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Partnership

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Individuals are called partners when it is in their best interest to help each other, if by doing so they increase the probability of being together in the future when, for similar reasons, they will continue to help each other. Kinsmen or individuals who often face (hedonic) situations in which helping is the dominating strategy are committed to help each other. Partnership may develop among them since the loss of the other means the loss of a guaranteed helper. Thus, they may be willing to take additional risks to help each other. Partnership may occur among unrelated individuals and with no hedonic situations. Partnership creates bonds between partners which may be much stronger than those between kinsmen; an individual may take more risks for his partner than he will ever take for a kin. Partnership may evolve without the sophistication and memory required for reciprocation altruism. Although kin selection, partnership and reciprocation are likely to appear fused as the causes for altruism, we argue that it may be possible to distinguish between them in some situations. We show that as the partners get older partnership may become less important to them. We also show that like cooperation, and for analogous reasons, malice may evolve among partners so that each will be willing to take additional risks in order to eliminate the other.

1. Introduction

Individuals are selected to behave in a way that increases the expected length of their reproductive life. In most studies of population game theory, individuals assume that their actions do not influence their own or their partners' survival to future periods. These considerations become important in social networks where the existence of a surviving "partner" may strongly affect one's own survival probability.

The case in which one's present actions affect the future *behavior* of his partners has been often considered in the literature. It has been shown how reciprocal altruism (cooperation) may evolve in such situations (Trivers, 1971; Axelrod, 1981).

The case in which an individual's action affects the welfare of others in the network and thus their potential ability to help in the future, has been rarely discussed in the literature, with the exception of Eshel & Cohen (1975) and Eshel & Motro (1981) who shows that kinship altruism amplifies itself. If an individual knows (as in kinship) that the other will help him in future dangers, then the death of the other means the loss of a reliable helper, and it is in the individual's interest to help the other survive. Thus, mutual altruistic behavior among such individuals will strengthen itself. We term this amplifying factor *partnership.* Partnership differs from reciprocation altruism in that it is the *ability* to help, not the willingness to help, which is

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conditional on past behavior. Thus, partnership is the relation established between two or more individuals when it is in the interest of one to help the other, since by doing so he increases the probability of the other to survive and be present in future situations where for similar reasons it will be in the other's best interest to help the first individual. In this work, we concentrate on partnership between non-related individuals.

Where one finds altruistic cooperation its reasons are likely to be mixed: kinship, partnership and reciprocation.* Hunting dogs, inbreeding within the pack, are likely to develop altruism due to kin selection. But their cooperation leads to a strong mutual dependence in their hunting and in skirmishes with rival packs or with other predators. The loss of a few members may be lethal to the pack and lead to its extinction, cooperation will therefore amplify itself and partnership will develop (van Lawick-Goodall, 1973). Elaborate alliances and social bonds develop in the pack and memory of past behavior leads to cooperation based on reciprocation. Although intense partnership may be established between young unrelated male lions who form a lifelong close bond based on mutual dependence (Schaller, 1972), it is more common for a sibling, when present, to be the chosen companion, amplifying dependency and creating a partnership. The common courtship-like behavior among kin-partners suggests that reciprocation plays an important role in maintaining and intensifying the relationship, perhaps even initiating it.

Although the three factors, kinship, partnership and reciprocation, are interwoven in establishing altruistic behavior, we demonstrate that they may each have a different effect on the resulting behavior. We suggest that each of the above factors leads to qualitatively different, if related, predictions that may be conceivably distinguished on the basis of field observations on a sufficiently wide range of situations.

In contrast to kinship and reciprocation, the effect of partnership on animal and human behavior has not been studied. In order to distinguish between partnership altruism on one side and kinship and reciprocation altruism on the other, we assume that the potential partners are unrelated, so that each aims to increase only his own expected lifespan. To isolate the effects of partnership from those of reciprocation we describe a situation in which the actions of one individual can affect only the survival probability of the others, not their future behavior, thus precluding punishments and rewards. This assumption, which is formally equivalent to assuming the absence of memory, fits a situation in which an organism developed physiological factors for symbiosis and partnership. Among humans, this may describe a case of help without the receiver being aware of it, a case which cannot be explained by reciprocal altruism (although it may be initiated by kinship).

Under these assumptions, we demonstrate that partnership altruism may evolve, beginning at a level in which the cost of helping the other is low, and amplifying itself to higher levels of mutual dependence. We show that, like in kinship altruism, an individual chooses his action to maximize his "inclusive survival" consisting of the sum of his own survival probability and the product of a *partnership coefficient* and the probability that *both* he and his partner survive. Unlike Hamilton's kinship coefficient, the partnership coefficient may assume arbitrarily high values or indeed negative values. High values of the coefficient correspond to situations of extreme mutual dependence when the probability of survival without the partner is low. Negative values of the partnership coefficient correspond to malice, when the individuals are bound together but the presence of one is detrimental to the survival of the other. In partnership altruism, unlike in kinship altruism, the altruistic behavior is aimed at increasing the partner's survival probability *conditional* on the altruist's own survival.

In later sections of the paper, we discuss how the age, mortality and ecological factors affect partnership altruism differently than kinship or reciprocal altruism.

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* Altruism may also evolve by natural selection in a structured population (see Wright, 1943). In a recent paper, Eshel *et al.* (1999) have shown that altruism which develops due to a neighborhood structure resembles altruism among kinsfolk. For a more general treatment of neighbors as kin see Hamilton (1972).

2. The Model

There is a large population of individuals who may be either paired or single and who face a stream of dangerous situations (events). The events that occur may kill one or more of any pair. The events differ in their nature but the individuals recognize the type of danger and can take some specific actions which affect their survival. In addition, individuals whether single or paired may die a natural death. Natural death is distinguished from death in one of the events in that the individuals have no effect on the probability of natural death. Natural death comes with intensity λ, i.e. at any infinitesimal time interval $\mathrm{d}t$ an individual (single or paired) may die of natural causes with probability $\lambda\,\mathrm{d}t$. A dangerous event occurs with intensity μ, and a single individual is matched with intensity ν. We refer to paired individuals as *partners*. Thus, a paired individual may die a natural death or be killed by an event. He remains with his partner for as long as both live, if his partner dies he remains single for a while and he may die a natural death or be killed in one of the dangerous events, he may find a new partner and continue his life in a pair.

At each encounter, the actions taken by the partners determine the survival probabilities of each of the and of their joint survival. Thus, the effect of them actions can be described by three probabilities: the survival probability of each partner and their joint survival probability (the probability of both dying is the residual probability). We assume that there are two strategies available at each encounter: C and D. The dependence of the survival probabilities on the actions taken by the two players can be written as a symmetric game, in which each cell contains two probabilities: the survival probability of the player taking the action and the joint survival rate. Thus, an encounter $\underline{V}$ can be described by

$$\underline{V} = \left\{ \begin{array}{c|c|c|} & C & D \\ \hline C & v_{11}, w_{11} & v_{12}, w_{12} \\ \hline D & v_{21}, w_{12} & v_{22}, w_{22} \\ \hline \end{array}\ , \theta \right\}.$$

Here v_{ij} is the first partner's probability of survival when he takes action i and the other partner has taken action j. The survival probability of the other partner is then v_{ji} and the probability of *both* surviving the event is w_{ij}. We assume that† $w_{ij} = w_{ji}$. Finally, when a single individual faces this encounter his probability of surviving it is θ.

An encounter is therefore characterized by eight probabilities (v_{ij}, w_{ij}, θ). The distribution of future encounters $\underline{V} \in \Omega = [0, 1]^8$ is assumed to be time independent and is given by $F(\underline{V})$.

The support of the distribution $F(\underline{V})$ may in general be wide, allowing for various types of encounters. In this paper, we will restrict the support to encounters of the Prisoners' Dilemma type, with the first strategy representing cooperation and the second defection, i.e. $v_{21} > v_{11} > v_{22} > v_{12}$. Thus, a player can always increase his survival probability by defecting. However, we will in most examples assume that $w_{11} > w_{12} = w_{21} \geqslant w_{22}$, so that defecting means a lower probability of surviving together. This introduces a conflict between wishing to increase one's own survival probability and wishing to have the other player alongside if, indeed, he is supposed to help in some future encounters.

In order to distinguish between partnership and reciprocation we assume that an individual always takes the same action in a particular event irrespective of the past. Thus, we assume that individuals cannot condition their behavior on past actions taken by their partners; this excludes reciprocation. A *global strategy* for an individual is therefore a plan of how to act at each possible encounter, i.e. a measurable function $\mathbf{x}$ from the set Ω of all possible encounters to the unit interval, such that for all $\underline{V} \in \Omega$, $\mathbf{x}(\underline{V})$ is a (mixed) *local strategy*, determining the probability of playing C in the encounter $\underline{V}$. Thus, at each moment in time when both partners are present, their future (which depends only on their global strategies) is independent of time.

Stability. We assume that the individuals in the population are selected to behave in a way that increases their expected lifespan. In this model, the longevity of an individual, either single or

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† For a mathematically oriented analysis of a special case of this model, with the restriction $\omega_{ij} = v_{ij}v_{ji}$, see Eshel & Weinshall (1988).

paired, depends on his own strategy and on the distribution of strategies in the entire population.

We shall be interested in strategies that when played by the whole population are in some sense evolutionarily stable. Denote by $S(\mathbf{x}, \mathbf{y})$ and $U(\mathbf{x}, \mathbf{y})$ the expected lifespan of (respectively), a single and paired $\mathbf{x}$-player in a population fixed on $\mathbf{y}$-players. Note that the strategy $\mathbf{x}$ affects the behavior of its player only when he is paired. It affects the lifespan $S(\mathbf{x}, \mathbf{y})$ of the single $\mathbf{x}$ player only via the conditional lifespan of this player in a pair $[U(\mathbf{x}, \mathbf{y})]$. Hence, a mutant strategy $\mathbf{x}$ increases $U(\mathbf{x}, \mathbf{y})$ if and only if it increases $S(\mathbf{x}, \mathbf{y})$. We can therefore define an ESS using either the payoff function $U(\mathbf{x}, \mathbf{y})$ or $S(\mathbf{x}, \mathbf{y})$:

Definition 1. A strategy $\mathbf{y}$, which is fixed in the population, is an ESS if it is strictly advantageous against any small group of mutants playing $\mathbf{x}$, i.e. $S(\mathbf{x}, \mathbf{y}) < S(\mathbf{y}, \mathbf{y})$, or equivalently $U(\mathbf{x}, \mathbf{y}) < U(\mathbf{y}, \mathbf{y})$.

In most of the paper, we use a weaker stability concept, *an agent equilibrium or agent ESS*, in which only a single local deviation from the global strategy $\mathbf{y}$ will be considered. In this equilibrium, the only mutants considered are those that deviate from $\mathbf{y}$ in a single event. This concept is similar to Selten's agent strategic form (see Selten (1975), or Section 12.5.2. in Osborne & Rubinstein, 1994).

A comment on the modeling. We have assumed a continuum of events, each occurring with probability 0, in order to achieve two aims:

- Our modeling guarantees that changing the action in a single event has no effect on the long-run survival probability, since this event will reoccur with probability 0.Thus, when considering what to play in a single event an individual need not take into account the long-run effects of this action. If, on the other hand, there is a finite number of events, or one of the events occurs with a positive probability then changing the action in that event will substantially change the global strategy and the long-run survival probabilities.
- A continuum of events enables us to assume, as we do later, that the events are densely ranked by a single parameter and each event is surrounded by close and similar events. Thus, it may be possible to deduce the behavior in one event from the behavior in the neighboring ones. In a discrete set of events, we would need an additional assumption to ensure that the distances between "neighboring" events are sufficiently small.

The continuum model can be seen as a limit case of a single-parameter discrete set of events each occurring with small probability and where neighboring events are close to each other.

Some notations. When both partners face an encounter $\underline{V}$ together and their (mixed) actions are $\mathbf{x}(\underline{V}) = (x_1, x_2)$, $\mathbf{y}(\underline{V}) = (y_1, y_2)$, the survival probability of partner 1 *to the end of the encounter* is given by

$$\pi^1(\underline{V}, \mathbf{x}(\underline{V}), \mathbf{y}(\underline{V})) = \sum_{i,j=1}^{2} v_{ij}\mathbf{x}_i(\underline{V})\mathbf{y}_j(\underline{V}).$$

The probability of both partners surviving the encounter $\underline{V}$ is

$$\pi^{12}(\underline{V}, \mathbf{x}(\underline{V}), \mathbf{y}(\underline{V})) = \sum_{i,j=1}^{2} w_{ij}\mathbf{x}_i(\underline{V})\mathbf{y}_j(\underline{V}).$$

The probability of partner 1 surviving a random future encounter, given the global strategies $\mathbf{x}, \mathbf{y}$ of the two players and the distribution of events $F(\underline{V})$, is therefore,

$$\tilde{\pi}^1 = \tilde{\pi}^1(\mathbf{x}, \mathbf{y}) = \int_\Omega \pi^1(\underline{V}, \mathbf{x}(\underline{V}), \mathbf{y}(\underline{V}))\, \mathrm{d}F(\underline{V}).$$

Similarly, the probability of both players surviving a forthcoming encounter is

$$\tilde{\pi}^{12} = \tilde{\pi}^{12}(\mathbf{x}, \mathbf{y}) = \int_\Omega \pi^{12}(\underline{V}, \mathbf{x}(\underline{V}), \mathbf{y}(\underline{V}))\, \mathrm{d}F(\underline{V}).$$

Finally, the probability of a single individual surviving such a (potential) encounter is

$$\tilde{\theta} = \int_\Omega \theta(\underline{V})\, \mathrm{d}F(\underline{V}).$$

2.1. PARTNERSHIP COEFFICIENT AND INCLUSIVE SURVIVAL

Let a mutant $\mathbf{x}$ player be paired with an individual taken from a population of $\mathbf{y}$ players and let the two face an encounter $\underline{V}$. Let the mutant consider his strategy choice in the event $\underline{V}$, assuming that his partner plays the global strategy $\mathbf{y}$ [in particular his partner will play $y = \mathbf{y}(\underline{V})$ in this event], and he himself plays the global strategy $\mathbf{x}$ in all other events and the strategy x in the event $\underline{V}$. Let his conditional lifespan, given this behaviour, be $U(x, y \,|\, \underline{V}, \mathbf{x}, \mathbf{y})$.

Definition 2. 1. A global strategy $\mathbf{x}$ is a *local best response* to $\mathbf{y}$ if for any encounter $\underline{V}$, except perhaps for a set of measure zero, the strategy $x = \mathbf{x}(\underline{V})$ maximizes the conditional expected lifespan $U(x, \mathbf{y}(\underline{V}) \,|\, \underline{V}, \mathbf{x}, \mathbf{y})$.

2. A global strategy $\mathbf{y}$ is an *agent equilibrium* if it is a local best response to itself.

Agent equilibrium is weaker than a Nash equilibrium: clearly, any best response is an agent best response and hence any equilibrium is an agent equilibrium but the reverse need not be true.

To calculate the conditional expected lifespan, note that if the two players play x, y in the encounter $\underline{V}$, then the probability that both survive the encounter is $\pi^{12}(\underline{V}, x, y)$ and the probability that only the mutant will survive it is $\pi^{1}(\underline{V}, x, y) - \pi^{12}(\underline{V}, x, y)$. In the first case, the expected lifespan of the mutant is $U(\mathbf{x}, \mathbf{y})$, and when he is left on his own it is $S(\mathbf{x}, \mathbf{y})$, hence,

$$\begin{aligned} U(x, y \,|\, \underline{V}, \mathbf{x}, \mathbf{y}) &= S(\mathbf{x}, \mathbf{y})[\pi^{1}(\underline{V}, x, y) - \pi^{12}(\underline{V}, x, y)] \\ &\quad + U(\mathbf{x}, \mathbf{y})\pi^{12}(\underline{V}, x, y) \\ &= S(\mathbf{x}, \mathbf{y})\pi^{1}(\underline{V}, x, y) + [U(\mathbf{x}, \mathbf{y}) \\ &\quad - S(\mathbf{x}, \mathbf{y})]\pi^{12}(\underline{V}, x, y) \\ &= S(\mathbf{x}, \mathbf{y})[\pi^{1}(\underline{V}, x, y) \\ &\quad + K(\mathbf{x}, \mathbf{y})\pi^{12}(\underline{V}, x, y)], \end{aligned}$$

where

$$K(\mathbf{x}, \mathbf{y}) = \frac{U(\mathbf{x}, \mathbf{y}) - S(\mathbf{x}, \mathbf{y})}{S(\mathbf{x}, \mathbf{y})}. \tag{1}$$

The values $K(\mathbf{x}, \mathbf{y})$, $S(\mathbf{x}, \mathbf{y})$ are determined by the two global strategies and do not depend on any particular encounter. When an individual chooses his action in an event $\underline{V}$, he leaves his global strategy unchanged and so $S(\mathbf{x}, \mathbf{y})$, $U(\mathbf{x}, \mathbf{y})$ and therefore $K(\mathbf{x}, \mathbf{y})$ can be taken as constants. Thus,

$$U(\mathbf{x}, \mathbf{y}) \propto \pi^{1} + K\pi^{12}.$$

We have shown that the conditional lifespan of an individual in an encounter $\underline{V}$ is proportional to his own survival probability in this event plus K times the *joint survival* of the two partners in this event. The constant K measures the affinity between the two partners and the extent to which one partner will want to sacrifice some of his survival probability in order to increase the joint survival probability.

Definition 3. 1. The constant $K(\mathbf{x}, \mathbf{y})$ is the *partnership coefficient* of the two players.

2. The function $I(x, y \,|\, \underline{V}, \mathbf{x}, \mathbf{y}) = \pi^{1}(\underline{V}, x, y) + K(\mathbf{x}, \mathbf{y})\pi^{12}(\underline{V}, x, y)$ is the *partnership inclusive survival* of player 1 when playing x against y in the encounter $\underline{V}$.

The conditional lifespan of an individual in an encounter $\underline{V}$ is proportional to his partnership inclusive survival in this encounter. Of particular interest to us is the symmetric case of a homogeneous population in which all individuals play $\mathbf{y}$. In that case, $\mathbf{y}$ is an agent equilibrium if and only if for almost all encounters $\underline{V}$ the pair of (local) strategies $[\mathbf{y}(\underline{V}), \mathbf{y}(\underline{V})]$ is a symmetric Nash equilibrium of the symmetric partnership inclusive survival game $I(x, y \,|\, \underline{V}, \mathbf{x}, \mathbf{y})$.

The partnership coefficient K is conceptually and significantly different from Hamilton's kinship coefficient r. Related individuals in Hamilton's theory care about their own survival probability plus r times their partner's survival; here they care about their own survival plus K times the *joint survival probability*. They care about their partner's survival conditioned on their own survival. This, as we show later, leads to different behavioral predictions of the two theories.

Definition 4. The global strategy $\mathbf{y}$ is an *agent-ESS* if and only if for almost all encounters $\underline{V}$, the local strategy $\mathbf{y}(\underline{V})$ is an ESS of the symmetric partnership inclusive survival game $I(x, y \mid \underline{V}, \mathbf{y}, \mathbf{y})$.

2.2. CALCULATION OF THE PARTNERSHIP COEFFICIENT

We begin by calculating the expected lifespan of an individual (single or paired) who plays the global strategy $\mathbf{x}$ in a population of $\mathbf{y}$ players. We denoted the expected lifespan of a paired individual by $U(\mathbf{x}, \mathbf{y})$ and by $S(\mathbf{x}, \mathbf{y})$ when he is single (recall that in this stationary model, the expected lifespan of an individual, whether paired or single, is independent of time).

We first calculate $U(\mathbf{x}, \mathbf{y})$. Consider a paired individual who plays the global strategy $\mathbf{x}$ in a population of $\mathbf{y}$ players. Equation (2) lists all that could happen to this individual in a *short* time interval τ, between time t and $t + \tau$. The time interval τ is assumed to be close to 0, which justifies ignoring terms with higher order of τ. Both individuals survive to the end of this time interval; at the end of it there is a probability $\lambda\tau$ that the individual will die and his expected remaining life is 0, with probability $\lambda\tau$ that only his partner will die[‡] and then he will be single and his expected lifespan will be $S(\mathbf{x}, \mathbf{y})$. With probability $\mu\tau$ the two partners will face a random encounter, in that case with probability $\tilde{\pi}^{12} = \tilde{\pi}^{12}(\mathbf{x}, \mathbf{y})$ both will survive it and with probability $\tilde{\pi}^{1} - \tilde{\pi}^{12}$ only the first will survive it. With the residual probability $1 - (2\lambda + \mu)\tau$ that none of the above will happen, our player remains with his partner and his conditional life expectancy is $U(\mathbf{x}, \mathbf{y})$. Other things could occur, e.g. that ■

Hence (ignoring terms with higher order of τ, i.e. by letting τ approach 0),

$$U = \tau + \lambda\tau 0 + \lambda\tau S + \mu\tau[(\tilde{\pi}^{1} - \tilde{\pi}^{12})S + \tilde{\pi}^{12}U] + [1 - (2\lambda + \mu)\tau]U \tag{2}$$

or

$$[2\lambda + \mu(1 - \tilde{\pi}^{12})]U = [\lambda + \mu(\tilde{\pi}^{1} - \tilde{\pi}^{12})]S + 1. \tag{3}$$

Similarly, we obtain an equation for $S(\mathbf{x}, \mathbf{y})$. A single individual may die from natural causes, or die in one of the events, or he may find a new partner

$$S = \tau + \lambda\tau 0 + \mu\tau(1 - \tilde{\theta})0 + \nu\tau U + [1 - \lambda\tau - \mu\tau(1 - \tilde{\theta}) - \nu\tau]S \tag{4}$$

or

$$[\lambda + \mu(1 - \tilde{\theta}) + \nu]S = 1 + \nu U. \tag{5}$$

Solving the equations for U, S and by eqn (1) we find that

$$K(\mathbf{x}, \mathbf{y}) = \frac{\mu(\tilde{\pi}^{1} - \tilde{\theta})}{2\lambda + \mu(1 - \tilde{\pi}^{12}) + \nu}.$$

Denote

$$p = \frac{2\lambda + \nu}{\mu}, \tag{6}$$

then the partnership coefficient K can be written as

$$K(\mathbf{x}, \mathbf{y}) = \frac{\tilde{\pi}^{1} - \tilde{\theta}}{1 + p - \tilde{\pi}^{12}}. \tag{7}$$

Note that for given global strategies, a positive partnership coefficient K decreases with p; note also that K increases with μ and decreases with λ, ν. Hence, it becomes less beneficial to take a risk for a partner who is likely to die (a high λ), when it is easy to find a new partner (a high ν),[§] or when the encounters are less likely to happen (a low μ).

The partnership coefficient K depends on the global strategies (through $\tilde{\pi}^{1}, \tilde{\pi}^{12}$). On the other

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[‡] The probability that only the partner dies is in fact $\lambda\tau(1 - \lambda\tau)$, but since τ is small we ignore the quadratic term $(\lambda\tau)^2$.

[§] We have taken ν, the ease of finding a new partner, to be an exogenous parameter. However, if ν depends on the size of the population, then the model can be extended to determine ν endogenously. A large population where it is easy to find a new partner (a high ν) lowers K which makes individuals cooperate less. Thus, individuals will have shorter lives and the population shrinks, leading to a low ν and more cooperation. In an equilibrium, of this extended model, both ν and the population size will be endogenously determined.

hand, the local stability of the strategies $\mathbf{x}, \mathbf{y}$ and therefore the (equilibrium) strategies themselves depend on K. We investigate this interrelation between the two in the following sections.

3. An Example: Mutual Help Among Partners

Assume that all encounters have the prisoners' dilemma form and that the survival probability in mutual defection equals that of being single, then defecting in all events is an ESS. If no one ever cooperates then individuals do equally well when single or when paired. If a small group of mutants begins to cooperate, they will be worse off since they sacrifice some of their survival probability for cooperation but receive nothing in return. However, non-cooperation is not always stable against small deviations of the *entire* population. If some small degree of cooperation has been established in the whole group, or in a sufficiently large group, then cooperation may amplify itself and reach a higher degree of cooperation. If the whole population cooperates in events in which some help can be offered for a small cost, and if such events occur often enough then each individual is no longer indifferent to the existence of the others. He may now help the others in situations in which help demands a greater sacrifice in order to secure the other's existence and thereby his help in situations for which cooperation has already been established. We demonstrate this argument in the example of this section.

An ESS is said to be continuously stable (CSS) if in addition to its stability against deviations of small groups it is also stable against small deviations of large groups (see Eshel & Motro, 1981; Eshel, 1982).

Consider a family of events each of which exposes an unaided individual (whether single or paired) to a fixed probability of death ε. A paired individual can help his partner survive by reducing his own survival probability by h. The events differ only in the cost h of helping the other. The events (parametrized by h) are distributed according to the function $F(h)$ on $(0, 1-\varepsilon]$. Mutual cooperation makes the partners survive or die together. An event of this type can be described by the following game matrix:

$$\begin{array}{c|c|c|} & C & D \\ \hline C & 1-h, 1-h & 1-h-\varepsilon, 1-h-\varepsilon \\ \hline D & 1, 1-h-\varepsilon & 1-\varepsilon, (1-\varepsilon)^2 \\ \hline \end{array}, \quad \theta = 1-\varepsilon.$$

The first number in each cell describes the row player's survival probability, the second number describes the joint survival probability, the number θ, outside the matrix, is the probability of a single player surviving this event. Note that the part of the matrix which describes the player's own survival probabilities corresponds to the situation of additive costs and benefits, analysed by Hamilton (1964) in his classic argument for kin- selection.

To defect in all events is an ESS. The partnership coefficient is 0, reflecting the fact that each partner is indifferent to the survival of the other.

We show that under certain conditions the partners will cooperate in some of the events. In particular, we show that

- Under certain conditions there exist agent ESSs in which the population cooperates in a wide range of events. These agent ESSs are also evolutionarily and continuously stable, i.e. they are stable against small groups of mutants and against small deviations of the whole population.
- When such cooperative ESSs exist then the totally non-cooperative ESS is continuously unstable, that is, if the whole population cooperates in events with very low costs of cooperation (h close to 0), then increasing rather than decreasing the range of cooperation is advantageous. In fact, when there is a high concentration of events around $h = 0$, and the entire population has, for some reason, begun to cooperate then it is beneficial for any individual to further increase his range of cooperation. Thus, little cooperation can amplify itself and reach high levels of cooperation.
- The partnership coefficient $K(\mathbf{x}, \mathbf{x})$ may assume arbitrarily large values for evolutionarily and continuously stable strategies $\mathbf{x}$. This ensures that the partners will cooperate in a wide range of events, including events in which the cost of cooperation is large.

We will consider only *simple strategies* in which there is cooperation in all events up to a certain h and defection for all other events:

$$\mathbf{x}_\alpha(h) = \begin{cases} 1 & \text{if } h \leqslant \alpha, \\ 0 & \text{if } h > \alpha. \end{cases}$$

Let $K(\alpha) = K(\mathbf{x}_\alpha, \mathbf{x}_\alpha)$ be the partnership coefficient when the population is fixed on a simple strategy $\mathbf{x}_\alpha$. By eqn (7)

$$K(\alpha) = \frac{\int_0^\alpha (\varepsilon - h)\,\mathrm{d}F(h)}{1 + p - [\int_0^\alpha (1-h)\,\mathrm{d}F(h) + \int_\alpha^\infty (1-\varepsilon)^2\,\mathrm{d}F(h)]}. \tag{8}$$

The partnership coefficient depends on the global strategy played. On the other hand, a given partnership coefficient determines the local best response to any strategy played by the partner. A strategy $\mathbf{x}_\alpha$ is an agent equilibrium if the partnership coefficient it induces makes cooperation the best response to cooperation for events below α and defection the best response to defection above α.

An agent equilibrium is stable against local mutations, i.e. against mutations occurring in the action of a single event. However, for this family of events local stability implies that no other mutation, however elaborate, can invade the population. An agent equilibrium in simple strategies is an ESS. The proof for this can be found in the appendix.

To find the agent equilibria we first investigate the best responses for a given coefficient K.

Cooperation is the best response to cooperation in an encounter h, if the partnership includes fitness of cooperating against a cooperator is higher than that of defecting against a cooperator:

$$(1-h) + K(1-h) \geqslant 1 + K(1-h-\varepsilon) \tag{9}$$

or

$$h \leqslant K\varepsilon. \tag{10}$$

Similarly, cooperation is the best response to defection in an event h if

$$(1-h-\varepsilon) + K(1-h-\varepsilon) \geqslant (1-\varepsilon) + K(1-\varepsilon)^2 \tag{11}$$

or

$$h \leqslant \frac{K}{1+K}\varepsilon(1-\varepsilon). \tag{12}$$

Denote

$$H_1(K) = K\varepsilon, \quad H_2(K) = \frac{K}{1+K}\varepsilon(1-\varepsilon). \tag{13}$$

Note that for any $K > 0$,

$$H_2(K) \leqslant H_1(K);$$

hence, C is the dominant strategy for events $h < H_2(K)$, defection D is the dominant strategy for events $h > H_1(K)$, and for intermediate events $H_2(K) < h < H_1(K)$ cooperation is the best response to itself and defection the best response to itself.

We have thus proved:

Lemma 5. 1. *If* $h < H_2(K)$ *then* C *is the local dominant strategy in event* h, i.e. *it is the unique best response to any strategy of the partner.*

2. *If* $h > H_1(K)$ *then* D *is the local dominant strategy in event* h, i.e. *it is the unique best response to any strategy of the partner.*

3. *If* $H_2(K) < h < H_1(K)$ *then* C *is the unique best response to* C *in event* h *and* D *is the unique best response to* D.

The following proposition follows directly from the lemma:

Proposition 6. *A simple strategy* $\mathbf{x}_\alpha$ *is an agent ESS if and only if* $H_2(K(\alpha)) \leqslant \alpha \leqslant H_1(K(\alpha))$.

Proof. If $\alpha < H_2(K(\alpha))$ then by Lemma 5 the local best response to $\mathbf{x}_\alpha$ in events $h : \alpha < h < H_2(K(\alpha))$ is to cooperate contrary to what $\mathbf{x}_\alpha$ prescribes, which cannot therefore be a local ESS. If $\alpha > H_1(K(\alpha))$ then the local best response in events $\alpha > h > H_1(K(\alpha))$ is to defect; hence $\mathbf{x}_\alpha$ cannot be a local ESS.

If, however, $H_2(K(\alpha)) \leqslant \alpha \leqslant H_1(K(\alpha))$ then for all events h, except $h = H_1(K(\alpha))$ and $H_2(K(\alpha))$, the strategy $\mathbf{x}_\alpha(h)$ is the strict best response to itself. □

If events with lost cost of cooperation rarely happen, then it is not worthwhile for any of the partners to sacrifice anything for a partner who, even if he were so inclined, would rarely have the opportunity to help.

If, on the other hand, there is a high concentration of events around $h = 0$ then there exist agent ESSs in simple strategies in which there is cooperation, and in any of these ESSs there is a minimal level of cooperation. This is shown in the following proposition.

Proposition 7. *Let the events be distributed according to a continuous function* $F(h)$, *with a density function* $f(h)$, *and let*

$$f(0) > \frac{1 + p - (1 - \varepsilon)^2}{\varepsilon^2(1 - \varepsilon)}.$$

Then:

1. *There are two events* $\alpha_1 > \alpha_2 > 0$ *such that for all events* $\alpha : \alpha_1 > \alpha > \alpha_2$ *the simple strategy* $\mathbf{x}_\alpha$ *is an agent ESS.*
2. *For* $\alpha < \alpha_2$ *the simple strategy* $\mathbf{x}_\alpha$ *is not an agent ESS.*
3. *The strategy* $\mathbf{x}_0$ (*defection in all events*) *is an ESS but is not continuously stable.*

Proof. Note first that $H_2(K(0)) = 0$ and that for any $K \geqslant 0$ $H_2(K) < \varepsilon(\mathbf{1} - \varepsilon)$; hence, for $\alpha > \varepsilon(1 - \varepsilon)$, $H_2(K) < \alpha$. If the derivative of $H_2(\mathrm{K}(\alpha))$ is greater than 1 at $\alpha = 0$ then $H_2(K(\alpha))$ is above the diagonal around $\alpha = 0$.

The derivative of $K(\alpha)$ at $\alpha = 0$ is [see eqn (8)]

$$K'(0) = \frac{\varepsilon f(0)}{1 + p - (1 - \varepsilon)^2};$$

hence, by the definition of $H_2(K)$:

$$\frac{\mathrm{d}}{\mathrm{d}\alpha} H_2(K(0)) = \frac{\varepsilon^2(1 - \varepsilon) f(0)}{1 + p - (1 - \varepsilon)^2}$$

the assumption of this proposition guarantees that this expression is greater than 1. Thus, $H_2(K(\alpha))$ is above the diagonal around $\alpha = 0$ and will (strictly) cross the diagonal for the first time at some $\alpha_2 < \varepsilon(1 - \varepsilon)$.

Since $H_2 < H_1$ it follows that $H_1(K(\alpha)) > \alpha$ for $0 < \alpha \leqslant \alpha_2$; hence, there exists $\alpha_1 > \alpha_2$ (possibly $\alpha_1 = 1 - \varepsilon$) such that for all $\alpha \in [\alpha_2, \alpha_1]$: $H_2(K(\alpha)) \leqslant \alpha \leqslant H_1(K(\alpha))$.

1. By Proposition 6 the strategy $\mathbf{x}_\alpha$, $\alpha \in [\alpha_2, \alpha_1]$, is an agent ESS.
2. For $\alpha < \alpha_2 : \alpha < H_2(K(\alpha))$, hence by Proposition 6, the strategy $\mathbf{x}_\alpha$ is not an agent ESS.
3. The strategy $\mathbf{x}_0$ is not continuously stable since when the entire population deviates from defection and cooperates up to an event α, for some $\alpha < \alpha_1$, then given this degree of cooperation each individual would want to increase his cooperation up to α_1. Hence, a small deviation of the entire population leads to even more deviations bringing the population further away from total non-cooperation.

This completes the proof of the proposition. □

Proposition 7 demonstrates that under certain conditions (a high concentration of events around $h = 0$) if some cooperation has been established, the population will cooperate at least up to the event α_2, and it is possible for the population to cooperate up to α_1.

The next lemma shows that by choosing an appropriate distribution of events the partnership coefficient can be made arbitrarily large. A large partnership coefficient makes both α_1, α_2 large and guarantees that if there is cooperation it will necessarily be in a wide range, at least up to α_2. Indeed, cooperation may be achieved even in events with h close to $1 - \varepsilon$. In such events the cooperators sacrifice so much for their partner that their survival probability is close to ε—their survival probability when they are singles.

Lemma 8. *The partnership coefficient K can be made arbitrarily large by choosing a high concentration of events around* $h = 0$ *in which the population cooperates and by letting p be close to* 0. *For sufficiently large K, the point* α_2, *at which* $H_2(K(\alpha))$ *crosses the diagonal for the first time, can be made arbitrarily close to* $\varepsilon(1 - \varepsilon)$ *and the point* α_1 *can be made arbitrarily close to* $1 - \varepsilon$.

Proof. From the definition of $K(\alpha)$ [eqn (8)] it is straightforward to see that $K(\alpha)$ can be made arbitrarily large for α's close to 0, by making p close to 0 and by choosing a distribution of events which puts nearly all weight on events with h close to 0. Moreover, where the density of events is low, the derivative of K w.r.t. α is close to 0. Thus, K can be made arbitrarily large around 0 after which it changes very little.

This ensures that $H_2(K(\alpha))$ will start close to $\varepsilon(1-\varepsilon)$ around 0, and will cross the diagonal for the first and last time arbitrarily close to $\varepsilon(1-\varepsilon)$.

For similar reasons, $H_1(K(\alpha))$ will be large around $\alpha = 0$ and will be above the diagonal for all $\alpha < 1-\varepsilon$. □

Thus, if events occur with a high probability and if most of them have small values of h, then partners will cooperate in nearly all events, even in those in which helping the other requires a great sacrifice. The intuition is simple: if most situations are such that helping the other is cheap, and situations in which helping is costly are very rare, then by risking a lot to keep the other alive, on the rare occasion when it is expensive to help, one secures help in the frequently occurring situations (the cheap ones) while another situation requiring costly help is unlikely to occur again.

Figure 1 illustrates Proposition 7 and Lemma 8.

Where $H_2(K(\alpha))$ is above the diagonal cooperation is the best response to defection (C/D), while defection is the best response to itself (D/D) when $H_2(K(\alpha))$ is below the diagonal. Similarly, cooperation is the best response to itself (C/C) when $H_1(K(\alpha))$ is above the diagonal. Thus, all simple strategies $\mathbf{x}_\alpha$ with $\alpha \in [\alpha_2, \alpha_1]$ are agent equilibria. The conditions of Lemma 8 ensure that both functions $H_i(K(\alpha))$ start above the diagonal and cross it for high values of α_2, α_1.

The events in our example have the property that the willingness to take high risks for a defecting partner is limited. When $h > \varepsilon(1-\varepsilon)$ an individual will not cooperate against a defective partner, since by cooperating he lowers both his own and the joint survival probabilities. One can easily imagine families of events for which this is not the case. In such families, the partners will be willing to cooperate even against a defecting partner in order to increase the joint survival probability.

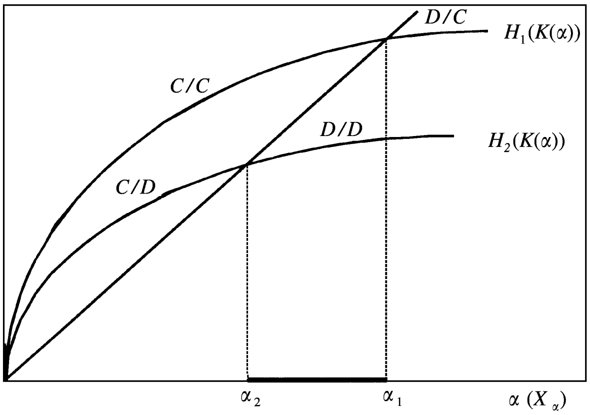

FIG. 1. Agent equilibria with cooperation.

4. Malice

The partnership coefficient need not always be positive as assumed until now. It can be negative and induce the individuals to take risks to their own life in order to *decrease* rather than increase the joint survival probability. Such behavior, in which an individual endangers himself in order to lower the probability of being with his partner in the future, we call *malice.*

Not all harm done to a partner is malice. Rivalry and direct competition between individuals is common in nature and in such situations it is often to the advantage of an individual to injure his partner opponent. In these cases, harming the other is due to egoism, not malice. In this sense, competitive behavior is analogous to hedonic altruism which is also derived from selfish behavior rather than goodwill.

A negative partnership coefficient can be established when the partners often meet in competitive situations. If then an event occurs in which both mutual cooperation and mutual defection are possible, the negative coefficient may tilt the balance in favor of malicious behavior. But, as the following example shows, a negative partnership coefficient may emerge without the presence of rivalry or competition, in situations where both competition and cooperation are possible.

Consider a variation of the additive help example of Section 3:

	C	D
C	$1-h, 1-h$	$1-h-\varepsilon, 1-h-\varepsilon$
D	$1, 1-h-\varepsilon$	$1-\varepsilon, (1-\varepsilon)^2$

, $\theta = 1-\varphi$,

with $\varphi < \varepsilon, 0 < h < \min\{\varphi, \varepsilon(1-\varepsilon)\}$ and with h distributed according to some function $F(h)$. The only difference between this event and the events of section 3, is that the survival probability of a single individual is higher than in mutual defection: $1-\varphi > 1-\varepsilon$. Defection creates a competitive situation: with the other defects he becomes a nuisance, since the survival probability is higher when single. Indeed, when both partners defect in all events the partnership coefficient is negative:

$$K(\mathbf{0}, \mathbf{0}) = \frac{(\varphi - \varepsilon)}{1 + p - (1-\varepsilon)^2} < 0.$$

A negative value of K ensures that defection is the dominant strategy in the partnership inclusive survival game defined by this K, since

$$1 + K(1-h-\varepsilon) > 1 - h + K(1-h),$$

$$1 - \varepsilon + K(1-\varepsilon)^2 > 1 - h - \varepsilon + K(1-h-\varepsilon)$$

[recall that $h < \varepsilon(1-\varepsilon)$].

In this example, there is no malice *per se*, confronted with a partner's defection an individual can only gain by defecting, he increases his own survival probability and reduces the joint one. However, total defection is an agent ESS for these events and it establishes a negative partnership coefficient. This negative coefficient prepares the ground for malice to appear when a suitable event occurs, then an individual will be willing to reduce his own survival probability in order to reduce their joint survival.

Note that in this example, like in Section 3, there can be a cooperative agent ESS when there is a high concentration of events around $h = 0$. Thus, in this family of events it is possible to establish cooperation with a positive partnership coefficient, leading to altruistic behavior in other events, or alternatively to have no cooperation with a negative coefficient which may lead to malice in other events.

The following example shows that malice, like cooperation, can amplify itself to extreme levels, even in situations where cooperation may also be established. Consider the following situation in which two neighbors could live independently and peacefully next to each other and may continue to do so, except that occasionally the opportunity arises for each to harm the other. In event $h \leqslant 1/2$, the aggressor survives a one-sided attack with probability $1-h$, while the peaceful neighbor survives it with probability h; the peaceful neighbor is never the sole survivor of such an attack, i.e. the joint survival probability is h. When both neighbors attack, one of them will die and each survives with a small probability σ. The risk h is distributed in $(0, 1/2]$ according to a function $F(h)$. The situation is described by the matrix:

$$\begin{array}{c|c|c|} & C & D \\ \hline C & 1, 1 & h, h \\ \hline D & 1-h, h & \sigma, 0 \\ \hline \end{array}, \quad \theta = 1.$$

Let $\mathbf{x}_\alpha$ be the simple strategy of attacking in all events in which the cost is lower than α: $h < \alpha$. The partnership coefficient when the entire population plays $\mathbf{x}_\alpha$ is

$$K(\alpha) = K(\mathbf{x}_\alpha, \mathbf{x}_\alpha) = -\frac{(1-\sigma)F(\alpha)}{1 + p - [1 - F(\alpha)]}$$

for $\alpha = 0$ (complete cooperation) the coefficient is 0, for $\alpha > 0$ it is negative, also $-1 < K(\alpha) \leqslant 0$.

Analogous to the discussion in Section 3 we show the following:

Proposition 9. 1. *The simple strategy of full cooperation* $\mathbf{x}_0$, *is an agent ESS.*

2. *If events are concentrated around* $h = 0$ *and events occur with high probability* ($p \sim 0$) *then there exist* $\alpha^* < 1/2$, *such that for all* $\alpha \in [\alpha^*, 1/2]$ *the simple strategy* $\mathbf{x}_\alpha$ *is an agent ESS. In that case no strategy* $\mathbf{x}_\alpha$ *with* $0 < \alpha < \alpha^*$ *is an agent ESS, and the strategy of complete cooperation* $\mathbf{x}_0$ *is not continuously stable.*[‖] *Moreover, when* σ *is small then* α^* *can be made close to* 1/2.

Proof. Following the lemmas and propositions of Section 3 it can be shown that:

- Cooperation is the best response to itself in the partnership inclusive game of event h if and only if $h > -K(1-K) = H_1(K)$.

[‖] Like in Section 3, it can be shown that an agent equilibrium in simple strategies is an ESS (see the appendix).

- Defection is the best response to itself in the partnership inclusive game of event h if and only if $h < \sigma/(1+K) = H_2(K)$.
- If events occur with high probability ($p \sim 0$), and if most events are concentrated around $h \sim 0$, then the value $K(0)$ can be made arbitrarily close to $-(1-\sigma)$, thereby making $H_1(K(0))$ arbitrarily close to $(1-\sigma)/(2-\sigma)$ and $H_2(K(0))$ to 1.
- Both functions $H_i(K(\alpha))$ increase with α but very slowly since most events are around $h = 0$. Hence, $H_1(K(\alpha))$ does not cross the diagonal in $(0, 1/2]$, and $H_2(K(\alpha))$ crosses the diagonal in the interval $[(1-\sigma)/(2-\sigma), 1/2]$.
- For all $\alpha \in [(1-\sigma)/(2-\sigma), 1/2]$ the simple strategy $\mathbf{x}_\alpha$ is an agent ESS.
- For small values of σ the expression $(1-\sigma)/(2-\sigma)$ is close to 1/2. This ensures that there are agent ESSs in which the partners defect in events with h close to 1/2. In this case, an individual is willing to forgo a survival probability of 1/2 for a low survival probability of σ in order not to be with his partner.

Part 1 follows immediately from the first two points and part 2 from the rest. □

Proposition 9 demonstrates the symmetry between cooperation and malice; both can start at a low level and be amplified. Here, full cooperation is an ESS, but (in some circumstances) when a small level of aggression establishes itself in the population then each individual will become more aggressive until a level of aggression α^*, or higher, is achieved.

Malice between partners may begin by competition while altruistic cooperation may start by hedonic cooperation. Although both competition and hedonic situations abound in nature, the first is probably more common. This does not necessarily indicate that malice is to be found more often than positive partnership. In situations of malice it is best for the partners to break the partnership, seek a new partner or new pastures, and generally avoid each other. Although it may not always be possible for the partners to move away from each other, some situations of malice will therefore not manifest themselves and will be avoided. On the other hand, in cooperation the partners' bond will be strengthened and they will be inclined to stay together.

5. Ageing

So far, we have taken the basic parameters of the model $\lambda, \mu, v, F(\cdot)$ to be constant. This, in general, need not be the case; one obvious situation to consider is ageing, when λ the natural death rate increases with the age of an individual. When two individuals are old and their death is imminent they will provide little help to each other since it is doubtful whether they will both survive to reap the benefits of their sacrifice. When they are both young and aware that old age gradually approaches they will help each other but less than in the absence of ageing, since they know that in the future they will help each other less.

A model taking the change in λ into account is very difficult to solve, particularly since we expect an individual to be familiar with his and his partner's ages. Thus, a strategy should depend not only on the individual's own age but also on the age of his current partner. To simplify matters we present here a special case of this model, in which the events consist mainly of hedonic situations with a very small chance of another event occurring and where a single individual cannot find a new partner, and therefore, once single will remain single for the rest of his life.

Let two partners be of the same age and have the same increasing natural death rate $\lambda(t) = \lambda_0 e^{\delta t}$. If left alone because of the partner's death an individual cannot find another partner ($v = 0$). Each moment an event may occur with intensity μ. The event is one in which mutual cooperation ensures survival and anything else ensures the death of both:

$$\begin{array}{c|c|c|} & C & D \\ \hline C & 1,1 & 0,0 \\ \hline D & 0,0 & 0,0 \\ \hline \end{array}, \quad \theta = 0.$$

The partners will always cooperate in this event irrespective of their age; here altruism is hedonic, one can only gain by cooperating, cooperation is the unique ESS of this game. This mass of hedonic events creates a positive partnership coefficient, so that each individual is prepared to forgo some of his own survival in order to increase the joint survival. The ratio of sacrifice to gain depends on the current value of K. Assume that, very rarely, an opportunity for such a sacrifice arises in the form of a non-hedonic event in which there is a possibility of making a sacrifice for the other, e.g. an event of the type discussed in Section 3. The higher their current partnership coefficient K, the wider is the range of such events in which they will cooperate. We show that K approaches 0 with time, so that when young the partners will cooperate in a range of events which shrinks as time goes on.

At each moment in time $K = (U - S)/S$, where U is the expected lifespan (at time t) when with a partner and S the expected lifespan when single. The intensity of death is higher when an individual is single, since in the absence of a partner he will certainly die when a hedonic event occurs, thus $U > S$. However, as the intensity of natural death λ increases both U, S approach 0, and since the occurrence of an event becomes insignificant relative to the looming (natural) death, the ratio U/S approaches1.¶ Thus, the partnership coefficient approaches 0 and the range of cooperation decreases with time.

Ageing has an effect on individuals only if their expected lifespan is long enough to enable them to reach old age. If individuals die young because of predators or events other than natural death, their strategy will not take into account the decrease of cooperation due to old age (see Hamilton, 1966). To show that the ageing effect plays a role in the actions taken by the young we need to show that they continue to live sufficiently long even after introducing ageing. Beginning with a world in which there is no ageing, i.e. the natural death rate λ is a constant ($\delta = 0$), we gradually introduce ageing: δ becomes positive. It can be easily shown that the expected lifespan of a young individual gradually decreases as δ increases. In formal terms, the derivative with respect to δ of the functions $U, S, U/S$ taken at $\delta = t = 0$, is finite, so that they live sufficiently long for ageing to affect the partners' behavior when they are young.**

6. Partnership, Kin Selection and Reciprocation

6.1. PARTNERSHIP AND KIN SELECTION

Differentiating between behavior which is motivated by kinship and one derived from partnership is not an easy task. One reason is that they are likely to appear intermingled, socially interacting kinsmen are likely to develop some degree of mutual dependence, becoming partners [Eshel & Cohen, 1975; Eshel & Motro, 1981], while partners are often chosen among kinsmen. Another reason is that, as we have shown in this work both types of behavior, kinship and partnership, can be similarly described each with the help of suitable coefficient by inclusive fitness or by partnership inclusive survival.

Partnership cannot be determined by observing only one interaction between the partners, even if it is of a repeated nature. The existence of other interactions and the behavior of the partners in those events is essential in determining the partners' behavior in a particular interaction.

Both kinship and partnership may lead an individual to exhibit altruistic behavior by helping another individual at a cost to himself, provided the cost is not too high. However, partnership-altruism qualitatively differs from kin-altruism in three factors:

- While the kinship-coefficient r can take values between 0 and 1 only, the partnership-coefficient K can assume arbitrarily high values or negative values.
- Kin-altruism can be described by assigning a fixed weight r to the survival of the kin. Partnership-altruism attaches weight to the survival of the other *conditioned* on one's own survival.
- While the kinship-coefficient r of two individuals is fixed for life, the partnership-coefficient K depends on the environmental parameters (λ, μ and v in our model). For example, K decreases when the exogenously given intensity of death increases, as a special case, K decreases with age.

¶ The differential equations for S, U are $S' = (\lambda + \mu) S - 1$, $U' = 2\lambda U - (1 + \lambda S)$. It is straightforward (but somewhat cumbersome) to solve the equations and prove the claimed properties. We omit the calculations.

** The simple but lengthy calculations are omitted.

The following examples demonstrate how kinship and partnership may lead to different behaviors in seemingly similar situations.

Consider two individuals interacting while facing a danger of a prisoner's dilemma type:

$$\begin{array}{c|c|c|} & C & D \\ \cline{2-3} C & v_{11} & v_{12} \\ \cline{2-3} D & v_{21} & v_{22} \\ \cline{2-3} \end{array}, \tag{14}$$

where $v_{21} > v_{11} > v_{22} > v_{12}$, and $v_{21} \leqslant \frac{1}{2}$, and where the payoff v_{ij} describes the survival probability of an individual when he has taken action i and the other action j.

If the two individuals are kinsmen with a kinship-coefficient r, cooperation (C) is evolutionarily stable (see Hamilton, 1964) when the expected advantage of defecting is smaller than r times the expected harm inflicted on the other, i.e.

$$r > \frac{v_{21} - v_{11}}{v_{11} - v_{12}}. \tag{15}$$

It is crucial for the theory of kin selection that the above condition ensures cooperation in this game matrix irrespective of the interpretation of the game, the age of the participants and other past or future interactions they have been or will be involved in.

We now consider the same situation between non-related *partners*; for this case we need to know their past and future interactions (summarized in the coefficient K) and also the joint survival probabilities. We first take the joint survival probability to be 0, i.e. whatever the partners do, at most one will survive the danger. The partnership matrix is

$$\begin{array}{c|c|c|} & C & D \\ \cline{2-3} C & v_{11}, 0 & v_{12}, 0 \\ \cline{2-3} D & v_{21}, 0 & v_{22}, 0 \\ \cline{2-3} \end{array}. \tag{16}$$

Regardless of the value of the coefficient K, the only globally stable strategy here is defection D. So, whereas kinsmen may cooperate in this situation, pure partners never will. Unlike kinsmen, partners are not interested in the other's existence after their own death.

Now consider a different way of adding the joint survival probabilities to the game:

$$\begin{array}{c|c|c|} & C & D \\ \cline{2-3} C & v_{11}, v_{11} & v_{12}, v_{12} \\ \cline{2-3} D & v_{21}, v_{12} & v_{22}, 0 \\ \cline{2-3} \end{array}. \tag{17}$$

Here if both cooperate they will survive and die together; if only one cooperates he has a lower chance of surviving and the defector has a higher chance, if both defect at most one will survive the danger. To illustrate the differences between kinship and partnership assume, in addition, that

$$\frac{v_{21} - v_{11}}{v_{11} - v_{12}} > 1;$$

this ensures that condition (15) of stability of cooperation among kinship cannot be satisfied ($r < 1$).

Given a partnership coefficient K, the condition for evolutionary stability of cooperation is

$$K > \frac{v_{21} - v_{11}}{v_{11} - v_{12}}. \tag{18}$$

This condition is identical to condition (15); however, the partnership coefficient K can take any positive value. Thus, if the partnership bonds are sufficiently strong the partners will cooperate in this situation as opposed to kinsmen who will not.

The difference between the behavior of kinsmen and partners, particularly since the strength of partnership changes with time, may explain many observed phenomena in human behavior, for example, the well-known human tendency to remember in their last will kinsmen rather than life-long friends.††

6.2. PARTNERSHIP AND RECIPROCATION

Like kinship altruism, altruism that relies on reciprocation leads to partnership, because once the other individual will provide help in the future (for whatever reason) he becomes

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†† A model incorporating this phenomenon would have to allow individuals to have different relations with different persons. Some would be relatives, others partners. The degree of cooperation will vary with the person and with age.

important, his mere existence is valuable and cooperation will amplify itself. However, partnership can develop without complex memory which is essential for reciprocation. Partnership may begin with hedonic situations so one needs to only identify the individuals with whom one encounters sufficiently many hedonic situations. It therefore becomes important for a potential partner to signal his willingness to cooperate. Unlike in reciprocation, the signal required for partnership is relatively primitive, there is no need to memorize how each individual behaved in the last period and to reward or punish them accordingly. For partnership it is enough to be aware that the other is a helper (or a menace) and to know the degree of the partnership (K). Thus, partnership may develop among primitive organisms as self-restraint in exploiting a limited resource (see Cohen & Eshel, 1976). For partnership all that is required is a signal that can be imprinted rather than a signal that needs to be continuously checked; it is therefore more primitive and cheap. Once such a signal evolves it is in the interest of the recipient to identify and accept it (Axelrod & Hamilton, 1981). The sender and the receiver of the signal would be able to reach higher levels of cooperation to their mutual benefit. Thus, partnership may enchance the evolution of simple signalling which may later expand to more complex signals and lead to reciprocation.

7. Conclusion

Partnership has been defined as the relation established between two or more individuals when it is in their best interest to help each other, since by doing so they increase the probability of being together in the future when, for similar reasons they will continue to help each other. Partnership is inevitable among kinsmen, and it may start among non-relatives when they face hedonic situations. In both cases, it is worthwhile to help the other because it will be in the other's best interest, if both survive, to provide help. We have shown that partnership may evolve even without hedonic cooperation.

Kin selection, partnership and reciprocation are likely to appear fused as the causes for altruism. However, we have shown that it may be possible to distinguish between kin altruism and partnership altruism by their different effects in some situations. We have also argued that partnership requires a lesser degree of sophistication than reciprocation. Our work may provide some theoretical ground for field biologists, anthropologists or sociologists in their observations of altruism.

In this work, we have concentrated on the *survival* aspect of partnership, since survival and life expectancy are significant factors in biology. However, the concept of partnership can be extended to include general payoffs like welfare, assets, income and power. Helping a partner to increase his income ensures a more powerful helper in the future. Such a generalization may provide tools for applying partnership to economics and the social sciences.

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APPENDIX

In Section 3, we presented an example of a family of encounters for which we have considered, as candidates for equilibrium, only simple strategies in which one cooperates up to a certain encounter and defects for all others. We have also considered only agent equilibria. Here we show that all agent equilibria in simple strategies are necessarily ESS.

Consider a family of encounters, parametrized by h, with a given distribution function. The first lemma applies to all such situations, the subsequent lemmas hold for the situations generalizing the example in Section 3.

First, we observe that if a strategy is a best response to another then it must also be a local best response to it.

Lemma A1. *Let* $\mathbf{x}(h)$ *be a best response global strategy to* $\mathbf{y}(h)$, *then* $\mathbf{x}(h)$ *is a local best response to* $\mathbf{y}(h)$.

Proof. The proof is straightforward, and we give here only a sketch of it. If there is an interval of events for which $\mathbf{x}(h)$ was not the local best response to $\mathbf{y}(h)$, then $\mathbf{x}$ can be corrected on a small set of events to the local best response. This will improve the expected lifetime of the player on this set of events and therefore in all other events. □

We define a family of events which generalizes in an intuitive way our additive example in Section 3. The encounters of family are ordered according to a parameter h, so that as h increases the benefits of cooperating become smaller both for the player's survival and for the joint survival of the partners.

We consider families of events ordered by a single parameter h; an event is described by the following survival probabilities (which are functions of h):

$$\begin{array}{|c|c|}\hline v_{11}, w_{11} & v_{12}, w_{12} \\ \hline v_{21}, w_{12} & v_{22}, w_{22} \\ \hline \end{array}, \quad \theta.$$

Assumption. 1. The gains of cooperating decrease with h, i.e. the following differences *decrease* with h:

$$v_{11}-v_{21}, \quad v_{12}-v_{22}, \quad w_{11}-w_{12}, \quad w_{12}-w_{22}.$$

2. For each h, the gains to the player and the gains to the joint survival from cooperating (rather than defecting) against a cooperator are higher than cooperating against a defector, i.e.

$$v_{11}-v_{21} > v_{12}-v_{22},$$

$$w_{11}-w_{12} > w_{12}-w_{22}.$$

It follows immediately from these assumptions that if for some positive K and some event h cooperating is the best response (in the inclusive survival game) against a pure strategy X then it is also the best response to X in events with lower h. Also, if for some h, the strategy C is the best response to D, then for all smaller h's the strategy C is the best response to C.

It is straightforward to see that the additive example of Section 3 satisfies the assumptions and that these ensure that $H_2(K) < H_1(K)$, and that C is the best response to D for events h below $H_2(K)$ and C is the best response to C for $h < H_1(K)$.

Lemma A2. *Let* $\mathbf{x}_\delta$ *be the simple strategy of cooperating up to the event* δ. *Let* $\mathbf{y}$ *be the best response to* $\mathbf{x}_\delta$, *then* $\mathbf{y}$ *is a simple strategy.*

Proof. From Lemma A1, $\mathbf{y}$ is a local best response. If $\mathbf{y}$ is not a simple strategy then there exist $h_1 < h_2$ such that $\mathbf{y}(h_1) = 0$, $\mathbf{y}(h_2) = 1$. There could be three cases concerning the location of δ relative to h_1, h_2. If $\delta < h_1 < h_2$ then the local best response to defection at h_2 is to cooperate; hence, by our assumption the best response to defection at h_1 should also be cooperation and it cannot be the case that $\mathbf{y}(h_1) = 0$. A similar argument holds for the case $h_1 < h_2 < \delta$. When δ is between the two values $h_1 < \delta < h_2$, the best response to defect at h_2 is to cooperate and hence by our assumption C is the best response to C at a lower event h_1, so that $\mathbf{y}(h_1)$ should be 1. □

The next lemma proves that if $\mathbf{x}_\delta$ is an agent equilibrium then it is a strict equilibrium and hence an ESS.

Lemma A3. *Let $\mathbf{x}_\delta$ be an agent equilibrium then $\mathbf{x}_\delta$ is the best response to itself.*

Proof. Let $\mathbf{y}$ be a best response to $\mathbf{x}_\delta$; then by Lemma A2 it is a simple strategy $\mathbf{y} = \mathbf{x}_\alpha$. We now show that $\alpha = \delta$.

Let $\alpha < \delta$, since $\mathbf{x}_\alpha$ is a best response it is (by Lemma A1) a local best response; hence, at $h = \alpha$ the best response to $\mathbf{x}_\delta$'s cooperation is both to defect and cooperate, i.e.

$$v_{11} + K(x_\alpha, x_\delta)w_{11} - v_{21} - K(x_\alpha, x_\delta)w_{21} = 0. \tag{A.1}$$

At $h = \delta$ the best response to cooperation is to cooperate and the best response to defection is to defect; hence,

$$v_{11} + K(x_\delta, x_\delta)w_{11} - v_{21} - K(x_\delta, x_\delta)w_{21} \geqslant 0. \tag{A.2}$$

Recall that v_{11}, w_{11}, etc., are functions of h.

We show that this leads to a contradiction, since as a function of h between α, δ the left-hand side cannot increase from equality to inequality. To show it we need to write $K(x_h, x_\delta)$ explicitly. The numerator of $K(x_h, x_\delta)$, for $h \leqslant \delta$, is

$$\left[\int_0^h v_{11}\,\mathrm{d}F(v) + \int_h^\delta v_{21}\,\mathrm{d}F(v) + \int_\delta^\infty v_{22}\,\mathrm{d}F(v) - \int_0^\infty \theta\,\mathrm{d}F(v)\right]$$

$$= \left[\int_0^\delta v_{11}\,\mathrm{d}F(v) + \int_\delta^\infty v_{22}\,\mathrm{d}F(v) - \int_0^\infty \theta\,\mathrm{d}F(v) + \int_h^\delta (v_{21} - v_{11})\,\mathrm{d}F(v)\right]$$

$$= \left[T + \int_h^\delta (v_{21} - v_{11})\,\mathrm{d}F(v)\right],$$

where

$$T = \int_0^\delta v_{11}\,\mathrm{d}F(v) + \int_\delta^\infty v_{22}\,\mathrm{d}F(v) - \int_0^\infty \theta\,\mathrm{d}F(v).$$

The denominator of $K(x_h, x_\delta)$ is

$$1 + p - \left[\int_0^h w_{11}\,\mathrm{d}F(v) + \int_h^\delta w_{21}\,\mathrm{d}F(v) + \int_\delta^\infty w_{22}\,\mathrm{d}F(v)\right]$$

$$= 1 + p - \left[\int_0^\delta w_{11}\,\mathrm{d}F(v) + \int_\delta^\infty w_{22}\,\mathrm{d}F(v)\right] - p\int_h^\delta (w_{21} - w_{11})\,\mathrm{d}F(v)$$

$$= 1 + p - B - \int_h^\delta (w_{21} - w_{11})\,\mathrm{d}F(v),$$

where

$$B = \int_0^\delta w_{11}\,\mathrm{d}F(v) + \int_\delta^\infty w_{22}\,\mathrm{d}F(v).$$

Substituting the explicit value of K on the left-hand side of eqn (A.1) and multiplying by the denominator of K, the following expression should not decrease as a function of h:

$$(v_{11} - v_{21})\left[1 + p - B - \int_h^\delta (w_{21} - w_{11})\,\mathrm{d}F(v)\right] - (w_{21} - w_{11})\left[T + \int_h^\delta (v_{21} - v_{11})\,\mathrm{d}F(v)\right].$$

However, we show that its derivative is negative and hence a contradiction is obtained. The derivative is

$$(v_{11}-v_{21})'_h\left[1+p-B-\int_h^{\delta}(w_{21}-w_{11})\,\mathrm{d}F(v)\right]$$
$$-(w_{21}-w_{11})'_h\left[T+\int_h^{\delta}(v_{21}-v_{11})\,\mathrm{d}F(v)\right]$$
$$+(v_{11}-v_{21})(w_{21}-w_{11})f(h)$$
$$+(w_{21}-w_{11})(v_{21}-v_{11})f(h)$$

the last two terms cancel, and we are left with

$$(v_{11}-v_{21})'_h\left[1+p-B-\int_h^{\delta}(w_{21}-w_{11})\,\mathrm{d}F(v)\right]$$
$$-(w_{21}-w_{11})'_h\left[T+\int_h^{\delta}(v_{21}-v_{11})\,\mathrm{d}F(v)\right].$$

By our assumption on the family of games this expression is negative and hence α cannot be less than δ.

By a completely analogous method it can be shown that α cannot be greater than δ. Hence, $\alpha=\delta$. □

We have shown that when $\mathbf{x}_\delta$ is an agent equilibrium then the *only* best response to $\mathbf{x}_\delta$ is $\mathbf{x}_\delta$ itself. Hence, $\mathbf{x}_\delta$ is a strict equilibrium and hence an ESS.

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