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Spatial evolutionary game theory: Hawks and Doves revisited

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SUMMARY

We consider a spatial generalization of evolutionary game theory in which strategies are distributed over a spatial array of sites. We assume that the strategy corresponding to a given site has local interactions with the strategies sitting on neighbouring sites, and that the strategies change if neighbouring strategies are doing better. After briefly setting the stage with a formal definition of spatial evolutionary game theory, we consider the spatial extension of the Hawk–Dove game, and we show that the results are qualitatively different from those obtained from classical evolutionary game theory. For example, the proportion of Hawks in the population is in general lower in the spatial game than in the classical one. We also consider spatial generalizations of the extensions of the Hawk–Dove game obtained by including strategies such as Retaliator and Bully. Here, too, the results from the spatial game are very different from the classical results. In particular, with space Retaliator is a much more successful strategy than one would expect from classical considerations. This suggests that, in general, spatial structure may facilitate the evolution of strategies such as Retaliator, which do not necessarily prosper classically, and which are reminiscent of the ‘nice’, ‘provokable’ and ‘forgiving’ strategies which seem to play a central role in the evolution of cooperation. The results indicate that including spatial structure in evolutionary game theory is a fruitful extension.

1. INTRODUCTION

Since the introduction of game theory concepts into biology by Maynard Smith & Price (1973), evolutionary game theory has developed into an important method for studying phenotypic evolution in situations when the fitness of particular phenotypes depends on their frequencies in the population (see Maynard Smith 1982). The central concept in evolutionary game theory is that of an evolutionary stable strategy (ESS). An ESS is a strategy such that, if almost all members of a population adopt it, then no mutant strategy can invade the population under the influence of natural selection. The ESS's (if there are any) are equilibrium states and evolutionary game theory attempts to study these equilibria. The ideas and methods of evolutionary game theory have been applied in a wide range of situations, including animal contests (Maynard Smith 1974; Maynard Smith 1982), the origin of anisogamy (Parker *et al.* 1972), the problem of sex allocation (Charnov 1982), animal dispersal in a uniform environment (Hamilton & May 1977), plant growth and reproduction (Mirmirani & Oster 1978), and the evolution of cooperation (Axelrod & Hamilton 1981; Axelrod 1984; Nowak & Sigmund 1993).

In this paper we shall consider evolutionary games

from a somewhat different perspective to that which is adopted in the classical work (as presented, for instance, in Maynard Smith 1982). This perspective has been first taken up by Nowak & May (1992, 1993) and involves studying evolutionary games in which strategies are distributed over some spatial region and have local interactions with strategies in neighbouring regions. The strategy at one particular location changes if neighbouring strategies are doing better. This corresponds to an evolutionary scenario in which successful phenotypes replace unsuccessful ones. In the spatial game, the analogue of the frequencies with which different strategies are adopted at an ESS is the proportions of the different strategies present at the spatial equilibrium distribution, or, if the spatial distribution is continually changing (as is often to be expected), the average proportion of the different strategies. If the fluctuations in the proportions are not too large, considering this average allows one to compare the outcome of spatial evolutionary games with the results of the classical ESS analysis.

The prototype of this kind of spatial extension of evolutionary game theory is the spatial Prisoner's Dilemma introduced by Nowak & May (1992) (see also Nowak & May 1993; Nowak *et al.* 1994*a, b*). Below we will first give a somewhat formal definition of a spatial evolutionary game to set up a general framework. We will then focus on one particular game and analyse the spatial generalization of the well-

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known Hawk–Dove game (Maynard Smith 1982) and some of its extensions. We show that the results from the spatial Hawk–Dove game are qualitatively different from the classical results. Together with the pioneering work of Nowak & May (1992, 1993) and of Nowak *et al.* (1994*a, b*), this suggests that the combination of spatial structures and evolutionary games may prove to be very fruitful: space literally adds a new dimension to evolutionary game theory.

2. SPATIAL EVOLUTIONARY GAMES: HAWKS AND DOVES

In this section we shall study the spatial Hawk–Dove game and discuss how the results from the spatial theory differ from the results of the classical Hawk–Dove game. However, we first give a precise general definition of spatial evolutionary game theory.

We consider a game allowing a finite number of strategies. The set of strategies will be denoted by Σ . Let $E(i, j)$ be the payoff to an individual adopting strategy $i \in \Sigma$ against an opponent adopting strategy $j \in \Sigma$. Now let us introduce a finite number of cells arranged in a lattice \mathcal{A} , which will represent space. In principle, the lattice \mathcal{A} may be of any dimension, but the cases of biological interest are dimensions one, two or three. The cells in \mathcal{A} are labelled by an index I , and at any point in time, each cell is occupied by a strategy from the strategy set Σ . Given any cell I the set of neighbouring cells to I (but not including I itself) is denoted by $N(I)$, and $N^*(I) = N(I) \cup I$ will denote the set of neighbouring cells to I together with I itself. For a given lattice \mathcal{A} the choice of the neighbourhood $N(I)$ is arbitrary and the final theory depends on this choice. However, there are usually a small number of natural choices for a minimal neighbourhood $N(I)$.

A spatial evolutionary game is defined by an association, at generation t , of a strategy $\sigma_t(I) \in \Sigma$ to each cell $I \in \mathcal{A}$, together with a dynamical process, that is, a rule which determines the association of a strategy to each cell of \mathcal{A} at generation $t+1$. Given an initial configuration of strategies $\sigma_0(I)$, for all $I \in \mathcal{A}$, this yields a recursive definition of the spatial evolutionary game once the dynamical process is specified.

The dynamical process is defined as follows. First the total score $s_t(I)$ of cell I at generation t is defined to be the sum of the payoffs resulting from playing all the neighbouring cells, i.e. all the cells in $N(I)$:

$$s_t(I) = \sum_{J \in N(I)} E(\sigma_t(I), \sigma_t(J)).$$

Using the scores s_t we can define the dynamical process which associates a strategy to each cell of \mathcal{A} at generation $t+1$. For any $I \in \mathcal{A}$ let $\hat{i} \in \Sigma$ be the strategy associated, at generation t , to the cell $J \in N^*(I)$ which has maximal score $s_t(J)$. Then we set $\sigma_{t+1}(I) = \hat{i}$; that is, the strategy at site I in generation $t+1$ is that strategy from among the neighbours of I and I itself which gets the highest score in generation t .

The dynamical process is well-defined either if the cell in $N^*(I)$ with maximal score is unique or if all the cells in $N^*(I)$ with maximal score have the same strategy associated to them. In general, however,

Table 1. *Pay-offs in the Hawk–Dove game*

	H	D
H	$1 - \beta$	2
D	0	1

neither of these will hold and in such cases it is necessary to introduce a tie-breaking mechanism to complete the description of the dynamics. One can in general choose to break any ties in either a deterministic or a stochastic fashion. In the former case the complete dynamic process is deterministic, whereas in the latter it has a stochastic element.

It is possible to give a slight variant of the above definition of spatial evolutionary game theory in which self-interactions at each site are included. The appropriate modification of the above definition is simply that the total score $s_t(I)$ of cell I is now defined by a sum over all cells $J \in N^*(I)$, rather than over $J \in N(I)$. Whether it is natural to include self-interactions in the theory depends on the biological assumptions underlying the model. In general, if each cell is viewed as being occupied by a single individual adopting a given strategy then it is natural to exclude self-interaction. However, if each cell is viewed as being occupied by a population, all of whose members are adopting a given strategy, then it may be more natural to include self-interaction.

We now make some remarks concerning the definition of spatial evolutionary game theory. First we note that for any game (that is, for any strategy set Σ and payoff matrix E) together with a spatial lattice \mathcal{A} and a choice of local neighbourhood $N(I)$, for all $I \in \mathcal{A}$, the corresponding spatial evolutionary game theory, as defined above, is a finite cellular automaton (Wolfram 1984, 1986). (Note, however, that as the score of the neighbours of a cell in turn depends on their neighbours, the actual neighbourhood involved in determining the new state of a cell is larger than in the simplest automata, in which the new state only depends on the nearest neighbours. For example, on a square lattice with $N(I)$ consisting of the eight cells surrounding I , the neighbourhood needed to obtain the new state of cell I is the 5×5 -block surrounding I .) Second, the above definition required a choice of local spatial neighbourhood $N(I)$ to be made. In general, for any given lattice, there are a small number of natural choices for $N(I)$. For example, if \mathcal{A} is the two-dimensional square lattice then natural choices for $N(I)$ are the eight cells which surround cell I and the four cells which lie to the left and right and to the top and bottom of cell I . As the lattice \mathcal{A} is finite it is necessary to specify boundary conditions to define $N(I)$ when I is close to the boundaries of \mathcal{A} . The most natural boundary conditions depend on the geometry of \mathcal{A} . If \mathcal{A} is the two-dimensional square lattice, for example, then the two natural choices are fixed boundary conditions, for which marginal cells have no neighbours on the outside of \mathcal{A} , and periodic boundary conditions, for which the neighbours of marginal cells are the corresponding cells at the opposite margin of the lattice \mathcal{A} .

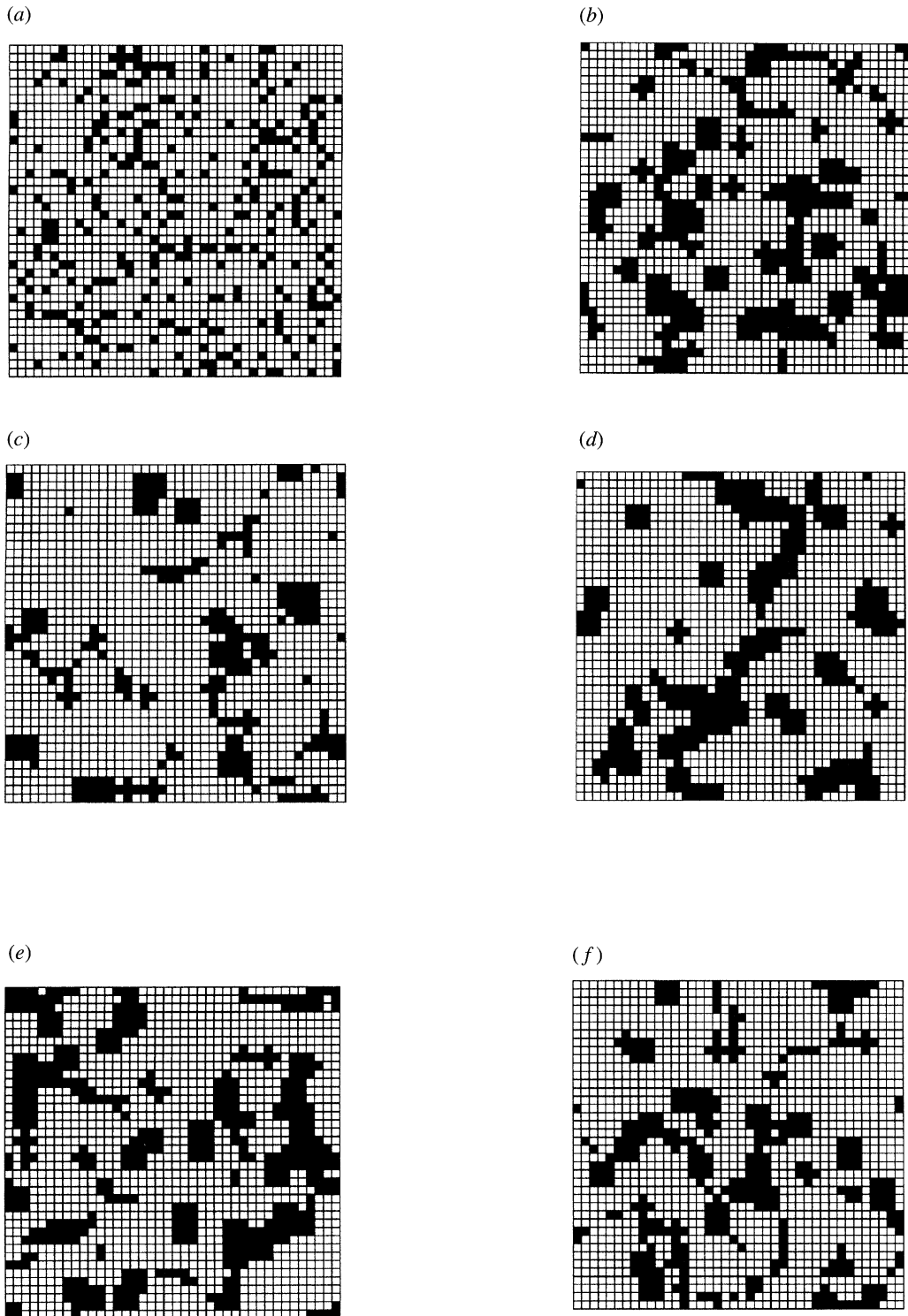


Figure 1. The results of a simulation of the spatial Hawk–Dove game on a 40×40 lattice with periodic boundary conditions and deterministic tie breaking at a value of $\beta = 2.2$. (If the neighbouring strategies with equal maximal scores are different, then the site remains unchanged.) Figure 1 (a) is the initial configuration with 80% Doves (white squares) chosen uniformly randomly, and (b), (c) and (d) show the system after 14, 63 and 166 iterations, respectively. The self-organizing nature of the system is apparent in these pictures: the spatial distribution of Hawks (black squares) varies from compact arrangements as in (b) and (d) to more elongated and disconnected structures as in (c). (e) Illustrates the sensitive dependence of the dynamics on the initial conditions. It shows the configuration obtained after the same number of generations as (c), starting from an initial condition which is identical to (a) with the exception that the top leftmost cell is changed from a Dove to a Hawk. The complete lack of similarity between (c) and (e) is a consequence of spatial chaos. (f) Demonstrates the sensitivity of the spatial game to a change in β . Starting from (a) with $\beta = 2.25$, (f) shows the result after the same number of generations as in (c) and (e). The difference between (c) and (f) results from the sensitive dependence of the theory on β .

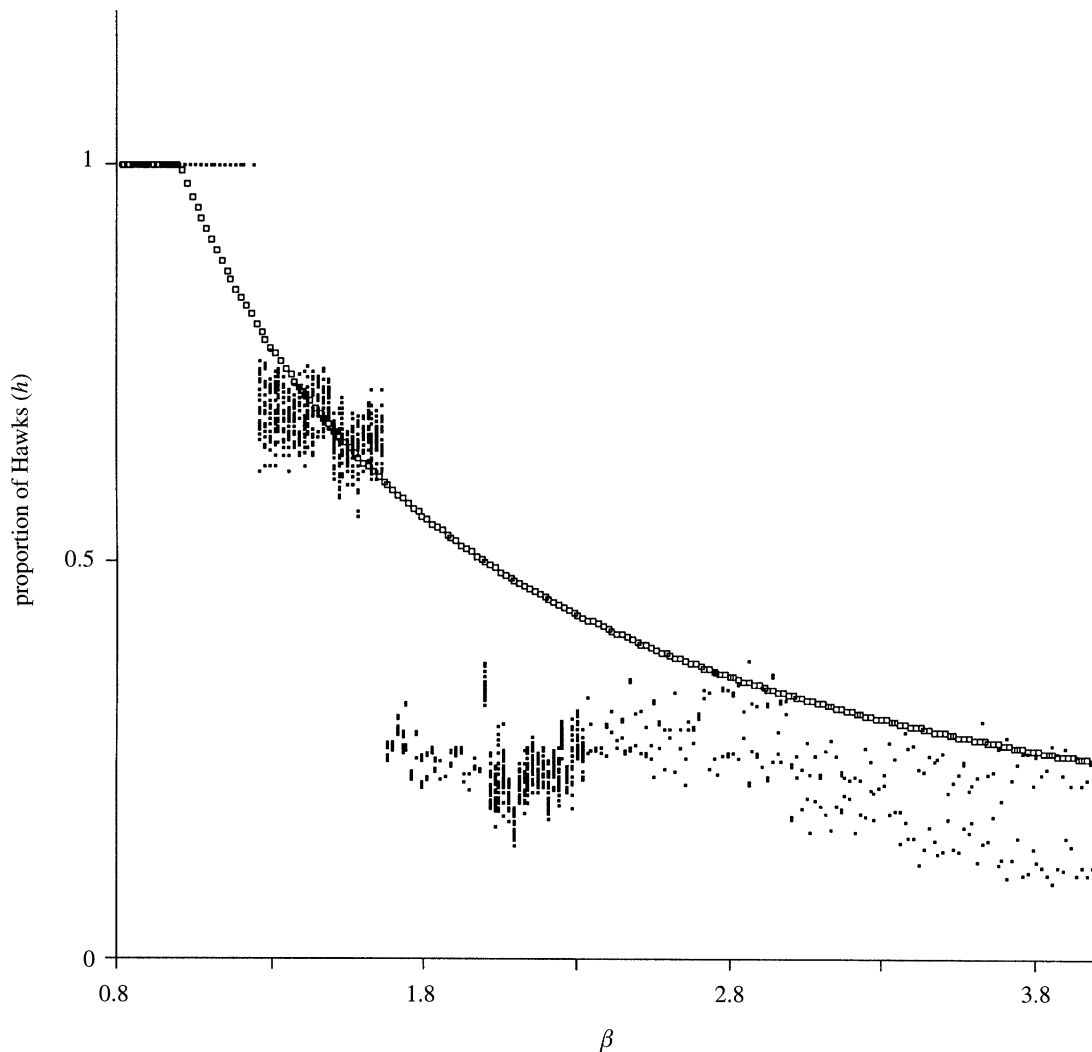


Figure 2. Variation of the proportion of Hawks h as a function of β . For 200 equidistant values of β in the range $0.8 \leq \beta \leq 4$ the dynamics of the system are followed for 175 generations, starting from a random uniform initial configuration with equal proportions of Hawks and Doves. To remove transient effects, only the h -values of the last 25 generations are plotted for each β . The different phases of h -values together with the phase transitions between them are apparent in this diagram, as is the qualitative difference between the spatial and the classical theory. The calculations were done on a 70×70 lattice with periodic boundary conditions and stochastic tie breaking. Dots = spatial game; squares = classical game.

It is worth remarking that although we assumed above that the game involved only a finite number of strategies, our definition of spatial evolutionary game theory applies equally well to cases in which the game has an infinite number of strategies.

Finally, we also note that if we take the game under consideration to be the classical Prisoners' Dilemma (Axelrod 1984) then the corresponding spatial theory which follows from our general definition is the spatial dilemma of Nowak & May (1992).

Now that we have given the general definition of a spatial evolutionary game we turn to consider one of the simplest such games: the spatial Hawk–Dove game. The possibility of studying the Hawk–Dove game in such a spatial context was alluded to by Nowak & May (1992) (cf. also Nowak & May 1993). We first recall that in the classical Hawk–Dove game (see Maynard Smith (1982) for a detailed account) it is assumed that during a contest an individual can behave in one of three ways, 'display', 'escalate', and

'retreat'. It is further assumed in the Hawk–Dove game that individuals in a given contest can adopt one of two strategies: 'Hawk' and 'Dove'. These strategies are defined as follows. Hawk (H): escalate and continue until injured or until opponent retreats. Dove (D): display, retreat at once if the opponent escalates. Under these assumptions we may write the payoff matrix for the Hawk–Dove game in the form shown in table 1. The entries in this matrix are the payoffs to the individuals adopting the strategy on the left if his opponent adopts the strategy above. The parameter β in the payoff matrix represents the cost incurred by an individual who adopts the strategy Hawk against a Hawk opponent.

The solutions of the classical Hawk–Dove game are well known (Maynard Smith 1982). If $\beta < 1$ then H is the only ESS. If $\beta > 1$ then neither H nor D is an ESS; however it is easy to show that in this case the only ESS is the mixed strategy: 'play H with probability p and D with probability $1-p$ ', where $p = 1/\beta$. This mixed

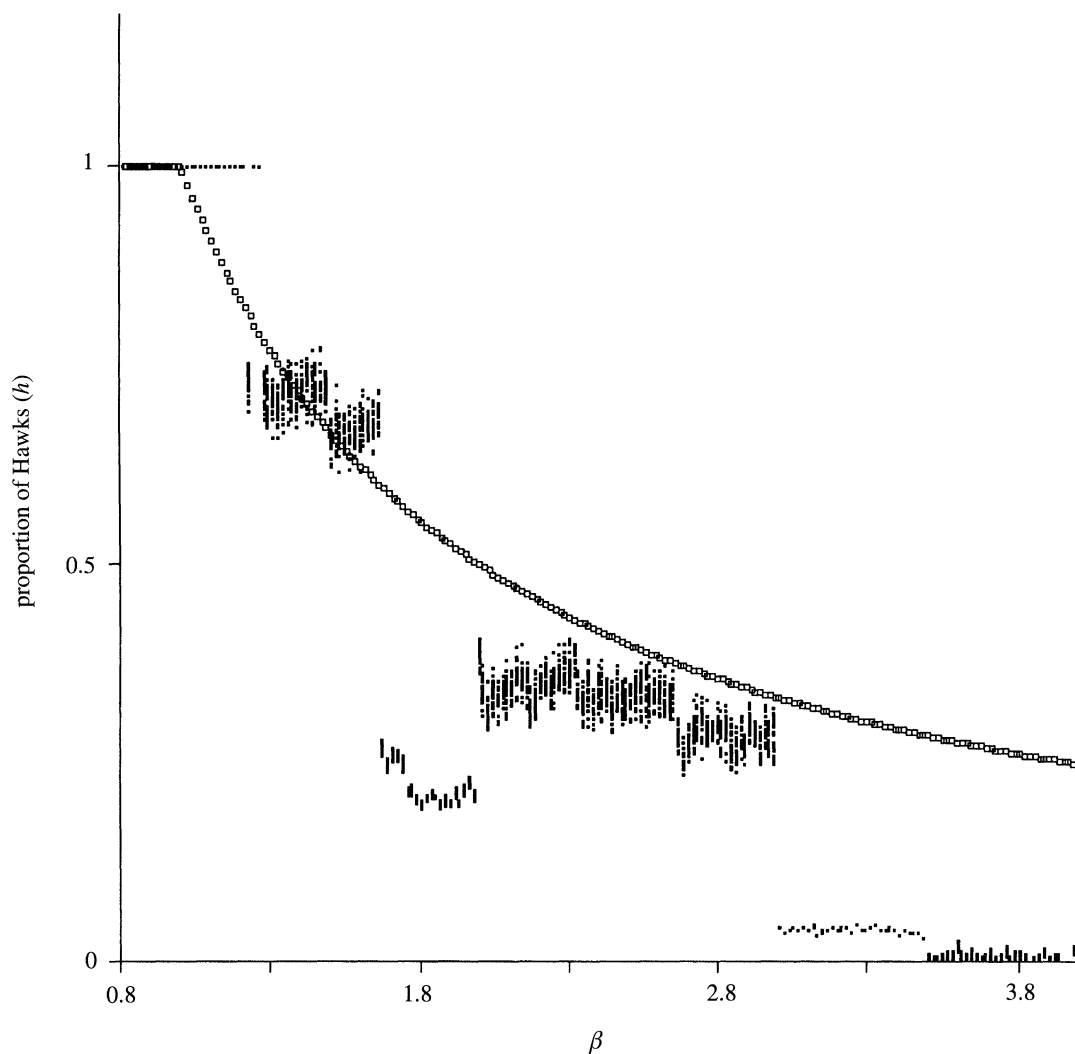


Figure 3. Same as figure 2, but with a 5% error in updating each cell. Here the phase structure and the form of the phase transitions is even more striking than in figure 2. For β -values larger than ~ 3 the proportion of Hawks present in the spatial game is very much lower than in the classical theory. Dots = spatial game with noise; squares = classical game.

strategy corresponds to a stable polymorphism consisting of a population of H and D in frequencies p and $1-p$, respectively.

Let us now consider the spatial Hawk–Dove game. We take the set of strategies and the payoff matrix to be as in the classical theory described above. The lattice A will be taken to be the $n \times n$ two-dimensional square lattice, and the local neighbourhood $N(I)$ of a cell $I \in A$ will be taken to be the eight cells which surround I . We will work with periodic boundary conditions. However, the results are qualitatively unchanged if we use fixed boundary conditions instead. These choices, together with the general definition of spatial evolutionary game theory given at the beginning of the section, define the spatial Hawk–Dove game that we shall study.

In general we found that if $\beta < 1$ then any initial configuration of Hawks and Doves becomes after a finite number of iterations all Hawks. Thus if $\beta < 1$ the results from the classical and from the spatial Hawk–Dove game are identical. Similarly, if β is very large then any initial configuration of Hawks and Doves

becomes essentially all Doves. However, for intermediate values of $\beta > 1$, the classical and spatial theories differ substantially. For these β -values we obtain a wide variety of dynamical behaviour ranging from limit points to limit cycles and to very complicated behaviour. An example of the complex spatial dynamics is shown in figure 1. In this region of β -values the dynamical behaviour of the system exhibits extreme sensitivity to the initial conditions (figure 1(e)). In addition, the discrete nature of the local updating rules implies that the dynamical time-development of the system will be unaltered if β is varied in a range whose magnitude is below a certain threshold. This threshold depends on the size of the lattice, but in general, it is surprisingly low (figure 1(f)), which again reflects the delicate effects of spatial structure.

Perhaps the most important quantity associated to the spatial Hawk–Dove game is the proportion h of Hawks in the total population in each generation. Figure 2 shows the dynamics of h for a range of β -values. One conclusion emerging from figure 2 is that the proportion of Hawks in the spatial game is in

general lower than expected from the classical results. Moreover, instead of roughly following the hyperbolic curve $1/\beta$ as β is varied, the proportion of Hawks undergoes what might be called ‘phase transitions’. Initially, when β just passes the threshold value 1, there is a small region of β -values for which no Doves survive, contrary to the classical theory. For values of $\beta > 9/7$, there is a first transition: instead of gradually decreasing as in the classical case, the proportion of Hawks drops suddenly and fluctuates around a mean that stays roughly constant as β is further increased. At $\beta = 5/3$, there is another sudden drop in the average proportion of Hawks, which rises again significantly at $\beta = 2$. Thus, as β is varied the spatial structure can lead to abrupt qualitative changes in the outcome of the Hawk–Dove interactions. In general, these transitions are associated with the success or failure of certain geometrical structures of Hawks or Doves to grow on the lattice. For example, the point at which a single Dove is able to grow in a sea of Hawks occurs at $\beta = 9/7$, which corresponds to the first transition. The second transition at $\beta = 5/3$ corresponds to the value of β at which a square of four Hawks is no longer able to grow in a sea of Doves, and the third transition occurs at $\beta = 2$, when a square of four Hawks can be invaded by a Dove. Similar observations hold for the transitions at larger β -values. As the cost of Hawk–Hawk contests becomes large, the dynamics of the Hawk proportion h become cyclic (figure 2). This is because of the appearance of ‘blinkers’: single Hawks surrounded by Doves are doing well, so that in the next generation there appears a cluster of nine Hawks, which reduces to a single Hawk again in the following generation because of the large cost β .

It has recently been observed that results from the spatial prisoner’s dilemma (Nowak & May 1992) may change qualitatively if some stochasticity in the updating rule is introduced (Mukherij *et al.* 1995). Here we do not refer to the stochasticity used to break ties, but rather to the chance of a cell failing to adopt neighbouring strategies even if they are doing better. Figure 3 shows the results from simulations in which every cell has a 5% chance of failing to update correctly. Interestingly, with stochasticity a second phase transition occurs at $\beta = 3$: the cyclic behaviour of the ‘blinkers’ for large β disappears when stochasticity is introduced. This is because the existence of the ‘blinkers’ depends on an exact symmetry in the updating rules which is broken by the introduction of stochasticity. With stochasticity it is still true that the proportion of hawks in the population is in general considerably lower than expected from the classical results. The difference is particularly pronounced for larger β after the second phase transition.

3. RETALIATION AND BULLYING

The classical Hawk–Dove game has two interesting extensions obtained by adding two further strategies: Retaliator (R) and Bully (B) (Maynard Smith 1982). These strategies are defined as follows. Retaliator: start by displaying, but escalate if opponent escalates;

Table 2. *Pay-offs in the three-strategy game*

	H	D	R
H	$1-\beta$	2	$1-\beta+\epsilon$
D	0	1	$1-\epsilon$
R	$1-\beta-\epsilon$	$1+\epsilon$	1

Bully: start by escalating, but retreat if opponent escalates. In this section we consider both the spatial Hawk–Dove–Retaliator game and the spatial Hawk–Dove–Retaliator–Bully game.

We start by considering the H – D – R game. The payoff matrix for this three-strategy game may be written in the form shown in table 2. The parameter $\epsilon \geq 0$ was introduced by Zeeman (1981) to allow for the fact that in a Retaliator versus Dove contest, the Retaliator may discover that its opponent will never escalate, and may exploit this advantage. Similarly, in a Hawk versus Retaliator contest the Hawk may have the advantage of escalating first. The case of $\epsilon = 0$ is the original model proposed by Maynard Smith & Price (1973). Here we shall consider the spatial H – D – R game for both $\epsilon = 0$ and $\epsilon > 0$.

First let us recall the solutions of the classical H – D – R game (Zeeman 1981; Maynard Smith 1982). For $\epsilon = 0$ the only ess is a polymorphism of Hawk and Dove. However, for $\epsilon > 0$ there are two alternative ess’s: pure Retaliator and a Hawk–Dove polymorphism.

The ‘solutions’ of the spatial H – D – R game are qualitatively different from the classical solutions. For $\epsilon > 0$ only Retaliators survive. Thus the Hawk–Dove polymorphism vanishes in the game with spatial structure. For $\epsilon = 0$ the final configuration in the spatial game is essentially a Retaliator–Dove polymorphism, which is again very different from the classically expected Hawk–Dove polymorphism. The results shown in figure 4 in a plot of the proportions of the various strategies as a function of β are at first sight counterintuitive: for large β , that is, high costs of Hawk–Hawk encounters, there are actually a few Hawks surviving in the population. As the cost decreases, all Hawks die, and the proportion of Retaliators increases. These results have the following explanation. A small β favours the Retaliators, which increase in frequency and drive the Hawks to extinction. As β increases, the advantage of the Retaliators decreases: eventually, the proportion of Doves is large enough to allow a few Hawks to survive. Because at most a few Hawks survive, the dynamics in the spatial H – D – R game are simpler than those in the spatial H – D game. As a consequence, updating errors do not have the strong effects apparent from figure 3 for the H – D game, and the results of figure 4 remain virtually unchanged if updating errors are introduced in the spatial H – D – R game.

We end this section by briefly turning to the spatial H – D – R – B game. The payoff matrix of the classical four-strategy game may be written in the form shown in table 3. The results of the classical H – D – R – B game are as follows (Zeeman 1981, Maynard Smith 1982). If $\epsilon = 0$ then no ess exists. Instead the system cycles indefinitely $R \rightarrow H$ – D polymorphism $\rightarrow H$ – B poly-

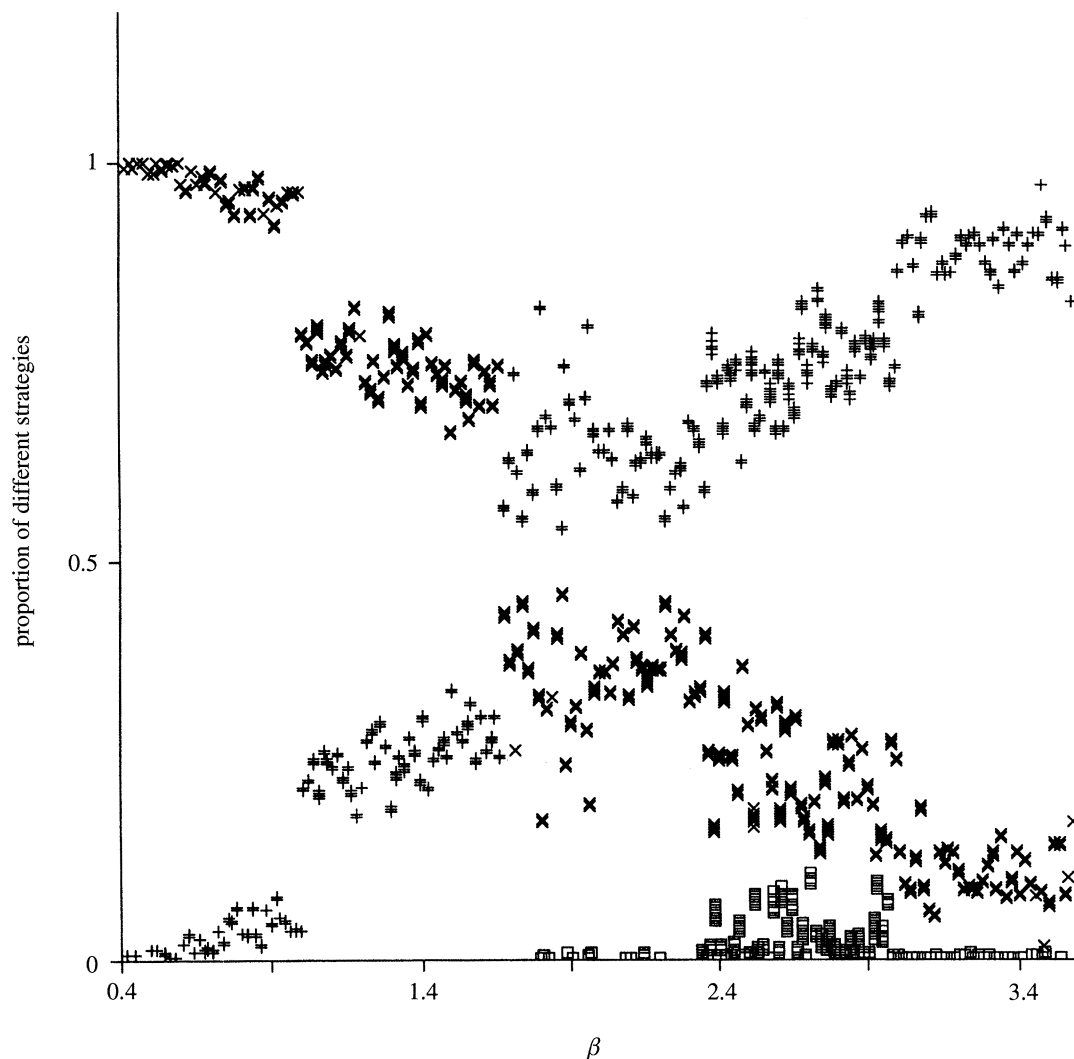


Figure 4. The proportions of Hawks (squares), Doves (plusses) and Retaliators (crosses) in the spatial H – D – R game with $\epsilon = 0$. Starting from uniform random configurations with equal proportions of H , D and R in ten generations after a transient of 150 generations was plotted for 200 β -values in the range $0.4 \leq \beta \leq 3.6$. Because at most a very small proportion of Hawks survive, these games have simpler dynamics than the game without Retaliators. Hawks can only survive if the cost of a Hawk–Hawk contest is relatively high (but not if it is too high), because only then are there enough Doves to support them. As β decreases, the Hawks vanish, while the proportion of R increases. The calculations were done on a 70×70 lattice with periodic boundary conditions and stochastic tie breaking.

Table 3. *Pay-offs in the four-strategy game*

	H	D	R	B
H	$1 - \beta$	2	$1 - \beta + \epsilon$	2
D	0	1	$1 - \epsilon$	0
R	$1 - \beta - \epsilon$	$1 + \epsilon$	1	2
B	0	2	0	1

morphism $\rightarrow R$. However, if $\epsilon > 0$ there are two ESS's, pure Retaliator and a Hawk–Bully polymorphism. The results of the spatial H – D – R – B game are again qualitatively different from the classical theory. For $\epsilon > 0$ the solution of the spatial game consists of pure Retaliators, and the same is true for $\epsilon = 0$, except if $\beta > 1$, in which case there may be (depending on initial conditions) a few Doves present among the Retaliators. Thus all the classical polymorphisms disappear with

space, and Retaliator is by far the most successful strategy.

4. DISCUSSION

In this paper we have sought to bring together two conventionally disparate aspects of modelling in evolutionary biology. The first of these aspects is the classical concept of an evolutionary game and the second is the idea of spatial dependence in a biological system. One possible route to a spatial generalization of evolutionary game theory is to associate a population of strategies to each cell of a spatial lattice and then to generalize the dynamics of classical evolutionary game theory in each cell by the addition of migration from the cell to its neighbours. This approach, which results

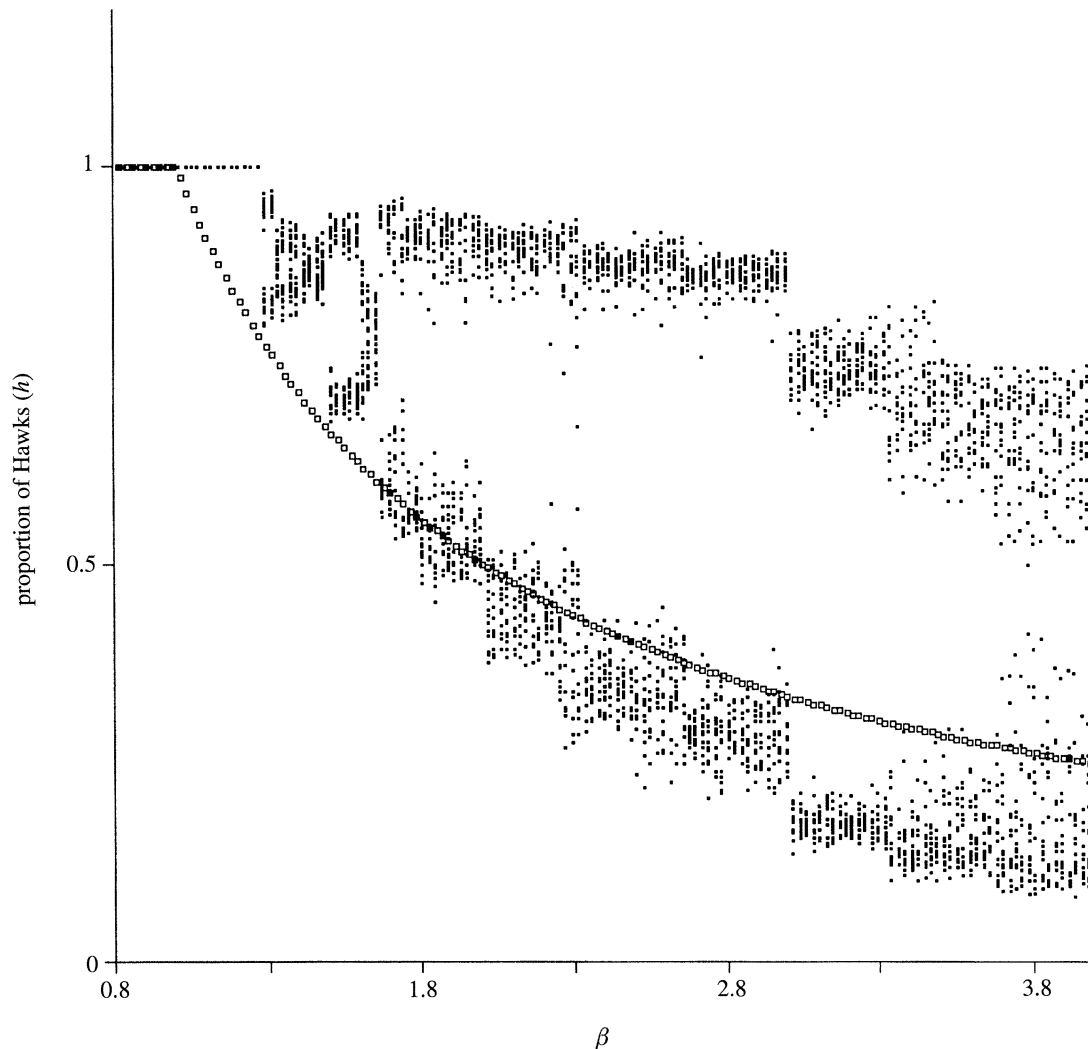


Figure 5. Same as figure 2, however after each updating the Hawks and Doves are randomly redistributed over the lattice. This procedure, which corresponds biologically to dispersal, results in dynamics which approximately lie on a two-cycle. It is clear that with this randomization Hawks are much more successful than in either the unrandomized spatial game or the classical game. Dots = spatial game; squares = classical game.

in a dynamical system of reaction–diffusion type, has been investigated by Brown & Hansell (1987) and by Durrett & Levin (1994).

Here we have chosen a quite different route to a spatial extension of classical evolutionary game theory. In our approach, which is modelled on the spatial dilemma's of Nowak & May (1992, 1993), a spatial extension of any evolutionary game is defined by associating a single strategy to each cell of the spatial lattice and giving a local rule for updating cells. The spatial generalization of an evolutionary game obtained in this way, which is defined in general in §2, is a finite cellular automaton. Such systems often display complex self-organizing behaviour (Wolfram 1984, 1986). As a consequence, spatial evolutionary game theory can be expected in general to have qualitatively different behaviour from the corresponding classical theory. Such a difference is apparent in the spatial Hawk–Dove game discussed in this paper. The spatial structure results in a series of polymorphic phases (with the proportions of Hawk and Dove approximately constant in each phase) with sudden phase transitions occurring at certain values of the cost of Hawk–Hawk

encounters. In addition, in the spatial theory the proportion of Hawks is smaller for most parameter values than would be expected from the classical theory.

It is interesting to note that the various phases seem to correspond to the different classes of complexity of cellular automata proposed by Wolfram (1986). Thus, in the region $1 < \beta < 9/7$, the system exhibits a limit point and therefore belongs to Wolfram's class I of cellular automata. For $5/3 < \beta < 2$, as well as for large β , the system exhibits limit cycles and belong to Wolfram's class II of cellular automata. For $9/7 < \beta < 5/3$, aperiodic behaviour occurs which appears to be chaotic and of the same type as that of cellular automata in Wolfram's class III. Finally, for $2 < \beta < 2.35$, the system seems to belong to Wolfram's class IV, which consists of cellular automata with extremely long transients. Such automata have been conjectured by Wolfram (1986) to support universal computation. For β in this range we find extremely long transients before the system relaxes to a simple cycle. This behaviour is typical of the critical slowing-down which has been identified by Langton (1990) as character-

izing class IV automata. In addition, the length of the transients increases very rapidly as the size of the lattice is increased, which is again typical of the behaviour found by Langton (1990) as identifying class IV systems.

The qualitative differences between the spatial theory and the classical theory are even more pronounced when the Hawk–Dove game is extended by the addition of the strategies Retaliator and Bully. As discussed in §3, either only Retaliators (for $\epsilon > 0$) or Retaliators and Doves (for $\epsilon = 0$) survive in the spatial Hawk–Dove–Retaliator game. Both of these outcomes are very different from the classical game, where one always has a Hawk–Dove polymorphism as evolutionary stable strategy, together with a pure Retaliator ESS for $\epsilon > 0$. In particular, Retaliator does considerably better in the spatial game than in the classical case.

The fact that Hawk does worse in the spatial game than in the classical game is a general consequence of spatial pattern formation. This can be made clear by considering randomized spatial games, in which after each round of updating, the strategies are randomly distributed over the lattice according to their overall frequencies. If this is done, Hawks do better, on average, than in the classical game (figure 5). This is because randomization produces smaller and more irregular clusters of Hawks, so that in one generation most Hawks have at least one Hawk as a neighbour that is surrounded by Doves, which in turn produces lots of Hawks in the subsequent generation. Consequently, the dynamics have an approximate two-cycle (figure 5). If we apply the same randomization procedure to the three strategy game, Retaliator almost always dies out. Biologically, randomizing corresponds to dispersal, so that these results suggest that thorough mixing of the population through dispersal increases the success of aggressive strategies such as Hawk.

Returning to the case of unrandomized spatial games, the success of Retaliator is even clearer when one considers the spatial Hawk–Dove–Retaliator–Bully game. In this case the final state of the spatial theory is always almost pure Retaliator, with occasionally some Doves present. In contrast, all the other strategies may survive in the classical theory. The efficiency of retaliation as a strategy in spatial evolutionary game theory is interesting given that the phenomenon of retaliation may help to explain the prevalence of ritualized behaviour in animal contests (c.f. Maynard Smith & Price 1973). The greater success of Retaliator in spatial evolutionary games than in the classical case illustrates the fundamental fact that spatial structure may allow a strategy to prosper when one would not expect this to occur on the basis of classical evolutionary game theory considerations. The analogous result for the Prisoner's Dilemma, that cooperators survive in the spatial theory, was the central observation made by Nowak & May (1992).

The strategy Retaliator is reminiscent of the 'nice', 'provokable' and 'forgiving' strategies (such as Tit for Tat) which appear to play a crucial role in the evolution of cooperation (Axelrod 1984; Nowak &

Sigmund 1993). It is tempting to speculate, therefore, that spatial evolutionary game theory favours such strategies. If this is so it suggests that, in general, cooperation may be more likely to occur in the presence of spatial structure. Indeed, studies of spatial versions of the iterated Prisoner's Dilemma seem to support this view (see, for example, Axelrod 1984).

Our formal definition of spatial evolutionary game theory given in §2 works equally well if the regular lattice \mathcal{A} is replaced by a 'random' lattice, in which the number of neighbours differs from site to site. This much more general structure may be biologically more realistic, and may also be of considerable mathematical interest. It will be interesting to study the outcomes of evolutionary games defined on these more general spatial structures. Some results in this direction have been obtained by Nowak *et al.* (1994*a, b*), who argue that, for the Prisoner's Dilemma, more general spatial structures again result in interesting spatial games.

A second interesting generalization of the work described here is to study the spatial Hawk–Dove game (and its extensions) in a continuous time formalism as opposed to the discrete time framework adopted here. Continuous time (which is appropriate in many biological situations) corresponds to the lattice cells being updated one by one in an asynchronous fashion rather than in the synchronous manner that corresponds to discrete time. The spatial Prisoner's Dilemma has been investigated in continuous time by Huberman & Glance (1993) and by Nowak *et al.* (1994*a, b*). In conclusion, in view of the results of Nowak & May (1992) and of the results presented here, we believe that the generalization of evolutionary game theory to spatially extended systems can lead to qualitatively new results that may shed light on unsolved problems.

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