Spatial Ultimatum Games, collaborations and the evolution of fairness

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It is often the case that individuals in a social group can perform certain tasks (such as hunting, for example) more efficiently if they collaborate with other individuals than if they act alone. In such situations one is necessarily faced with the problem of how the resource obtained as the result of such a collaboration should be divided among the collaborating individuals. If one of the individuals in the collaboration is in a position (through its dominance rank, for example) to impose a particular division of the resource on the other members of the collaboration then we show that an evolutionary dilemma arises which prevents such collaborations being evolutionarily stable. This dilemma, which is closely related to the well-known Ultimatum Game, results from the fact that in such situations natural selection favours individuals who, if dominant, offer smaller and smaller shares of the resource to the others and, if subdominant, will accept lower and lower offers. We also show, however, that this dilemma is naturally resolved in a spatially structured population with selection favouring the evolution of a fair division of the resource and consequently ensuring the evolutionary stability of collaborations of this type.

Keywords: Ultimatum Game; spatial games; collaborations; evolution of fairness; evolution of cooperation

1. INTRODUCTION

Many activities that are engaged in by animals are more effective if undertaken by more than one animal rather than by a single individual. Examples of such activities include hunting, defending territory and guarding a group of females (Wilson 1975; Krebs & Davies 1993, 1997). In the simplest case two individuals collaborate (in hunting, for example) to try to obtain an objective, which if achieved results, on average, in the pair gaining a resource (food, for example) which is more than twice as great as that which would be obtained by each animal acting alone. Thus the pair obtains, as a result of a successful collaboration, an excess resource of size R . The following question then naturally arises: how should the resource be divided between the two collaborators? Clearly no collaboration will be evolutionarily stable if either one of the participants is no better off than if it had acted alone. Thus each animal must receive at least as much of the resource as it could have obtained by acting independently. The essential question therefore reduces to: how should the excess resource R be split between the pair? Splitting the excess equally so that each individual receives one-half of R would accord with our idea of a fair division, but is there any reason why we should expect such a fair division to evolve by natural selection?

In practice there will often be an asymmetry between the two prospective collaborators, such as size, strength or fighting ability, or more generally, position in a dominance hierarchy (Wilson 1975; Krebs & Davies 1993, 1997), which results in one of the individuals being able to impose a particular division of the excess resource resulting from a successful collaboration on the other individual. We therefore consider here the following situation: a potential collaboration consists of two individuals,

one of whom is in a position to determine how the excess resource resulting from a successful collaboration will be divided, while the other individual is only in a position to accept or reject the proposed collaboration. Here we shall assume that the division that an individual will impose if dominant and the minimum offer an individual is prepared to accept if subdominant are genetically determined characteristics of that individual, and, in addition, that every individual is aware of the value of the division it would receive from any animal that is dominant over it, either through past interactions with the individual or through observing this animal interacting with others. Given these assumptions, the question that we consider here is: what division of the excess resource will evolve under the influence of natural selection?

In order to study this question we give a precise formulation of the division problem in terms of an evolutionary game and then show that the evolutionary outcome predicted by game theory is somewhat paradoxical. The evolutionary outcome of the division problem is that the dominant individual offers a zero share of the excess resource to the other animal, and the subdominant individual is prepared to accept any share that it is offered. Thus the subdominant animal is no better off than if it had acted alone and no such collaboration could be evolutionarily stable. Consequently, since such collaborations will not take place and therefore the excess resource R will not be available to either animal, the dominant individual will be worse off than it would have been had it been genetically programmed to offer a more generous share to any prospective partner and therefore allowed successful collaborations to take place. Thus individual selection results in a paradoxical situation, in some ways reminiscent of the Prisoner's Dilemma (Axelrod & Hamilton 1981; Axelrod 1984), in which both individuals are worse off than they would have been had the dominant individual been programmed to offer a fairer

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division of R . This outcome is closely related to the behaviour of the celebrated Ultimatum Game (Güth *et al.* 1982; Thaler 1988), which has recently been considered from the point of view of evolutionary game theory (Nowak *et al.* 2000; Page *et al.* 2000).

In this paper we consider how this Collaborator's Dilemma can be resolved. We show here that if this problem is considered in a spatially structured context then much fairer divisions automatically evolve. Hence spatial structure resolves the difficulties associated with the division problem and provides a natural explanation for why collaborations of the form considered here are evolutionarily stable. A more detailed discussion of these issues, covering a number of extensions of the basic case considered here together with various analytical results, which we will simply state, will be given elsewhere.

2. THE COLLABORATOR'S DILEMMA

We now give a precise formulation, in terms of evolutionary game theory (Maynard Smith 1982), of the division problem that arises in collaborations of the type considered above. The amount of the resource obtained by a successful collaboration which is in excess of the sum of the resources that could be obtained by each animal independently is denoted by R . Without any loss of generality we can always take $R = 1$. We consider a population $\mathcal{P}$ of N individuals labelled by $i = 1, 2, \dots, N$. In addition we assume that there exists in the population a dominance hierarchy of height n : that is, every member of the population has a dominance rank associated to it, which is specified by an integer $1, 2, \dots, n$. More formally, if we let $D = \{1, 2, \dots, n\}$ then the dominance rank of an individual $i \in \mathcal{P}$ is $d(i) \in D$. An individual i is said to be dominant over an individual j if and only if $d(i) < d(j)$. To formulate the division problem in terms of evolutionary game theory we associate to each member of the population $i \in \mathcal{P}$ a strategy $\sigma_i = (p_i, q_i) \in \mathcal{S} = [0, 1] \times [0, 1]$, defined as follows: if in any pairwise interaction between i and another member of the population j , where i and j have different dominance ranks and $d(i) < d(j)$ then $p_i \in [0, 1]$ is the fraction of the excess resource $R = 1$ that i offers to j ; if, however, $d(i) > d(j)$ then $q_i \in [0, 1]$ is the smallest offer that i will accept. To complete the specification of the game we must give the pay-off that results from an interaction between i and j . The pay-off is defined as follows: if $d(i) < d(j)$, say, then the pay-off obtained by i against j is $E(i, j) = B(1 - p_i)$ if $p_i \geq q_j$ and $E(i, j) = 0$ if $p_i < q_j$, and the pay-off obtained by j against i is $E(j, i) = B(p_i)$ if $p_i \geq q_j$ and $E(j, i) = 0$ if $p_i < q_j$. In these formulae for the pay-off, B is a fitness function which expresses the increase in fitness that an individual obtains from a given share of the excess resource. We shall assume here that $B(0) = 0$ and that $B(x)$ is a strictly increasing function of x . A particularly simple form of the game results from the choice $B(x) = x$. However, we shall also consider here the case in which B is a concave function, reflecting the fact that the benefit obtained from a resource will often obey a law of diminishing returns.

In the definition of this game we assumed that individuals of the same dominance rank do not play against one another. This seems a reasonable assumption in view of the fact that such individuals do not possess any

asymmetry which would allow either of them to impose a division of the resource on the other. We will make this assumption throughout this paper, although we note here the following two interesting alternative possibilities. The first is that individuals of equal dominance rank agree to a fair splitting of the excess resource instead of not playing at all. The second possibility is that if individuals with the same dominance rank form collaborations then they may attempt to divide the resource by engaging in a sequence of alternating offers for how much the other will receive, with the sequence terminating when an offer is accepted. If it is also assumed that the value of the resource decreases with time then it follows from bargaining theory (Rubinstein 1986) that a division close to the fair one will evolve.

The game defined above, which we will call the *Level n Ultimatum Game*, gives a precise evolutionary game theory formulation of the type of division problem considered earlier. In the case $n = 2$ and $B(x) = x$ this game reduces to the Classical Ultimatum Game (see Güth *et al.* (1982); Thaler (1988); Binmore (1992, 1994, 1998); Binmore *et al.* (1995); Samuelson (1997); and also Nowak *et al.* (2000); Page *et al.* (2000)). However, in general, the Level n Ultimatum Game is more complex than the Classical Ultimatum Game as it allows a given individual to both propose divisions of the resource to those individuals in the population over which it is dominant and to respond to divisions offered by individuals who are dominant over it.

We can deduce from the Level n Ultimatum Game the evolutionary outcome of the division problem. The basic argument can be described intuitively in the following way: consider, for simplicity, a situation (closely related to the Classical Ultimatum Game) in which the population $\mathcal{P}$ is composed of two subpopulations $\mathcal{P}_1$ and $\mathcal{P}_2$, where all the members of $\mathcal{P}_1$ have dominance rank l_1 and all the members of $\mathcal{P}_2$ have dominance rank l_2 . We shall assume that $l_1 < l_2$. Furthermore, let us assume that the populations $\mathcal{P}_1$ and $\mathcal{P}_2$ are homogeneous in the sense that all members of $\mathcal{P}_1$ use the same strategy (p_1, q_1) and all members of $\mathcal{P}_2$ use the same strategy (p_2, q_2) . In interactions between $\mathcal{P}_1$ and $\mathcal{P}_2$, individuals in $\mathcal{P}_1$ only use strategy p_1 and individuals in $\mathcal{P}_2$ only use q_2 . Hence, we shall refer to p_1 and q_2 simply as p and q , respectively. If $p > q$ then any mutant strategy p' in $\mathcal{P}_1$ which satisfies $p > p' > q$ will receive a higher pay-off than p and will invade. This process will continue until the $\mathcal{P}_1$ population consists of individuals with $p = q$. A mutant q' in $\mathcal{P}_2$ with $q' < q$ will be neutral and such mutations can invade $\mathcal{P}_2$ by drift. Invasion by such q -lowering mutants results in a decrease in the mean q -level of $\mathcal{P}_2$, which can in turn be exploited by p -lowering mutants in the $\mathcal{P}_1$ population. The continuation of this process results in the mean p and q values of $\mathcal{P}_1$ and $\mathcal{P}_2$, respectively, evolving to zero. It is not hard to generalize this argument to the case of more than two homogeneous subpopulations with individuals in different subpopulations having different dominance ranks, to show that the offer and acceptance levels of all individuals evolve to zero.

Under the assumption that $\mathcal{P}_1$ and $\mathcal{P}_2$ are homogeneous the standard framework of adaptive dynamics (Hofbauer & Sigmund, 1990, 1998; Nowak & Sigmund, 1990; Metz *et al.*, 1996; Geritz *et al.* 1997, 1998) can be applied, giving the time evolution of p and q to be

Figure 1. The evolutionary dynamics of the mean offer (p) made by the dominant individuals in the population and the mean acceptance level (q) of the subdominant individuals in the population for the Level 2 Ultimatum Game with linear benefit function $B(x) = x$, as a function of time. The dynamics are determined using an evolutionary simulation in which the individuals in a population of 1000 have either dominance rank 1 or 2 and strategies (p_i, q_i) . Each individual plays against all other individuals in the population that have a different dominance rank and receive pay-offs from the games as described in the text. The fitness of each individual in a given generation is taken to be the sum of the pay-offs it obtains in these games. Each individual then reproduces in proportion to its total fitness to yield the distribution of individuals in the next generation. We note that when an individual reproduces its offspring are assumed to inherit both its strategy (p_i, q_i) and its dominance rank. The mechanism which results in offspring having the same dominance rank as that of their parents could, in principle, involve either genetics, with offspring inheriting the attributes which were responsible for their parents' position in the dominance hierarchy, or imitation, with offspring copying the behaviour which was responsible for the parents' dominance rank. Mutations in the strategies (p_i, q_i) (which are chosen from a normal distribution with mean equal to the strategy mutating and variance equal to 10% of the mean) are introduced at a rate of 1% per generation. We see here that the mean values of p and q evolve to zero as discussed in the text. The same result is true for any number of dominance ranks and any fitness function $B(x)$.

$\dot{p} = -B'(1-p)$ if $p \geq q$ or $\dot{p} = 0$ if $p < q$, and $\dot{q} = 0$ (see also Nowak *et al.* (2000); Page *et al.* (2000)). Thus for $p > q$, p will decrease until p reaches the line $p = q$ and for $p < q$ the system will not change. According to the definition of the game used here the behaviour on the diagonal $p = q$ cannot be described by adaptive dynamics. The inability to describe the behaviour on the diagonal is due to the discontinuous nature of the step function used in the definition of the game. However, if the game is modified by replacing the step function by an arbitrarily good smooth approximation, which is a reasonable change in view of the fact that in the real world changes cannot occur instantaneously, then it may be shown using adaptive dynamics that both p and q evolve to zero (for an alternative argument establishing this result see Page & Nowak (2000)). This adaptive dynamics argument can be extended to more than two homogeneous subpopulations, with individuals in different subpopulations having different dominance ranks, to show formally that for any fitness function B the offer and acceptance levels evolve to zero.

The result that the offer and acceptance level evolve to zero is confirmed by evolutionary simulations for heterogeneous populations with interactions between individuals with different strategies and dominance ranks. Figure 1 shows the results of evolutionary simulations for a population with $n = 2$ and a linear fitness function. The same qualitative behaviour is obtained for hierarchies of any height and for any fitness function—in all cases the offer and acceptance levels of the individuals in the population evolve to zero.

3. SPATIAL ULTIMATUM GAMES

We have seen above that the Collaborator's Dilemma is paradoxical in a sense that is reminiscent of the Prisoner's Dilemma. In view of the success in resolving many of the problems associated with the evolution of cooperation that results from the introduction of spatial structure (Nowak & May 1992; Nowak *et al.* 1994; Killingback *et al.* 1999), it is natural to consider the effect of spatial structure on the division problem defined in § 2 (the effect of spatial structure on the Classical Ultimatum Game has been discussed very recently by Page *et al.* (2000)).

To define the spatial version of the Level n Ultimatum Game introduced in § 2 according to the principles of spatial evolutionary game theory (Killingback & Doebeli 1996) we introduce a two-dimensional lattice Λ , which could be, for example, a square lattice, a hexagonal lattice or even a random lattice given by an arbitrary tessellation of the plane. For a given lattice Λ we define a set of neighbours for each cell in Λ . For example, if Λ is a square lattice the neighbours of any given cell can be taken to be the eight cells immediately surrounding it; if Λ is a hexagonal lattice then the neighbours of a cell can be taken to be the six cells immediately surrounding it; in the case of a random lattice each cell can have a different number of neighbours, given by the cells which immediately surround the cell. Here we will take Λ to be a hexagonal lattice, although all our results are qualitatively unchanged on any other two-dimensional lattice. The case in which Λ is a random lattice defined by the Voronoi diagram (see de Berg *et al.* (1997)) of a set of points in the plane will be discussed in detail elsewhere. We assume that each cell is occupied by an individual which has associated to it both a dominance rank $l \in D$ and a strategy $(p, q) \in \mathcal{S}$, as in the non-spatial game. At the start of a given generation an individual in cell $I \in \Lambda$ plays against each of the individuals in its neighbouring cells, where the game between each pair of individuals is as defined above. The fitness of an individual in a given cell is taken to be the sum of the pay-offs it receives from playing against its neighbours. Repeating this procedure for each cell results in all individuals on the lattice being assigned a fitness. At the start of the next generation the occupant of cell I is replaced by the occupant of the neighbouring cells of I and I itself which has the highest fitness (in case of a tie one of the fittest individuals is chosen at random). Applying this procedure to every cell of the lattice results in the entire spatial lattice being updated each generation. We shall refer to the spatial game defined in this way as the *Level n Spatial Ultimatum Game*.

To follow the evolutionary dynamics of this spatial game we start from an initial configuration consisting of

Figure 2. The evolutionary dynamics of the Level n Spatial Ultimatum Game, for $n = 2, 3$ and linear benefit function $B(x) = x$, on a hexagonal lattice of 40 000 cells (i.e. 200×200) with fixed boundary conditions. (a) The evolution of the mean phenotypes for the Level 2 Spatial Ultimatum Game. The asymptotic value of the mean offer $\bar{p}$ is seen to be very close to the theoretical prediction $\bar{p} = 1/3$ and this value is maintained indefinitely. (b) The evolutionary dynamics of the Level 3 Spatial Ultimatum Game. The mean phenotypes now display greater variations than in the Level 2 case; however, all phenotypes are again maintained at significant levels. In this figure, p_1 and p_2 are the offers made by individuals of dominance ranks 1 and 2, respectively, and q_2 and q_3 are the acceptance levels of individuals of dominance ranks 2 and 3, respectively. In both cases the initial strategies in each cell were picked uniformly randomly from $(0, 0.5)$ and mutations (which had the same characteristics as in the non-spatial case) occurred at a rate of 1% per generation. In addition, we include a stochastic element in the updating procedure so that in 5% of cases an individual is not taken over by the fittest individual in its neighbourhood, but instead remains unchanged.

individuals whose dominance levels are picked uniformly randomly from D and whose strategies are picked randomly from $\mathcal{S}$. The evolutionary dynamics of the system follow from the updating rule defined for the spatial game together with the occasional appearance of mutations in the strategies associated to the individuals on the lattice. We show in figure 2 the evolutionary dynamics of the Level n Spatial Ultimatum Game for $n = 2, 3$ and the linear fitness function $B(x) = x$. The introduction of spatial structure clearly results in a striking difference in the evolutionary outcome of the Ultimatum Game, with the mean of the strategies used by the population being reasonably close to a fair division, and with these fair strategies being maintained indefinitely.

Figure 3. The evolutionary dynamics of the Level 2 Spatial Ultimatum Game for the nonlinear fitness function $B(x) = 1 - e^{-4x}$. Again all phenotypes are maintained indefinitely at non-zero levels; however, the value of $\bar{p} \simeq 0.16$ is lower than in the linear case. All parameter values are as in figure 2.

For $n = 2$ we can deduce analytically, by an extension of the methods used by Killingback *et al.* (1999) and Hauert (2001) to study the behaviour of spatial games, that an estimate of the asymptotic value of the mean offer made by the dominant individuals in the population is $\bar{p} = 1/3$. We see from figure 2a that this estimate is in extremely good agreement with the results of our evolutionary simulations. We can also show that the Level n Spatial Ultimatum Game defined on a lattice with a local neighbourhood that consists of m cells maintains individuals at all dominance ranks if and only if $n \leq \lfloor m/2 \rfloor$. If this condition is initially not satisfied then subpopulations of individuals with a given dominance rank successively go extinct until the inequality is satisfied, at which point all dominance ranks are maintained indefinitely. This inequality is confirmed by our simulations. We find on the hexagonal lattice (i.e. $m = 6$) that for $n = 2, 3$ individuals of all dominance ranks are maintained indefinitely in the Level n Spatial Ultimatum Game. However, for $n > 3$ all individuals with certain dominance ranks are eliminated until only three dominance ranks remain in the population.

Qualitatively very similar results are obtained for nonlinear fitness functions $B(x)$. Figure 3 shows the evolutionary dynamics of the Level 2 Spatial Ultimatum Game for $B(x) = 1 - e^{-4x}$. While the qualitative behaviour is identical to the linear case there is the obvious quantitative difference that the asymptotic mean value of the offers made by the dominant individuals in the population ($\bar{p} \simeq 0.16$) is now significantly lower than in the linear case. The qualitative behaviour of the Level n Spatial Ultimatum Game for $n > 2$ for nonlinear $B(x)$ is the same as in the linear case. In particular, the condition that individuals at all dominance ranks are maintained if and only if $n \leq \lfloor m/2 \rfloor$ still holds.

4. CONCLUSIONS

The formation of collaborations which enable a resource to be obtained more efficiently than by a solitary individual, are a common feature of animal behaviour. Here we have shown that certain types of collaborations—namely those in which one individual is in a position to determine how the excess resource resulting from a successful collaboration will be divided, while the

other can only accept or reject the proposed collaboration—suffer from a fundamental evolutionary instability. This instability, which is closely related to the behaviour of the Classical Ultimatum Game, follows from the fact that natural selection will favour the outcome in which an individual in the dominant role will always offer a zero share of the excess resource to the animal in the subdominant role, and an individual in the subdominant role will accept any share that is offered. Because this results in the subdominant individual being no better off than if it acted alone, no collaboration of this type will be stable. This breakdown in collaboration results in all individuals in the population being worse off than they would have been had individuals, when dominant, made a non-zero offer.

We have shown here that the introduction of spatial structure radically changes the situation. In a spatially structured population selection leads to individuals both offering and aspiring to non-zero divisions of the excess resource. Thus spatial structure yields a natural resolution of the Collaborator's Dilemma and provides a fundamentally simple explanation for the evolutionary stability of collaborative actions.

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