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The emergence of kinship behavior in structured populations of unrelated individuals*

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Abstract. The paper provides an explanation for altruistic behavior based on the matching and learning technology in the population.

In a infinite structured population, in which individuals meet and interact with their neighbors, individuals learn by imitating their more successful neighbors. We ask which strategies are robust against invasion of mutants: A strategy is *unbeatable* if when all play it and a finite group of identical mutants enters then the learning process eliminates the mutants with probability 1. We find that such an unbeatable strategy is necessarily one in which each individual behaves as if he is related to his neighbors and takes into account their welfare as well as his. The degree to which he cares depends on the radii of his neighborhoods.

Key words: Population dynamics, Local interaction, altruism, inclusive fitness

1. Introduction

Kinship has been suggested as a plausible explanation of altruism and cooperative behavior between blood relations. When individuals are related and

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share some common genes then cooperation increases the fitness of their common genes and altruistic behavior is likely to be selected (Hamilton Hamilton [9]).

Kinship arguments are not suitable for explaining cooperation in human society at large: Two randomly chosen individuals are not likely to be related. Yet humans very often behave as if the well being of others enters their considerations and influences their actions. Many explanations have been offered for this seeming paradox: Recently some models have calculated the degree of altruism which is in some sense stable given that altruistic behavior exists and can be identified as such by others (see e.g. Fershtman and Weiss [7]).

It is likely that humans learned to behave altruistically in situations in which this type of behavior was called for and was justified e.g. within a family, and later have extended this behavior to other situations (Axelrod and Hamilton [1]). In this paper we suggest that (seemingly) altruistic behavior may have also originated in situations in which individuals were not related but met often with a subset of the population: their neighbors. We show how the matching and the learning technology in an infinite population causes individuals to behave as if they are altruistic and care about their neighbor's welfare. It is assumed that the population has a local interaction structure: Each individual meets and interacts only with individuals in his interaction neighborhood. The interaction takes the form of a game, payoffs are obtained as a result of these interactions. Occasionally, an individual is permitted to learn and change his strategy. He will then imitate at random one of the individuals in his learning neighborhood and he is more likely to imitate a more successful individual. The learning neighborhood may differ from the interaction neighborhood. We also assume that individuals are *conservative* and are reluctant to introduce a new strategy to their environment. This assumption is only suitable for cultural evolution. In a biological setup, replacing a dead individual is analogous to learning. However, a dead individual can be replaced by the seed of any of his neighbors irrespective of whether the dead individual was identical to his neighbors. Hesitation and fear of novelty are cultural rather than biological features. Thus, the results of this model should not be directly applied to biological models.

In the spirit of the Evolutionarily Stable Strategies (ESS) we look for an unbeatable strategy: A strategy, that if all individuals play it and a finite group of identical mutants enters, the dynamic process defined by the interaction and learning procedure will eliminate the mutants with probability 1. We find that if such an unbeatable strategy exists it is one in which individuals behave as if they care about their neighbors: The unbeatable strategy is an ESS in a game derived from the original interaction game by changing the payoffs so that the new payoffs take account of the *inclusive fitness* as defined by Hamilton. The player cares about the welfare of his opponents to a degree which is determined by the sizes (radii) of the relevant neighbors. When taking the ESS of this new derived game we no longer take account of the local interaction structure, this is taken care of by the inclusive fitness.

The intuition for this result is straightforward. The learning process consists of imitation. The individuals in a player's learning neighborhood are likely to play the same strategy that he does, since he is likely to imitate them and they him. However, an individual interacts with players in his interaction neighborhood, who may or may not have imitated him. A strategy is likely to be unbeatable if it earns a higher payoff than others in these changing environment (else a player of this strategy is likely to switch to another that does better). To do better than others, a strategy has to strike a balance between cooperating with identical strategies and beating other strategies. Players are not assumed to have the sophistication required for this calculation, circumstances lead them to behave as if they do. Balancing between the two aims depends on the ratio between the two radii of the interacting and learning neighborhoods. If n, the radius of the learning neighborhood is much greater than k (the radius of the interaction neighborhood) then a player is likely to interact with identical individuals and under these circumstances a strategy that takes into account the opponents welfare will do well. While if $k \gg n$ then a player will face mostly other strategies and in this case he will do better by being selfish and not taking into account his opponent's welfare.

2. The model

2.1. Interaction and learning on a line

Three components are needed to describe the model:

- How do individuals interact?
- When is an individual allowed to change his strategy?
- How does he change his strategy (learning)?

Denumerable individuals are located at the integer points $(0, \pm 1, \pm 2 \ldots)$ of an infinite line. Each individual affects and is affected by his immediate $2k$ neighbors, the interaction takes the form of a game. Each individual chooses a strategy in a symmetric finite game Ω, this strategy interacts with the strategies of all his immediate $2k$ neighbors and produces his payoff. The payoff is the sum of the payoffs he gets from his interaction with all his neighbors. Time is continuous and interaction takes place at each time t. We assume that all payoffs in Ω are strictly positive.

Occasionally, an individual is allowed to change his strategy: Each individual waits an exponential time, independent of others and independent of past events, and with the same intensity parameter as others, which, without loss of generality, we take to be 1. When called upon to revise his strategy an individual will not necessarily be keen to do so. Ours is not a model of inspiring innovations but rather of sluggish imitation. A player will start looking around for a new strategy to adopt, but uniformity and homogeneity are the enemies of change. If he sees no new strategies in his nearest environment he is very likely to stop his search for a new strategy. Very few players will continue despite this discouragement to search for inspiration in a wider neighborhood. In this paper we assume extreme *conservatism* of learning: An individual will learn only if at least one of his *two immediate* neighbors plays a strategy different to the one he currently plays. That is, we assume that if the immediate neighborhood does not encourage change then the player will look no further.

However, when an individual is activated to learn and when the above condition is satisfied then he will consider his learning neighborhood: $2n + 1$ individuals, including himself and his immediate $2n$ neighbors. Individual i

will switch to the strategy[1] used by individual j with a rate given by the relative success of j in i's learning neighborhood. Thus, the momentary probability $p_{i,j}$ of i switching to j's strategy at time t (for j in i's learning neighborhood) is given by:

$$p_{i,j} = \frac{\omega_j}{\sum_{h=-n}^{n} \omega_{i+h}} \tag{1}$$

where ω_h is player h's current payoff (the sum total of all his interactions). Note that our assumption that all payoffs are positive implies that a player who is permitted to learn has a positive probability to switch to a different strategy.[2]

This dynamic system is a special case of an Interacting Particle System in which particles can be in one of a finite number of states and in which the momentary transition rates at each location are uniformly bounded and determined by the state of particles within a finite radius. The derived evolutionary dynamics of such a system is uniquely determined and is a Markov process in the space of all population states (see Ligget 1985, Ligget 1985, [11], p. 122).

The dynamic process is thus fully defined by the game Ω and the radii of the two neighborhoods: k, n. We denote the dynamic process defined in this way by $\langle \Omega, k, n \rangle$.

The conservative learning assumption, that an individual may learn only when at least one of his immediate neighbors is different, ensures that only players directly on the border of clusters between two strategies may change their strategies. The continuous time of the dynamics ensures that no two (close) individuals learn simultaneously (a zero probability event). Hence borders only shift but no new borders and no new clusters are formed, although clusters may shrink and disappear. For a discussion of conservative assumption see section 5.

2.2. Unbeatable Strategies

We shall look for strategies which are in some sense robust against invasion of mutants. Our definition of robustness, like the Evolutionarily Stable Strategies (ESS) tests the robustness of a strategy against a single type of mutant at a time. We assume that all individuals on the line play the same strategy and that a finite number of identical mutants has entered. The indigenous strategy is stable against the invasion if, when beginning at this state, the dynamic process of interaction and learning eliminates the mutants with probability 1.

Definition. *A strategy* $\underline{\mathbf{x}}$ *is an* ***unbeatable strategy*** *of* $\langle \Omega, k, n \rangle$ *if for any strategy* $\underline{\mathbf{y}}$*, beginning from a state in which all but a finite number of individuals play*

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[1] We allow individuals to learn and imitate mixed strategies. In a genetic context this raises no problems. For cultural evolution one may argue that when an individual adopts a new mode of conduct he learns a set of rules that determine his random behavior.

[2] The payoffs of the game Ω may be interpreted as the excess payoff above a payoff level 0. Transforming all payoffs of Ω (and 0) by an affine transformation, $x \to \alpha x + \beta$ with $\alpha > 0$, leaves the dynamics defined above unchanged. Thus the payoffs of the game Ω can be taken to be von Neumann Morgenstern utility levels.

strategy $\underline{\mathbf{x}}$ *and the rest play* $\underline{\mathbf{y}}$*, the dynamic process* $\langle \Omega, k, n \rangle$ *converges with* probability 1 to a state in which all play $\underline{\mathbf{x}}$.

The difference between an ESS and an Unbeatable Strategy is that the latter is defined for populations with a local interaction structure, and that the process by which mutants are eliminated is explicitly defined.

Due to the *conservative learning* assumption, the strength of an unbeatable strategy is revealed when the mutants have succeeded and won over a large interval on the line. Any short string of mutants has a positive probability of vanishing. It also has a positive probability of becoming sufficiently long so that, due to the local interaction structure, whatever happens on its one side is unaffected by the other side. If a large string of mutants is guaranteed to shrink then it must eventually vanish. Thus it suffices to test the strength of an unbeatable strategy against a long string of mutants. It therefore suffices to consider the movement of the boundary between two large strings of strategies. This intuitive argument is made clear in the definitions and the lemma of this section.

Consider a *Frontier State*, a state in which all players on one side of a certain player, his left side say, play a strategy $\underline{\mathbf{y}}$, while all players to his other side (his right side) including this player, play a strategy $\underline{\mathbf{x}}$. Beginning with this state, only the players on the border between the two strategies may revise their strategies, thus the dynamic process becomes a continuous time random walk of the border (between $\underline{\mathbf{x}}$ and $\underline{\mathbf{y}}$). For a strategy $\underline{\mathbf{x}}$ to win means that each player will eventually play $\underline{\mathbf{x}}$, or alternatively that the frontier, the border between the two strategies, will move to the left, to $-\infty$, with probability 1.

Which strategy will win in this simple situation? Consider the frontier between the regions in which $\underline{\mathbf{x}}$ and $\underline{\mathbf{y}}$ are played. We can calculate the momentary rate of transition $P_{\underline{\mathbf{x}}\to\underline{\mathbf{y}}}$, for a frontier $\underline{\mathbf{x}}$ agent to become a $\underline{\mathbf{y}}$ agent. This probability is, of course, independent of the precise location of the frontier on the line. The position of the frontier behaves like a continuous time random walk with rates of jumps $P_{\underline{\mathbf{x}}\to\underline{\mathbf{y}}}$ and $P_{\underline{\mathbf{y}}\to\underline{\mathbf{x}}}$ to the right and to the left respectively. From basic properties of random walks we know that if $P_{\underline{\mathbf{x}}\to\underline{\mathbf{y}}} > P_{\underline{\mathbf{y}}\to\underline{\mathbf{x}}}$ then a frontier $\underline{\mathbf{x}}$ player is more likely to turn to $\underline{\mathbf{y}}$ than the reverse, in that case strategy $\underline{\mathbf{y}}$ takes over, each individual will eventually play the strategy $\underline{\mathbf{y}}$ and the frontier will move to $+\infty$ with probability 1. If $P_{\underline{\mathbf{x}}\to\underline{\mathbf{y}}} < P_{\underline{\mathbf{y}}\to\underline{\mathbf{x}}}$ then strategy $\underline{\mathbf{x}}$ will take over. In the singular case $P_{\underline{\mathbf{x}}\to\underline{\mathbf{y}}} = P_{\underline{\mathbf{y}}\to\underline{\mathbf{x}}}$, no strategy will take over and the borderline between the strategies will meander over all positions on the line.

When $P_{\underline{\mathbf{y}}\to\underline{\mathbf{x}}} > P_{\underline{\mathbf{x}}\to\underline{\mathbf{y}}}$ we denote it by: $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$.

The following lemma establishes the first connection between unbeatability and winning in a simple frontier state.

Lemma 1. *Let the initial state be one in which all individuals play strategy* $\underline{\mathbf{x}}$ *except for a finite number who play* $\underline{\mathbf{y}}$*, then:*

1. *If* $\underline{\mathbf{y}} \succ \underline{\mathbf{x}}$ *then with positive probability the process will converge to a fixation of* $\underline{\mathbf{y}}$*, i.e. to a state in which all play* $\underline{\mathbf{y}}$.
2. *If* $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$ *then with probability 1 all* $\underline{\mathbf{y}}$ *players will be driven to extinction and all will play* $\underline{\mathbf{x}}$.

Proof. 1. Consider the case $\underline{\mathbf{y}} \succ \underline{\mathbf{x}}$. There is a positive probability that a sufficiently large single cluster (interval) of $\underline{\mathbf{y}}$ players will be formed (recall that an $\underline{\mathbf{x}}$ player whose immediate neighbor is a $\underline{\mathbf{y}}$ player has a positive probability of becoming a $\underline{\mathbf{y}}$ player). Once a single cluster of $\underline{\mathbf{y}}$ players has been formed whose length is $> n + k$ the transition probabilities $P_{\underline{\mathbf{x}} \to \underline{\mathbf{y}}}, P_{\underline{\mathbf{y}} \to \underline{\mathbf{x}}}$ on the left and right borders of the long cluster are the same as in a simple frontier state, i.e. the system behaves as if there are only $\underline{\mathbf{x}}$ player on one side and only $\underline{\mathbf{y}}$ players on the other (or vice versa). This is so because a player observes a neighborhood of radius n, the individuals in this neighborhood interact with individuals who are all included in a neighborhood of radius k of this neighborhood. Thus, if all clusters are longer than $n + k$ then each border behaves as a simple frontier. Since $\underline{\mathbf{y}} \succ \underline{\mathbf{x}}$, a long cluster has positive probability of becoming infinite without ever being shorter than $k + n + 1$. The process is then supercritical and therefore a cluster of $\underline{\mathbf{y}}$ has a positive probability of winning over the whole population.

2. Now consider the case $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$. First we show that beginning with a general population state, each single cluster will either vanish or will become infinite. All transition rates at a boundary location are bounded above by 1 and below by some $p > 0$, since by assumption all payoffs in the interaction game are strictly positive. It therefore follows that any cluster of length N has a probability larger than $(p/p + 1)^N$ of vanishing before it reaches length $N + 1$.

This means that for any $N > 0$, with probability 1 there is only a finite number of times that a cluster can be shorter than N before it disappears. Hence any cluster will either vanish or will become larger than N.

Since we begin with a state that has only a finite number of clusters and no new clusters can appear (although clusters may vanish) it follows that after a finite random time all remaining clusters will be longer than $n + k + 1$ forever and therefore their borders will behave like simple frontiers. The length of a (long) cluster is then a continuous time Markov process. Since $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$ the process is subcritical and from any length $> n + k$ a cluster of $\underline{\mathbf{y}}$ players will shrink to length $n + k$ with probability 1, from whence it has positive probability of vanishing. It therefore follows that with probability 1 a cluster of $\underline{\mathbf{y}}$ can be longer than $n + k$ only a finite number of times before vanishing. Thus all clusters of $\underline{\mathbf{y}}$ will disappear with probability 1. ■

A direct corollary from this lemma is:

Corollary.

1. *A strategy $\underline{\mathbf{x}}$ is unbeatable in $\langle \Omega, k, n \rangle$ if and only if for all strategies $\underline{\mathbf{y}} \neq \underline{\mathbf{x}}$: $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$ (i.e. $P_{\underline{\mathbf{y}} \to \underline{\mathbf{x}}} > P_{\underline{\mathbf{x}} \to \underline{\mathbf{y}}}$).*
2. *There exists at most one unbeatable strategy.*

Corollary 1 follows from the definition of unbeatable strategy and from part 1 of the lemma. Corollary 2, the uniqueness of the unbeatable strategy follows directly from the lemma: If both $\underline{\mathbf{x}}$ and $\underline{\mathbf{y}}$ are unbeatable then $P_{\underline{\mathbf{y}} \to \underline{\mathbf{x}}}$ should, at the same time, be strictly bigger and strictly smaller than $P_{\underline{\mathbf{x}} \to \underline{\mathbf{y}}}$.

Unbeatable strategy was defined as one that cannot be invaded by any mutant, however from lemma 1 it follows that an unbeatable strategy is also the unique strategy that can with positive probability invade and take over any other strategy: If a finite number of mutants playing the unbeatable strategy invade a line in which all play another strategy, the mutants have a positive probability of taking over the whole line.

2.3. Algebraic characterization of unbeatable strategies

In this section we find an algebraic characterization of unbeatable strategies based on Lemma 1. We have established that a strategy $\underline{\mathbf{x}}$ is unbeatable in $\langle \Omega, k, n\rangle$ if for all strategies $\mathbf{y} : \underline{\mathbf{x}} \succ \underline{\mathbf{y}}$. The latter property can be easily described in terms of the game Ω and k, n the radii of the interaction and learning neighborhoods.

Consider a frontier state in which a strategy $\underline{\mathbf{y}}$ is played to the left of the boundary and $\underline{\mathbf{x}}$ to its right. We enumerate the individuals according to their distance from the frontier and the strategy they play:

$$\ldots . y_4 y_3 y_2 y_1 x_1 x_2 x_3 x_4 \ldots ..$$

The payoff of an individual x_i (y_i) will be denoted by $\omega(x_i)$ $(\omega(y_i))$. Since a player interacts with $2n$ of his neighbors, the infinitesimal switch rates of the border players are given by:

$$P_{\underline{\mathbf{x}} \to \underline{\mathbf{y}}} = \frac{\sum_{i=1}^{n} \omega(y_i)}{\sum_{i=1}^{n} \omega(y_i) + \sum_{i=1}^{n+1} \omega(x_i)} \tag{2}$$

$$P_{\underline{\mathbf{y}} \to \underline{\mathbf{x}}} = \frac{\sum_{i=1}^{n} \omega(x_i)}{\sum_{i=1}^{n} \omega(x_i) + \sum_{i=1}^{n+1} \omega(y_i)} \tag{3}$$

The condition for $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$ or: $P_{\underline{\mathbf{y}} \to \underline{\mathbf{x}}} > P_{\underline{\mathbf{x}} \to \underline{\mathbf{y}}}$, becomes:

$$\sum_{i=1}^{n} \omega(x_i) \left\{ \sum_{i=1}^{n} \omega(y_i) + \sum_{i=1}^{n+1} \omega(x_i) \right\} > \sum_{i=1}^{n} \omega(y_i) \left\{ \sum_{i=1}^{n} \omega(x_i) + \sum_{i=1}^{n+1} \omega(y_i) \right\}$$

or:

$$\sum_{i=1}^{n} \omega(x_i) \sum_{i=1}^{n+1} \omega(x_i) > \sum_{i=1}^{n} \omega(y_i) \sum_{i=1}^{n+1} \omega(y_i) \tag{4}$$

Dividing both sides by $n(n+1)$:

$$\frac{1}{n} \sum_{i=1}^{n} \omega(x_i) \frac{1}{n+1} \sum_{i=1}^{n+1} \omega(x_i) > \frac{1}{n} \sum_{i=1}^{n} \omega(y_i) \frac{1}{n+1} \sum_{i=1}^{n+1} \omega(y_i) \tag{5}$$

We now calculate each player's payoff. Denote by $\omega(\underline{\mathbf{a}}, \underline{\mathbf{b}})$ the payoff of strategy $\underline{\mathbf{a}}$ against strategy $\underline{\mathbf{b}}$ (in Ω) then:
for $i \leq k$:

$$\omega(x_i) = \frac{(k+i-1)\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) + (k-i+1)\omega(\underline{\mathbf{x}}, \underline{\mathbf{y}})}{2k} \tag{6}$$

and similarly:

$$\omega(y_i) = \frac{(k+i-1)\omega(\underline{\mathbf{y}}, \underline{\mathbf{y}}) + (k-i+1)\omega(\underline{\mathbf{y}}, \underline{\mathbf{x}})}{2k} \tag{7}$$

while for $i > k$:

$$\omega(x_i) = \omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) \quad ; \quad \omega(y_i) = \omega(\underline{\mathbf{y}}, \underline{\mathbf{y}}) \tag{8}$$

By summing over equations (6), (7), (8) we find that the averages in equation (5) can be written as:

$$\frac{1}{n}\sum_{i=1}^{n}\omega(x_i) = \begin{cases} \dfrac{2k+n-1}{4k}\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) + \dfrac{2k-n+1}{4k}\omega(\underline{\mathbf{x}}, \underline{\mathbf{y}}) & \textit{if} \quad n \leq k \\ \dfrac{4n-k-1}{4n}\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) + \dfrac{k+1}{4n}\omega(\underline{\mathbf{x}}, \underline{\mathbf{y}}) & \textit{if} \quad n \geq k \end{cases} \tag{9}$$

and similarly for strategy $\underline{\mathbf{y}}$. The coefficient of $\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}})$ in the above equation can be easily explained, it is the proportion of $\underline{\mathbf{x}}$ players with whom the n strategy $\underline{\mathbf{x}}$ players next to the border interact. That is, for each of these n players find the number of $\underline{\mathbf{x}}$ players he interacts with, add those numbers and divide by the total number of players these n players interact with: $2kn$. The future actions of a frontier individual are partly influenced by the n players who play his strategy. The coefficient of $\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}})$ in (9) measures the extent to which the influence of these n players is derived from interactions with their kin, players who play the same strategy. Thus this coefficient assesses the total effect of his kinsman on a boundary player. We will see later that this indeed corresponds to a measure of degree of relatedness among kinsmen.

Rewrite the condition for $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$ (equation (5)), to obtain:

Proposition 2. *For strategies* $\underline{\mathbf{x}}, \underline{\mathbf{y}}$: $\underline{\mathbf{x}} \succ \underline{\mathbf{y}}$ *if and only if*
for $n \leq k$:

$$\begin{aligned} &[(2k+n-1)\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) \\ &\quad + (2k-n+1)\omega(\underline{\mathbf{x}}, \underline{\mathbf{y}})][(2k+n)\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) + (2k-n)\omega(\underline{\mathbf{x}}, \underline{\mathbf{y}})] \\ &\quad > [(2k+n-1)\omega(\underline{\mathbf{y}}, \underline{\mathbf{y}}) + (2k-n+1)\omega(\underline{\mathbf{y}}, \underline{\mathbf{x}})][(2k+n)\omega(\underline{\mathbf{y}}, \underline{\mathbf{y}}) \\ &\quad + (2k-n)\omega(\underline{\mathbf{y}}, \underline{\mathbf{x}})] \end{aligned}$$

and for $n \geq k$:

$$[(4n-k-1)\underline{\mathbf{x}},\underline{\mathbf{x}}) + (k+1)\omega(\underline{\mathbf{x}},\underline{\mathbf{y}})][(4n-k+3)\omega(\underline{\mathbf{x}},\underline{\mathbf{x}}) + (k+1)\omega(\underline{\mathbf{x}},\underline{\mathbf{y}})]$$

$$[(4n-k-1)\omega(\underline{\mathbf{y}},\underline{\mathbf{y}}) + (k+1)\omega(\underline{\mathbf{y}},\underline{\mathbf{x}})][(4n-k+3)\omega(\underline{\mathbf{y}},\underline{\mathbf{y}}) + (k+1)\omega(\underline{\mathbf{y}},\underline{\mathbf{x}})]$$

The proof is immediate. ■

2.4. *The case $n = 1$*

When $n = 1$, an individual will imitate one of his immediate neighbors. In this case the learning process is automatically conservative for all values of k. Before continuing with the general case (which requires the conservative learning assumption) we point out how when $n = 1$ the unbeatability concept selects a particular equlibrium in simple $2x2$ games.

From proposition 2, for $n = 1$, strategy $\underline{\mathbf{x}}$ is unbeatable if for all strategies $\underline{\mathbf{y}}$:

$$[\omega(\underline{\mathbf{x}},\underline{\mathbf{x}}) + \omega(\underline{\mathbf{x}},\underline{\mathbf{y}})][(2k+1)\omega(\underline{\mathbf{x}},\underline{\mathbf{x}}) + (2k-1)\omega(\underline{\mathbf{x}},\underline{\mathbf{y}})]$$
$$> [\omega(\underline{\mathbf{y}},\underline{\mathbf{y}}) + \omega(\underline{\mathbf{y}},\underline{\mathbf{x}})][(2k+1)\omega(\underline{\mathbf{y}},\underline{\mathbf{y}}) + (2k-1)\omega(\underline{\mathbf{y}},\underline{\mathbf{x}})].$$

- Consider a simple coordination game:

a, a	$0, 0$
$0, 0$	b, b

when $\underline{\mathbf{x}}$ is the first strategy and $\underline{\mathbf{y}}$ the second strategy (or indeed any other mixed strategy), the above condition translates to:

$$a^2 > b^2$$

i.e. a strategy is unbeatable if and only if it yields the pareto payoff.

- Consider the Stag Hunt game:

a, a	$0, b$
$b, 0$	b, b

and test when the second strategy is unbeatable.
The condition for the second strategy to be unbeatable is:

$$(2b)^2 > a^2\left(1 + \frac{1}{2k}\right).$$

When (b, b) is the risk dominant equilibrium, i.e. when $2b > a$, then it will also be the unbeatable strategy for sufficiently large k. Unbeatability chooses the risk dominant equilibrium for sufficiently large $k's$.

2.5. Large neighborhoods

The above characterization of unbeatable strategies becomes particularly simple when we take the limit $n, k \to \infty$ while holding the ratio $n/k = \theta$ constant. The strict inequalities we obtain imply that the inequalities of proposition 2 hold for sufficiently large n, k with $n/k = \theta$:

for $\theta \leq 1$:

$$\left(\frac{1}{2}+\frac{\theta}{4}\right)\omega(\underline{\mathbf{x}},\underline{\mathbf{x}}) + \left(\frac{1}{2}-\frac{\theta}{4}\right)\omega(\underline{\mathbf{x}},\underline{\mathbf{y}})$$
$$> \left(\frac{1}{2}+\frac{\theta}{4}\right)\omega(\underline{\mathbf{y}},\underline{\mathbf{y}}) + \left(\frac{1}{2}-\frac{\theta}{4}\right)\omega(\underline{\mathbf{y}},\underline{\mathbf{x}}) \tag{10}$$

and for $\theta > 1$:

$$\left(1-\frac{1}{4\theta}\right)\omega(\underline{\mathbf{x}},\underline{\mathbf{x}}) + \frac{1}{4\theta}\omega(\underline{\mathbf{x}},\underline{\mathbf{y}})$$
$$> \left(1-\frac{1}{4\theta}\right)\omega(\underline{\mathbf{y}},\underline{\mathbf{y}}) + \frac{1}{4\theta}\omega(\underline{\mathbf{y}},\underline{\mathbf{x}}) \tag{11}$$

The limit process should be interpreted in the following way: If, for a given θ, a strategy $\underline{\mathbf{x}}$ satisfies $(10, 11)$ for all strategies $\underline{\mathbf{y}}$, then for sufficiently large n, k such that $n/k = \theta$, strategy $\underline{\mathbf{x}}$ is unbeatable in the process $\langle \Omega, k, n \rangle$.

The two conditions for unbeatability $(10, 11)$, can be combined by defining $r(\theta)$ as:

$$r(\theta) = \begin{cases} \frac{\theta}{2} & \text{if } \theta < 1 \\ 1-\frac{1}{2\theta} & \text{if } \theta \geq 1 \end{cases} \tag{12}$$

Note that r takes values between 0 and 1. It is small when the interaction neighborhood k is bigger than the learning neighborhood n, and r is closer to 1 when the learning neighborhood is the larger one.

The condition for unbeatability can now be written as:

$$\frac{(1+r(\theta))}{2}\omega(\underline{\mathbf{x}},\underline{\mathbf{x}}) + \frac{(1-r(\theta))}{2}\omega(\underline{\mathbf{x}},\underline{\mathbf{y}})$$
$$> \frac{(1+r(\theta))}{2}\omega(\underline{\mathbf{y}},\underline{\mathbf{y}}) + \frac{(1-r(\theta))}{2}\omega(\underline{\mathbf{y}},\underline{\mathbf{x}}) \tag{13}$$

Definition. *A strategy $\underline{\mathbf{x}}$ is unbeatable in $\langle \Omega, r \rangle$ if $\underline{\mathbf{x}}$ satisfies inequality* (13) *for all strategies $\underline{\mathbf{y}} \neq \underline{\mathbf{x}}$.*

If such strategy exists we denote it by $\hat{B}\langle \Omega, r \rangle$.

From our previous comment it is clear that when $\hat{B}\langle\Omega, r\rangle$ exists for $r = r(\theta)$ then it is unbeatable in $\langle\Omega, k, n\rangle$ for sufficiently large n, k with $n/k = \theta$.

3. Unbeatable strategy and kinship behavior

In this section we show how the property of unbeatability relates to kinship behavior. Following Hamilton [10], if an individual is related to a degree r to his opponents his *inclusive fitness* (see Hamilton [9], Taylor [14]) is his own payoff plus r times that of his kin-opponent. If the game played between individuals is Ω the corresponding matrix of inclusive fitness is:

$$\Omega^r = \Omega + r\Omega^t \tag{14}$$

(where Ω^t is the transpose of Ω).

An unbeatable strategy is shown to be an ESS in the game Ω^r in which a player takes into account his opponent's payoff. Here there is no longer any local interaction structure in the population, the population is fully mixed, however, the payoff of each individual has been changed to take into account that the individuals care about each other. More precisely: We show that a strategy is unbeatable in $\langle\Omega, r\rangle$ if and only if it is unbeatable in $\langle\Omega^r, 0\rangle$, and that if it is unbeatable in $\langle\Omega^r, 0\rangle$ then it is an ESS of Ω^r.

The case $k \gg n$, where an individual interacts with a large number of players but learns from few, is similar to a totally mixed population. In the limit, where $k, n \to \infty$, i.e. $r = 0$ each interacts with the whole population and learning is rather insignificant, it is therefore not surprising that an unbeatable strategy in this case is an ESS. The main result of this section is that $\langle\Omega, r\rangle$ and $\langle\Omega^r, 0\rangle$ have the same unbeatable strategies, i.e. instead of considering a population with the local structure r we may ignore the local structure and consider a panmictic population in which the interaction between player is according to the game Ω^r, a game in which each player cares to a certain extent about his opponents: Caring substitutes the local structure. Since in this setup an unbeatable strategy is an ESS of Ω^r it follows that an unbeatable strategy of $\langle\Omega, r\rangle$ must be an ESS of Ω^r.

We begin with the case $r = 0$. We show that $\hat{B}\langle\Omega, 0\rangle$, an unbeatable strategy of the dynamic process $\langle\Omega, 0\rangle$, is an ESS of Ω.

For $r = 0$ the condition for unbeatablity (13) becomes:

$$\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) + \omega(\underline{\mathbf{x}}, \underline{\mathbf{y}}) > \omega(\underline{\mathbf{y}}, \underline{\mathbf{y}}) + \omega(\underline{\mathbf{y}}, \underline{\mathbf{x}}) \qquad \forall \underline{\mathbf{y}} \neq \underline{\mathbf{x}} \tag{15}$$

or:

$$\omega\left(\mathbf{x}, \frac{\underline{\mathbf{x}} + \underline{\mathbf{y}}}{2}\right) > \omega\left(\mathbf{y}, \frac{\underline{\mathbf{x}} + \underline{\mathbf{y}}}{2}\right) \qquad \forall \underline{\mathbf{y}} \neq \underline{\mathbf{x}} \tag{16}$$

This implies that if the indigenous population of $\underline{\mathbf{x}}$ players were to be massively invaded by a mutant $\underline{\mathbf{y}}$ which took over half the population, then the $\underline{\mathbf{x}}$ players would do better than the mutant. The following lemma shows that $\underline{\mathbf{x}}$ will also do better than a mutant invading in small groups, i.e. $\underline{\mathbf{x}}$ is an ESS of Ω.

Lemma 3. *(i) If an unbeatable strategy $\hat{B}(\Omega, 0)$ exists then it is an ESS of Ω.*
(ii) If $\underline{\mathbf{x}}$ is a fully mixed ESS of Ω then $\underline{\mathbf{x}} = \hat{B}(\Omega, 0)$.

Proof. (i) If an unbeatable strategy $\underline{\mathbf{x}} = \hat{B}(\Omega, 0)$ exists it satisfies (16) for all $\underline{\eta} \neq \underline{\mathbf{x}}$:

$$\omega\left(\mathbf{x}, \frac{\mathbf{x} + \underline{\eta}}{2}\right) > \omega\left(\underline{\eta}, \frac{\mathbf{x} + \underline{\eta}}{2}\right) \tag{17}$$

For a given $\underline{\mathbf{y}} \neq \underline{\mathbf{x}}$ and for any $\frac{1}{2} > \varepsilon > 0$ choose:

$$\underline{\eta} = (1 - 2\varepsilon)\mathbf{x} + 2\varepsilon\mathbf{y}$$

then:

$$\frac{\underline{\mathbf{x}} + \underline{\eta}}{2} = (1 - \varepsilon)\underline{\mathbf{x}} + \varepsilon\underline{\mathbf{y}}$$

from (17) it follows that:

$$\omega(\underline{\mathbf{x}}, (1 - \varepsilon)\underline{\mathbf{x}} + \varepsilon\underline{\mathbf{y}}) > \omega(\underline{\mathbf{y}}, (1 - \varepsilon)\underline{\mathbf{x}} + \varepsilon\underline{\mathbf{y}}) \qquad \forall\underline{\mathbf{y}} \neq \underline{\mathbf{x}}, \quad 0 < \varepsilon < \tfrac{1}{2}$$

This ensures that $\underline{\mathbf{x}}$ is an ESS of the game Ω.

(ii) Let $\underline{\mathbf{x}}$ be a fully mixed ESS of Ω, then by the definition of ESS the following two properties $(i), (ii)$ hold for all $\underline{\mathbf{y}} \neq \underline{\mathbf{x}}$:

$$\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) = \omega(\underline{\mathbf{y}}, \underline{\mathbf{x}}) \tag{i}$$

$$\omega(\underline{\mathbf{x}}, \underline{\mathbf{y}}) > \omega(\underline{\mathbf{y}}, \underline{\mathbf{y}}) \tag{ii}$$

adding $(i), (ii)$ we find that (16) is satisfied, i.e. $\underline{\mathbf{x}}$ is an unbeatable strategy of the game Ω for $r = 0$. ■

We now consider the general case: $r \geq 0$. The next lemma shows that a strategy is unbeatable in $\langle\Omega, r\rangle$ if and only if it is unbeatable in $\langle\Omega^r, 0\rangle$.

Lemma 4. *For all* $0 \leq r \leq 1 : \hat{B}(\Omega, r) = \hat{B}(\Omega^r, 0)$, *provided at least one side of the equation exists (i.e. if one side exists then the other exists as well and they are equal)*

Proof. Denote by $\omega^r(\underline{\mathbf{x}}, \underline{\mathbf{y}}) = \mathbf{x}\Omega^r\mathbf{y}$ the payoff of $\underline{\mathbf{x}}$ against $\underline{\mathbf{y}}$ in the game Ω^r.

The strategy $\underline{\mathbf{x}}$ is unbeatable in the game $\Omega^r : \mathbf{x} = \hat{B}(\Omega^r, 0)$, iff (15) holds for all $\underline{\mathbf{y}} \neq \underline{\mathbf{x}}$, i.e.

$$[\omega^r(\underline{\mathbf{x}}, \underline{\mathbf{x}}) + \omega^r(\underline{\mathbf{x}}, \underline{\mathbf{y}})] - [\omega^r(\underline{\mathbf{y}}, \underline{\mathbf{y}}) + \omega^r(\underline{\mathbf{y}}, \underline{\mathbf{x}})] > 0$$

using the definition of $\omega^r(\underline{\mathbf{x}}, \underline{\mathbf{y}})$, this can be rewritten as:

$$(1 + r)[\omega(\underline{\mathbf{x}}, \underline{\mathbf{x}}) - \omega(\underline{\mathbf{y}}, \underline{\mathbf{y}})] + (1 - r)[\omega(\underline{\mathbf{x}}, \underline{\mathbf{y}}) - \omega(\underline{\mathbf{y}}, \underline{\mathbf{x}})] > 0$$

which is the condition for $\underline{\mathbf{x}}$ to be an unbeatable strategy in $\langle \Omega, r \rangle$, $\underline{\mathbf{x}} = \hat{B}(\Omega, r)$. ∎

Combining lemmas (3), (4) we get:

Proposition 5. *1. If* $\mathbf{x} = \hat{B}(\Omega, r)$, *an unbeatable strategy of* $\langle \Omega, r \rangle$, *exists then it is an ESS of* Ω^r. *Moreover, comparing* $\underline{\mathbf{x}}$ *to any other strategy or any other ESS of* Ω^r $(\underline{\mathbf{y}})$, *the strategy* $\underline{\mathbf{x}}$ *does better than* $\underline{\mathbf{y}}$ *against a* 50:50 *mix of the two*[3]*:*

$$\omega^r\left(\mathbf{x}, \frac{\underline{\mathbf{x}} + \underline{\mathbf{y}}}{2}\right) > \omega^r\left(\mathbf{y}, \frac{\underline{\mathbf{x}} + \underline{\mathbf{y}}}{2}\right)$$

2. Any fully mixed ESS of Ω^r *is an unbeatable strategy of* $\langle \Omega, r \rangle$.

An unbeatable strategy does not necessarily exist even if Ω^r has an ESS. We provide an example in which Ω^r has a unique ESS, and this only candidate for an unbeatable strategy of $\langle \Omega, r \rangle$ fails to be unbeatable.

Example. Let Ω be given by:

$\Omega =$

1	0	1
0	2	0
0	3	0

$\Omega^r =$

$1 + r$	0	1
0	$2(1 + r)$	$3r$
r	3	0

it is easy to verify that for $r < \frac{1}{2}$ the pure strategy $\underline{\mathbf{x}} = (1, 0, 0)$ is the unique ESS of Ω^r. Let $\underline{\mathbf{y}} = (0, 1, 0)$ be the second pure strategy, then:

$$\omega^r\left(\underline{\mathbf{x}}, \frac{\underline{\mathbf{x}} + \underline{\mathbf{y}}}{2}\right) = \frac{1 + r}{2}, \quad \omega^r\left(\underline{\mathbf{y}}, \frac{\underline{\mathbf{x}} + \underline{\mathbf{y}}}{2}\right) = (1 + r)$$

so $\underline{\mathbf{x}}$, $\underline{\mathbf{y}}$ do not satisfy (16) for ω^r which is a necessary condition for $\underline{\mathbf{x}}$ to be an unbeatable strategy in $\langle \Omega^r, 0 \rangle$ and in $\langle \Omega, r \rangle$.

4. Altruistic traits

In this section we demonstrate that for some neighborhood structures the unbeatable strategy is an altruistic one. Consider the games Prisoners' Dilemma and Chicken, we show that for a sufficiently large r the unbeatable strategy is the cooperative one. A large r corresponds to the case where the learning neighborhood is much larger than the interaction neighborhood.

[3] Any $\hat{B}(\Omega, r)$ is an unbeatable strategy of $\langle \Omega^r, 0 \rangle$ and as such it satisfies (16) in Ω^r for all $\mathbf{y}$.

Let Ω be the game:

	C	D
C	a	b
D	c	d

For Ω to be a Prisoners' Dilemma game a, b, c, d should satisfy: $c > a > d > b$.

For Ω to be a Chicken game its parameters should satisfy: $c > a > b > d$.

For both games we will further assume that $2a > b + c$ so that cooperating (C, C) is the utilitarian outcome of the game.

We now show that cooperating (C) is an unbeatable strategy in $\langle \Omega, r \rangle$ for a sufficiently large r. By proposition 4, strategy C is unbeatable in $\langle \Omega, r \rangle$ iff it is unbeatable in $\langle \Omega^r, 0 \rangle$. The game Ω^r is given by:

$$\Omega^r = \begin{array}{|c|c|}\hline a(1+r) & b+rc \\ \hline c+rb & d(1+r) \\ \hline \end{array}\,.$$

By (15) strategy C is unbeatable in $\langle \Omega^r, 0 \rangle$ if for every strategy $\underline{\mathbf{y}} = (y_1, y_2)$ with $y_2 > 0$:

$$a(1+r) + a(1+r)y_1 + (b+rc)y_2 > \omega^r(\underline{\mathbf{y}}, \underline{\mathbf{y}}) + a(1+r)y_1 + (c+rb)y_2$$

where $\omega^r(\underline{\mathbf{y}}, \underline{\mathbf{y}})$ is the payoff $\underline{\mathbf{y}}$ obtains against itself in Ω^r. This reduces to:

$$a(1+r) - \omega^r(\underline{\mathbf{y}}, \underline{\mathbf{y}}) > (1-r)y_2(c-b)$$

Expanding the left hand side by writing $\omega^r(\underline{\mathbf{y}}, \underline{\mathbf{y}})$ explicitly, and dividing by y_2, the above can be written as:

$$(1+r)[(2a-b-c)y_1 + (a-d)y_2] > (1-r)(c-b)$$

Since for both the Prisoners' Dilemma and Chicken $a - d > 0$ and since we assumed that $2a - b - c > 0$, it follows that the above will hold for r sufficiently close to 1, for all strategies $\underline{\mathbf{y}}$.

In contrast, the above inequality does not hold for r close to 0, thus to cooperate (C) is not an unbeatable strategy in that case.

5 Summary and conclusions

The distinguished population biologist S. Wright [17], [18] was the first to suggest that evolution may lead to altruism in large populations in which individuals are, as he called it, isolated by distance. He believed that in large populations individuals tend to meet only a relatively small number of their neighbors and that this adds to the evolutionary process more than random noise, it substantially changes the direction of the evolutionary process.

This paper presents a model that agrees with Wright's intuition. In our model individuals imitate and interact with a small subset of the population: their neighbors. A player is occasionally allowed to learn and change his strategy, he learns by imitating the strategy of one of his more successful neighbors. We have shown that if a strategy is unbeatable, in the sense that when all play it, the evolutionary process eliminates any finite number of mutants with probability 1, then this strategy must take into account the payoff of its opponent. The degree it cares about the opponent's welfare depends on the ratio between the radii of the interacting and the learning neighborhoods. We found that the evolved behavior will be more altruistic the bigger the learning neighorhood is (given an interaction neighborhood).

Our result seems, on first sight, to be in disagreement with some of the literature. Learning new strategy makes strategies mobile, a small learning (or propagation) neighborhood corresponds to low mobility of new ideas. We have found that altruistic behavior is more likely to occur when the learning neighborhood is large. Following Wright's logic, Eshel [4] presented a model of *demes*, in which the population is divided into subgroups and individuals normally interact only within their group. Occasionally, with a given probability, an individual may move to another deme. The probability of a move measures mobility in this model. When mobility is high the model approaches a panmictic model. Eshel shows that in a deme model altruism is more likely to develop when mobility is low. D.S. Wilson in [15], [16], was the first to introduce different learning and interaction environments. He gave intuitive arguments suggesting that altruism should evolve when the radius of the interaction neighborhood is substantially larger than the radius of the learning neighborhood. Our results, however, are derived with the additional assumption that learning is conservative. This assumption makes mobility low even when learning neighborhoods are large, one does not import a new strategy into a neighborhood if it was not there to begin with. There is, therefore, no disagreement between the intuition and results of our model and those of Eshel and Wilson.[4]

Our result crucially depends on the *conservative learning* assumption. We assumed that an individual learns only when one of his 2 immediate neighbors plays a strategy different to his. This assumption can be seen as an extreme form of reluctance to learn or requiring an incentive to learn. A player needs to observe something new and different in his immediate environment before he will begin to look for a new strategy. Reluctance to learn in uniform environments fits cultural learning rather than biological propagation. In biological models a dead individual is replaced by the seed of one of his neighbors, depending on this neighbor's strength to project his seed to the vacant location and with no reference to the dead individual or his 'wishes'. We believe that reluctance to learn describes human behavior in many situations and thus this assumption, or variations of it, is suitable for models of cultural evolution. Conservative learning tends to create large patches of identical strategies in

[4] When we set $n = 1$ in the biological propagation model then conservative learning is trivially satisfied. A simple calculation (based on the inequalities of proposition 2) shows that contrary to Wilson's intuition the interaction neighborhood should, in fact, be not too large in order to support altruism.

the population. Causal observation of cities or nations confirms that patches of uniform behavior ocur frequently. Patches of altruists earn, on average, more than patches of egoists, when the interaction neighborhood is small compared to the learning one, hence conservatism leads to altruistic behavior.

Relaxing the assumption not only makes the mathematics too complicated for us to solve analytically, it also changes the results, as we have found in related computer simulations. In another paper (Eshel at al. [5]) we have tested what happens when the conservative learning assumption is relaxed. We found that the results of this paper no longer hold when we move to a model of biological propagation in which there is no restriction on 'learning': when an individual dies he is replaced by one of his $2n$ neighbors with no conservative restrictions. In that case, a strategy which is unbeatable in our model (with the conservative learning assumption) is no longer unbeatable, it can be beaten by another, less altruistic strategy. However, we found that even in the biological propagation model altruism can be sustained in circumstances which are extremely favorable to it, like when it costs an individual very little to confer a great favor on his neighbors.

When we remain in the cultural realm and relax the assumption by degrees simulations show that our results still hold. Permitting an individual to learn with small probability even when his two immediate neighbors play the same strategy as he does, but one of his four immediate neighbors plays a different strategy then the results of our paper seem to be robust. A strategy which is unbeatable with the conservative assumption remains unbetable when the assumption is gradually relaxed.

A similar model was developed by Bergstrom & Stark [2] and by Eshel, Samuelson & Shaked [6]. It differs from this model in that it does not allow stochastic learning when neighborhoods have a radius >1. Other models of local interaction can be found in: Cohen & Eshel [3], Matessi & Jayakar [12], Nunney [13] and Grafen [8].

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