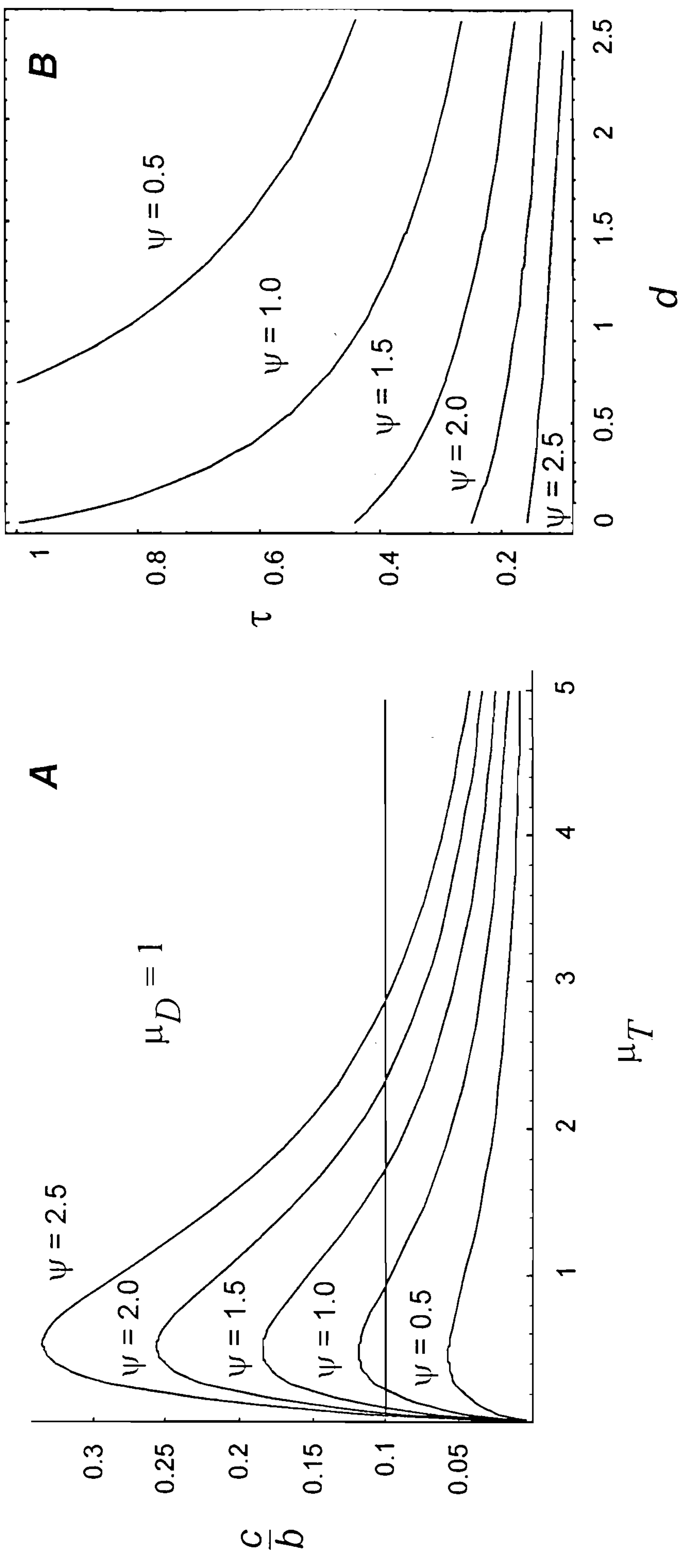

A
$\mu_D = 1$
$\psi = 2.5$
$\psi = 2.0$
$\psi = 1.5$
$\psi = 1.0$
$\psi = 0.5$
$\frac{c}{b}$
0.3
0.25
0.2
0.15
0.1
0.05
1
2
3
4
5
μ_T
B
$\psi = 0.5$
$\psi = 1.0$
$\psi = 1.5$
$\psi = 2.0$
$\psi = 2.5$
τ
1
0.8
0.6
0.4
0.2
0
0.5
1
1.5
2
2.5
d

Figure 3

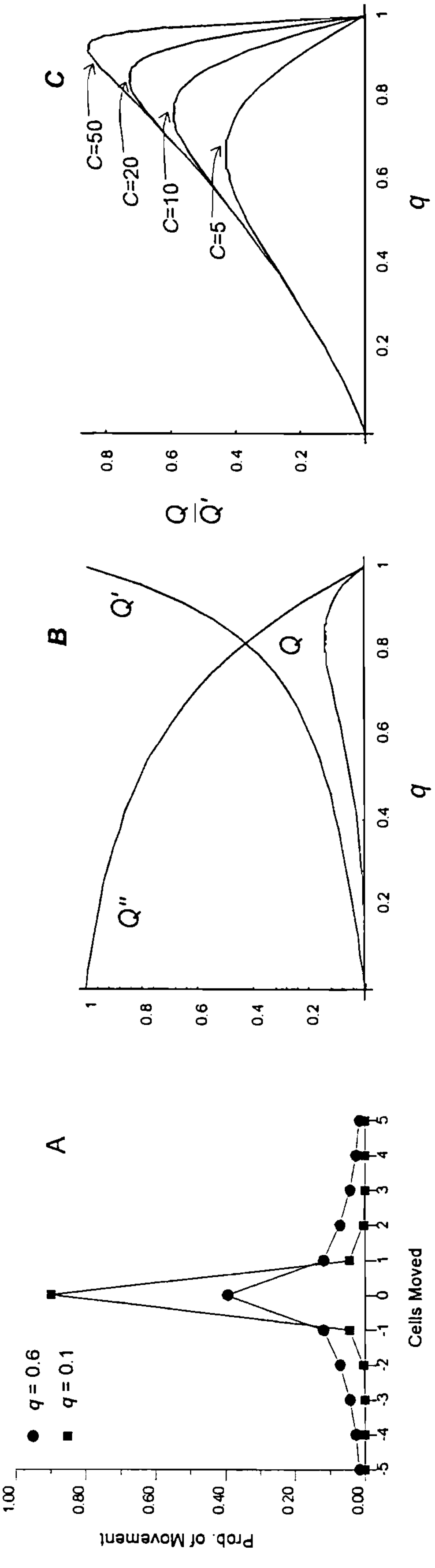

A
q = 0.6
q = 0.1
Prob. of Movement
1.00
0.80
0.60
0.40
0.20
0.00
Cells Moved
-5
-4
-3
-2
-1
0
1
2
3
4
5
B
Q''
Q'
Q
1
0.8
0.6
0.4
0.2
q
C
C=50
C=20
C=10
C=5
Q/Q'
0.8
0.6
0.4
0.2
q
1

Figure 4

Figure 5

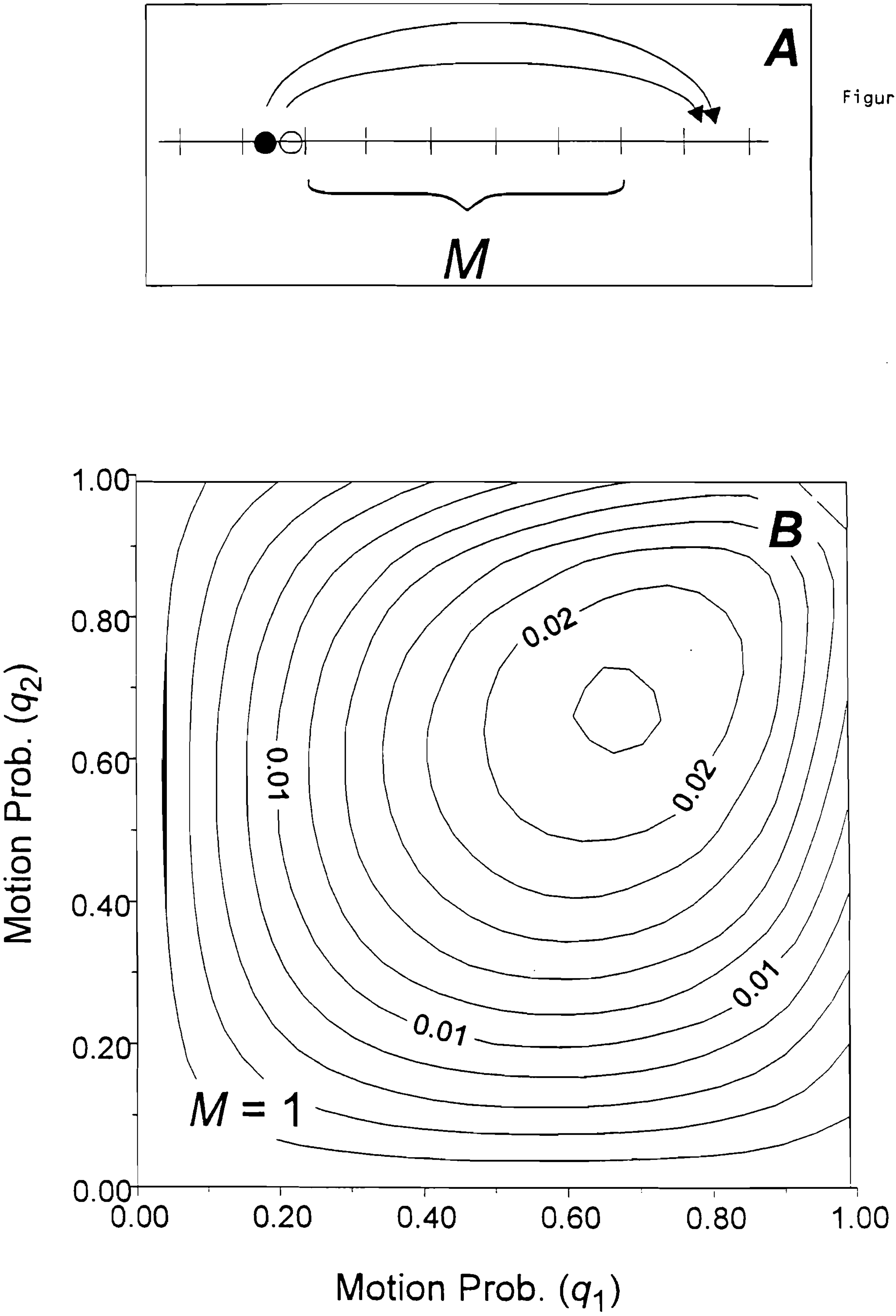
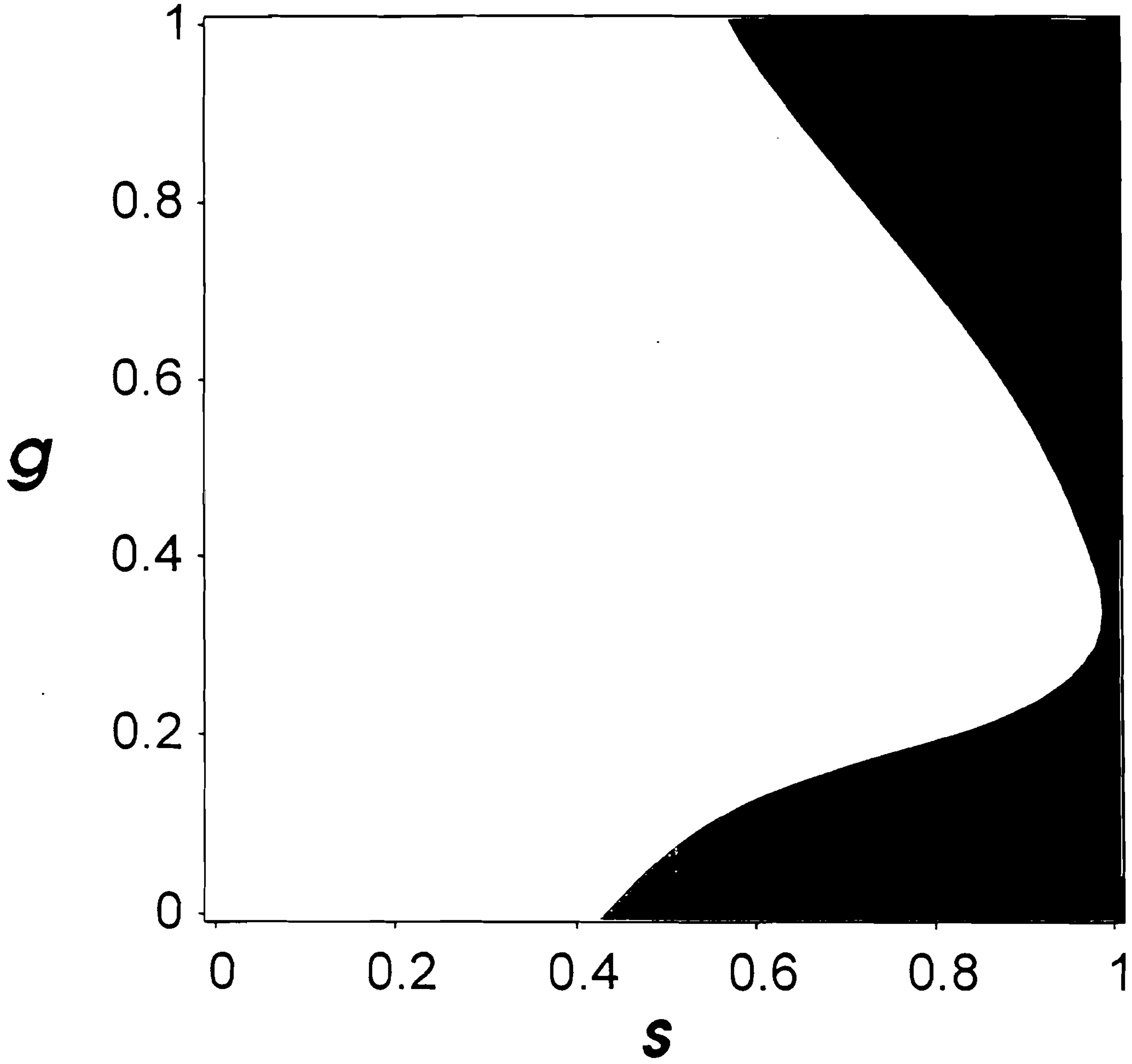

A
M
B
0.02
0.02
0.01
0.01
0.01
M = 1
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
Motion Prob. (q_2)
Motion Prob. (q_1)

Figure 6



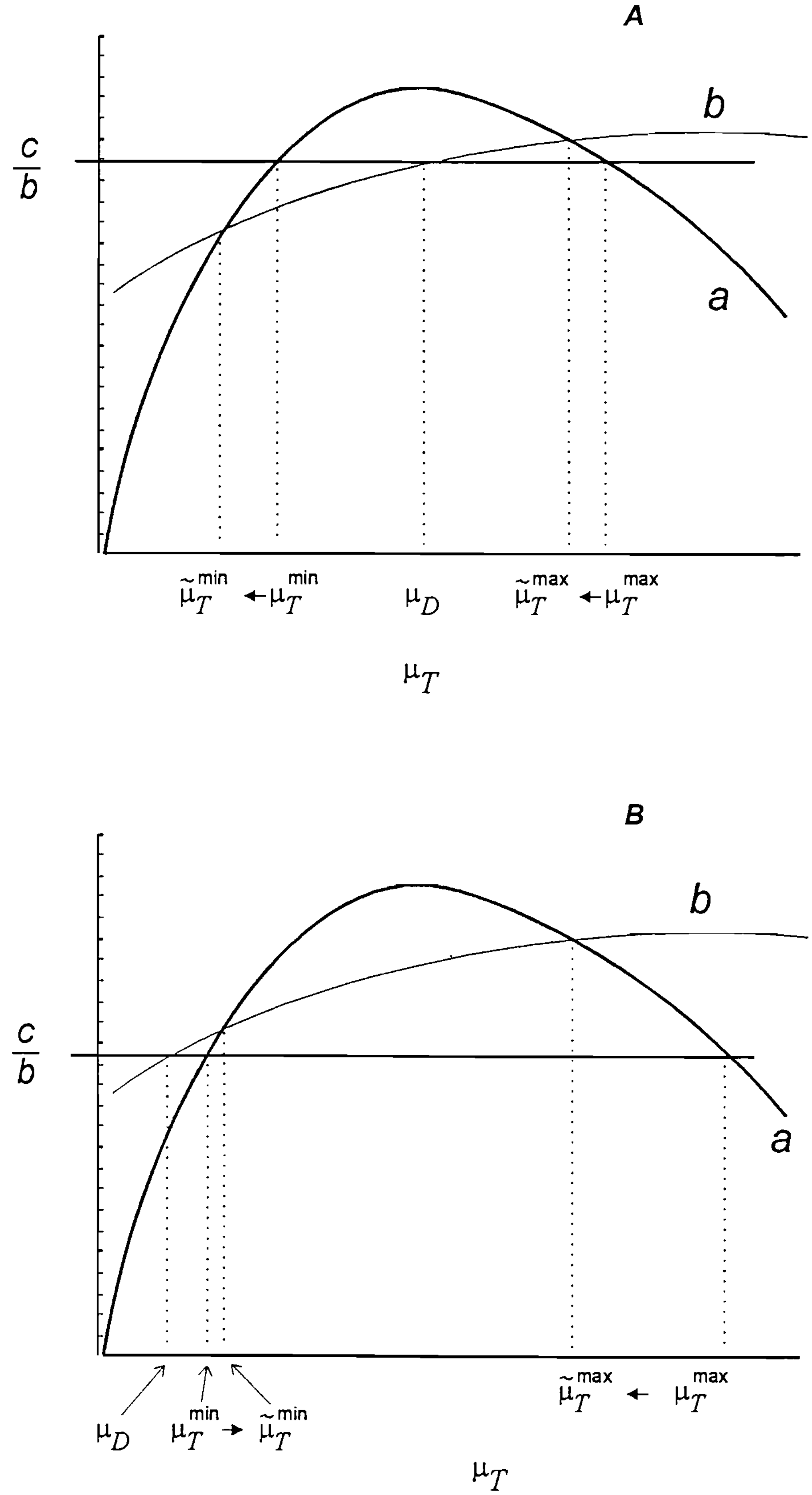

A
b
c/b
a
μ̃_T^min ← μ_T^min
μ_D
μ̃_T^max ← μ_T^max
μ_T
B
b
c/b
a
μ_D
μ_T^min → μ̃_T^min
μ̃_T^max ← μ_T^max
μ_T

Figure A1