On the evolutionary edge of altruism:
a game-theoretic proof of Hamilton's rule for a simple case of siblings

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for a simple case of siblings[⋆]

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Abstract. We offer a game-theoretic proof of Hamilton's rule for the spread of altruism. For a simple case of siblings, we show that the rule can be derived as the outcome of a one-shot prisoner's dilemma game between siblings.

Keywords: Evolution of altruism – Hamilton's rule – One-shot prisoner's dilemma game

JEL Classification: A13, C70, D64

1 Introduction

Evolutionary biologists have developed a powerful theory of the evolutionary foundations of altruism between relatives. The theory is based on the idea that individuals who are related by blood share genes. Consider a gene that governs a particular behavior. The likelihood that the gene will be replicated is higher when the gene takes into account not only the extra reproductive opportunities that the behavior confers on the host who carries the gene but also the extra reproductive opportunities that the behavior confers on relatives of the host who also carry the gene. William Hamilton, the pioneer of this theory, describes it as follows: "The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbor's fitness against his own according to the coefficients of relationship appropriate to that situation" (Hamilton, 1964,

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p.19). The coefficient of relationship between two individuals is the probability that a randomly selected gene in one of these individuals will have an exact copy located in the other individual as a result of descent from a common ancestor. In the case of a haploid population in which each parent has a single gene for being altruistic or selfish and mating is monogamous, the coefficient of relationship between two siblings is $1/2$.

"Hamilton's rule" is that altruism will spread in a population if the benefit obtained from giving times the coefficient of relationship exceeds the cost of giving. If c is the cost to oneself of helping a sibling, and b is the benefit to a sibling from receiving help, altruism will spread if $b \cdot 1/2 > c$, that is, if the benefit obtained from help exceeds twice the cost of helping.
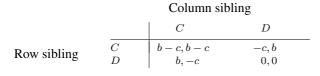
The purpose of this paper is to complement the large and important literature that followed Hamilton's pioneering articles, both in evolutionary biology (notably Dawkins, 1976; Grafen, 1984; Wilson, 1987) and beyond (Axelrod, 1984; Hofbauer and Sigmund, 1988; Binmore and Samuelson, 1992; Nowak and May, 1992), with a formal game-theoretic proof of Hamilton's rule. Building on Bergstrom and Stark (1993), Bergstrom (1995), and Stark (1999), this paper provides a proof of the rule for a simple case of siblings.

In evolutionary economics, the study of altruism is motivated by two questions: where does altruism come from and what does it give rise to. The incentive to explore inclinations is not independent, however, from the density of implications. If the motivation to produce, the propensity to redistribute, and the tendency to accumulate and transfer – within families, societies, and across generations – matter both for individual well-being and for social welfare, and if these processes are governed or significantly affected by the incidence and intensity of altruism as a trait, we would like to find out how the trait evolves. The interest in economics, and beyond, in the evolution, survival, and extinction of institutions of various types cannot be orthogonal to the interest in the prevalence and intensity of altruism *if* altruism gives rise to patterns and predispositions that completely or partially substitute for institutional mandates, impinge on the design of institutions, crowd out their roles, or render their mission superfluous. All the more so when there is a close correspondence between altruism and cooperation.[1] Since altruism is practiced and manifested socially, it is natural to start the search for its prevalence and origins in small social groupings such as the family. It is more likely that altruism will pervade large groupings such as the population at large if it evolves between siblings than if it fails to gain a foothold even within families.

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[1] The inquiry pursued in this paper relates to the study of institutions in yet another way. Schelling (1960, 1971, 1978) has shown how the interactions of individuals in environments characterized by bounded rationality and imperfect information coalesce over time into customs, norms, and institutions that govern economic and social life. Schelling's pioneering work was recently supplemented significantly by Young's study of economic and social institutions. To Young (1998) an institution is an established law, custom, usage, practice, organization. (Examples of institutions are aplenty: rules of the road, time of lunch, patterns of marriage, forms of economic contracts.) Young develops a theory that predicts how institutions evolve and characterizes their welfare properties. Viewing Hamilton's rule as an institution places this paper's inquiry in that research vein.

2 The game and a general result

In each period there is an old generation and a young generation. A fraction of the old generation consists of altruists, a complementary fraction consists of nonaltruists. Members of the old generation are matched with uniform probabilities into pairs. Each pair breeds two children. The children constitute the young generation. The two siblings play a one-shot prisoner's dilemma game with each other. A sibling can help the other sibling at a cost to himself. Let c be the cost to a sibling of helping a sibling, and let b be the benefit to the sibling who receives the help, $b > c > 0$. We obtain the following payoff matrix:

<div align="center">

Column sibling

		C	D
Row sibling	C	$b-c, b-c$	$-c, b$
	D	$b, -c$	$0, 0$

</div>

where playing C stands for providing help and playing D stands for not offering help. A sibling who plays C is altruistic, a sibling who plays D is nonaltruistic. To see this suppose the column sibling selects C. If the row sibling selects C rather than D, he gives up b to receive the smaller $b - c$, whereas the column sibling gains since he receives $b - c$ which is larger than $-c$. Suppose, alternatively, that the column sibling selects D. Again, if the row sibling selects C rather than D, his payoff declines (by c), while the column sibling's payoff rises (by b). This defines altruism: giving up something for the sake of another. Thus, throughout the rest of this paper we identify altruism with playing cooperatively in the one-shot prisoner's dilemma game.

Let $(p, 1-p)$ denote the mixed strategy in which the row sibling plays C with probability p; and let $(q, 1-q)$ denote the mixed strategy in which the column sibling plays C with probability q. Then, for any given (p, q), the expected payoffs of the row and column siblings are $qb - pc$ and $pb - qc$, respectively. Let p_1 and p_0 be the probabilities that the row sibling plays C if the column sibling plays C and D, respectively. We now provide a game-theoretic proof of Hamilton's rule for a simple case of siblings.

Proposition (Hamilton's rule). If c is the cost to oneself of helping a sibling, and b is the benefit to a sibling from receiving help, altruism will spread if $b \cdot (p_1 - p_0) > c$, that is, $p_1 - p_0$ is the equivalent of the coefficient of relationship.

Proof. Cooperation will be globally stable if the expected payoff of a randomly selected cooperator child is larger than the expected payoff of a randomly selected defector child. Without loss of generality, we randomly select the column sibling. The expected payoff of a randomly selected cooperator column sibling is $p_1 b - c$ since $(p, q) = (p_1, 1)$, and the expected payoff of a randomly selected defector column sibling is $p_0 b$ since $(p, q) = (p_0, 0)$. Hence, cooperation will be globally stable if $p_1 b - c > p_0 b$, yielding the statement of the proposition. □

3 The rule of imitation, survival, and the outcome: a special case

We assume that how a child plays, C or D, is determined through the imitation of his parents, and that each child imitates one of his parents with equal probabilities. The probability that a child survives to reproduce (to have his own children) is proportional to the payoff in the game. For example, consider a case in which the payoff positively influences the probability of reaching maturity and of being able to procreate.

Let x be the proportion of cooperative parents, and let $1 - x$ be the proportion of defector parents.

Claim 1. The probability that a randomly chosen child is a cooperator is x.

Proof. Let N be the number of individuals in the old generation. Hence, the number of parent pairs is $\dfrac{N}{2}$. Cooperator children come either from cooperator-cooperator parent pairs or from cooperator-defector parent pairs. The number of cooperator-cooperator marriages is $\dfrac{N}{2}x^2$. All $\dfrac{N}{2}x^2 \cdot 2 = Nx^2$ children of these marriages are cooperators. The number of cooperator-defector marriages is $\dfrac{N}{2}\left[x\left(1-x\right)+\left(1-x\right)x\right] = Nx\left(1-x\right)$ which is also the number of cooperator children produced by such marriages. Hence, the total number of cooperator children is $Nx^2 + Nx\left(1-x\right) = Nx$. In a population of N children, the probability then that a randomly chosen child is a cooperator is $\dfrac{Nx}{N} = x$. □

Claim 2. Given that a child is a cooperator, the conditional probability that its sibling is a defector is $\dfrac{1-x}{2}$.

Proof. A cooperator-defector pair of children results from a mixed marriage. Half of these $Nx\left(1-x\right)$ marriages produce mixed sibling pairs. The number of cooperator children in the mixed sibling pairs from these marriages is $\dfrac{1}{2}Nx\left(1-x\right)$. As already shown, the total number of cooperator children is Nx. Given that a child is a cooperator, the conditional probability that its sibling is a defector is $\dfrac{\frac{1}{2}Nx\left(1-x\right)}{Nx} = \dfrac{1-x}{2}$. □

Given that a child is a cooperator, the conditional probability that its sibling is a cooperator is the complementary probability $1 - \dfrac{1-x}{2} = \dfrac{1+x}{2}$.

By replacing x for $1-x$ we get that given that a child is a defector, the conditional probability that its sibling is a cooperator is $\dfrac{x}{2}$. (Given that a child is a defector, the conditional probability that its sibling is a defector is the complementary probability $1 - \dfrac{x}{2}$.)

Claim 3. Cooperation will be globally stable if $b > 2c$.

Proof. Since in this case $p_1 = \dfrac{1+x}{2}$ and $p_0 = \dfrac{x}{2}$, the claim follows from the proposition.

Evolutionary biologists refer to "inclusive fitness" of an individual. In the present model the inclusive fitness of a cooperator parent is the expected payoff of a randomly selected cooperator child, and the inclusive fitness of a defector parent is the expected payoff of a randomly selected defector child. The inclusive fitness of a cooperator is larger than the inclusive fitness of a defector, and cooperation is globally stable if the benefit to a child from playing cooperatively (helping) exceeds twice the child's own cost of playing cooperatively (helping).   □

4 Conclusion

We have shown that in a simple case of siblings, Hamilton's rule can be derived as the outcome of a prisoner's dilemma game between siblings. We employed several simplifying assumptions. These may be relaxed. For example, the formation of couples can be more selective than random. As shown in the Appendix, however, this change will only strengthen the case for cooperation.

Appendix

To substantiate the claim that a non-random formation of couples will only strengthen the case for cooperation, note that if matching is purely (positively) assortative, the fractions of cooperator marriages and defector marriages are, respectively, x and $1 - x$. To allow matching patterns that are intermediate between the polar cases of purely random matching and purely assortative matching, we define a parameter m where $0 \le m \le 1$, such that when matching is purely random $m = 0$, and when matching is purely assortative $m = 1$. The number of cooperator-cooperator marriages is then $\dfrac{N}{2}[x^2 + mx(1 - x)]$, and the number of cooperator-defector marriages is $N(1 - m)x(1 - x)$.

It follows that the probability that a randomly chosen child is a cooperator is x; given that a child is a cooperator, the conditional probability that its sibling is a defector is $(1 - m)\dfrac{1 - x}{2}$; given that a child is a cooperator,   the conditional probability that its sibling is a cooperator is $1 - (1 - m)\dfrac{1 - x}{2}$; and given that a child is a defector, the conditional probability that its sibling is a cooperator is $(1 - m)\dfrac{x}{2}$. (Given that a child is a defector, the conditional probability that its sibling is a defector is $1 - (1 - m)\dfrac{x}{2}$.) Since in this case $p_1 = 1 - (1 - m)\dfrac{1 - x}{2}$ and $p_0 = (1 - m)\dfrac{x}{2}$, it follows from the proposition that cooperation will be globally stable if $b\left[1 - (1 - m)\dfrac{1 - x}{2} - (1 - m)\dfrac{x}{2}\right] > c$ that is, if $b(1 + m) > 2c$.

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