Siblings, Strangers, and the Surge of Altruism

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Abstract

We demonstrate how altruism can surge in a population of nonaltruists. We assume that each individual plays a one-shot prisoner's dilemma game with his or her sibling, or with a stranger, and that the probability that an individual survives to reproduce is proportional to his or her payoff in this game. We model the formation of couples and the rule of imitation of parents and of nonparents. We then ask what happens to the proportion of altruists in the population. We specify a case where the unique and stable equilibrium is one in which the entire population will consist of altruists.

Contents

1. Introduction

An example is provided to illustrate how evolution can select for altruism. It is shown that evolution can sustain altruistic behavior even in a single-shot prisoner's dilemma model in which altruism benefits one's opponent at a cost to oneself, and conditions are derived under which altruism persists and flourishes to the extent that the entire population will consist of altruists. The case presented is of interest also because it goes beyond an earlier case in which one's opponent was exclusively a sibling (Bergstrom and Stark, 1993; Stark, 1995). Siblings are more likely to be similar than random pairs of individuals. Therefore, an altruist matched with a sibling is more likely to have an altruistic counterpart than an altruist who is matched with a randomly selected individual. This was shown to favor the evolution of altruism. In the present paper we show that even if an altruist is not necessarily matched with a sibling, altruism can surge.[1]

In section 2 we present the game and the payoffs and define altruism. In sections 3 through 6 we assume that each individual plays a one-shot prisoner's dilemma game with his or her sibling and that the probability that an individual survives to reproduce is proportional to his or her payoff in this game. We present the rule of imitation of parents and of nonparents and model the formation of couples. We then ask what happens to the proportion of altruists in the population. We specify a case where the unique and stable equilibrium is one in which the entire population will consist of altruists. In section 7, while retaining the structure of the preceding sections, we relax the assumption that the game is played with a sibling. We specify a case wherein the entire population will consist of altruists even if the game is played with a sibling with probability $u < 1$, and with a randomly selected stranger with the complementary probability $1 - u > 0$.

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[1] Referring to the earlier studies, Rose-Ackerman writes: "Altruism towards one's kin has intergenerational survival value in some models. Parents sacrifice for their children, and as a result, the children are more capable of reproduction than other, less fit, children (Theodore C. Bergstroem and Oded Stark 1993). Siblings whose genes or upbringing predispose them to cooperate will, under some conditions, do better than non-cooperators and end up dominating society (Stark 1995)." Bester and Güth (1998) write: "The strategic role of preferences distinguishes our approach from alternative explanations of altruism that rely on 'kin selection' arguments. These arguments show that evolution can sustain altruism between genetically linked individuals (see e.g. Bergstroem and Stark, 1993)." There appears then to be an implicit concern that the evolution of altruism result of the earlier studies hinges critically on a 'kin selection' argument. The present paper addresses this concern.

2. The game and the payoffs

Consider the following two-player, two-strategy game in which a player who cooperates gets a payoff of R if his opponent cooperates, and S if the opponent defects. A player who defects gets T if his opponent cooperates, and P if the opponent defects. In a prisoner's dilemma game, $S<P<R<T$, so that defection is a dominant strategy for each player.

We equate altruism with cooperating in a prisoner's dilemma game. To see this suppose the column player selects C.

Column Player

		C	D
Row Player	C	R,R	S,T
	D	T,S	P,P

If the row player selects C rather than D, he gives up T to receive the smaller R, whereas the column player gains since he receives R, which is larger than S. Suppose, alternatively, that the column player selects D. Again, if the row player selects C rather than D, his payoff declines (by $P-S$), while the column player's payoff rises (by $T-P$). This is what altruism is about: giving up something for the sake of another. Thus, throughout the rest of this paper we identify altruism with playing cooperate in the one-shot prisoner's dilemma game.

3. The rule of imitation

An individual's strategy, to play C or D against one's sibling, is determined by imitating the behavior of parents or nonparents. Note that strategy here stands for a programmed pattern of behavior, not an object of choice. Assume that with probability v a child randomly selects one parent as a role model and adopts that parent's strategy. With probability $1-v$ the child chooses a random nonparent as a role model. Each individual has a sibling with whom

the individual plays a game of prisoner's dilemma. The probability that an individual survives to reproduce is proportional to the payoff in this game. For example, consider a case in which the payoff positively influences the probability of reaching maturity and of being able to procreate.

4. The formation of couples

Assume that mating is monogamous. Parent-couples can be one of three possible types: two-cooperator couples, "mixed couples" with one cooperator and one defector, and two-defector couples. Let x be the fraction of cooperators in the adult population. If marriage is purely random, the fraction of marriages with two cooperators is $x \cdot x = x^2$, the fraction with two defectors is $(1-x)(1-x) = (1-x)^2$, and the fraction with mixed couples is $2x(1-x)$. If marriage is purely (positively) assortative, the fractions of cooperators and defectors are, respectively, x and $1-x$. To allow mating patterns that are intermediate between the polar cases of purely random mating and purely assortative mating, we define a parameter m where $0 \le m \le 1$, such that when mating is purely random $m = 0$, and when mating is purely assortative $m = 1$. In the population at large, the proportion of two-cooperator couples is thus $x^2 + mx(1-x)$; the proportion of two-defector couples is $(1-x)^2 + mx(1-x)$; and the remaining proportion of mixed couples is $2(1-m)x(1-x)$.[2]

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[2] The matching process can be characterized in the following way. Interpret m as the fraction of each of the two types who systematically marry members of their own type, and interpret $1-m$ as the fraction of each of the two types who marry randomly (that is, independently of type). We refer to cooperators as type C and to defectors as type D. Thus, a fraction mx of the population are individuals of type C who systematically marry individuals of type C, whereas a fraction $m(1-x)$ of the population are individuals of type D who systematically marry individuals of type D. Of the 1-m who marry randomly, x^2 are of type CC and $(1-x)^2$ are of type DD. Therefore, the total fraction of marriages that are of type CC is $mx + (1-m)x^2 = x^2 + mx(1-x)$, and the total fraction of marriages that are of type DD is $m(1-x) + (1-m)(1-x)^2 = (1-x)^2 + mx(1-x)$. Finally, of the fraction 1-m of type C who marry randomly, $x(1-x)$ are of type CD and of the fraction 1-m of type D who marry randomly, $(1-x)x$ are of type CD. Therefore, the total fraction of marriages that are of type CD is $(1-m)x(1-x) + (1-m)(1-x)x = 2(1-m)x(1-x)$.

5. The outcome

Given the assumptions about the rule of imitation and the formation of couples, what happens to the share of cooperators in the population, x? We specify a case where the unique and stable equilibrium is one in which the entire population will consist of cooperators.[3] For this monomorphic outcome to occur, two conditions must be satisfied. First, that a population of defectors would be "invaded" by cooperators. Second, that a population of cooperators could not be "invaded" by defectors.

The proportion of cooperators in the population will increase or decrease depending on whether the average payoff to cooperators is higher or lower than that of defectors. If defectors were as likely as cooperators to have cooperative siblings, then defectors would get higher expected payoffs than cooperators. However, siblings are more likely to be similar than random pairs of individuals.

Claim 1: As the proportion of one type in the population becomes rare, the *probability* that an individual of the rare type is married to an individual of the rare type approaches m.

Proof: Consider, for example, the case of rare cooperators. If an individual is a married cooperator, what is the probability that he will be married to a cooperator, when cooperators are rare in a population consisting of, say, N couples? This conditional probability is the total number of cooperators married to cooperators, divided by the total number of cooperators who are married at all, that is:

$$\frac{2\left[x^2 + mx(1-x)\right]N}{2\left[x^2 + mx(1-x)\right]N + 2(1-m)\,x(1-x)\,N} = x + m - mx,$$

which, when $x \to 0$, is equal to m. □

Thus, when cooperators are rare, the *probability* of a cooperator-cooperator match is m.

When the proportion of one type in the population approaches zero, what is the probability that an individual of the rare type has a sibling of the rare type?

Claim 2: The probability that an individual of the rare type has a sibling of the rare type approaches $(1+m)\,v^2/2$.

Proof: Denote the fractions of marriages that are of the three types, that is, two cooperators, cooperator-defector, and two defectors, by, respectively, $\boldsymbol{g}_{CC}$, $\boldsymbol{g}_{CD}$, and $\boldsymbol{g}_{DD}$. Then,

(1) $\boldsymbol{g}_{CC} = x^2 + mx(1-x)$,

(2) $\boldsymbol{g}_{CD} = 2(1-m)x(1-x)$,

(3) $\boldsymbol{g}_{DD} = (1-x)^2 + mx(1-x)$.

The probabilities that a child in a marriage of each type is of type C are

(4) $\boldsymbol{d}_{CC} = (1-v)x + v$,

(5) $\boldsymbol{d}_{CD} = (1-v)x + \dfrac{v}{2}$,

(6) $\boldsymbol{d}_{DD} = (1-v)x$.

Assuming that the number of children on average is the same in all types of marriages, the total fraction of children who are of type C is

(7) $\Delta = \boldsymbol{g}_{CC}\,\boldsymbol{d}_{CC} + \boldsymbol{g}_{CD}\,\boldsymbol{d}_{CD} + \boldsymbol{g}_{DD}\,\boldsymbol{d}_{DD} = x$.[4]

Given that a child is of type C, denote by $\boldsymbol{e}_{CC}$, $\boldsymbol{e}_{CD}$, and $\boldsymbol{e}_{DD}$ the conditional probabilities that the marriage into which the child was born is of a particular type. Thus,

(8) $\boldsymbol{e}_{CC} = \dfrac{\boldsymbol{g}_{CC}\,\boldsymbol{d}_{CC}}{\Delta}$.

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[4] Exploiting the similarity between the $\boldsymbol{d}$s, this result can be obtained as follows: $\boldsymbol{g}_{CC} + \boldsymbol{g}_{CD} + \boldsymbol{g}_{DD}$

$= x^2 + 2mx(1-x) + 2(1-m)x(1-x) + (1-x)^2 = x^2 + 2x(1-x) + (1-x)^2 = 1$, and

$\boldsymbol{g}_{CC} + \dfrac{1}{2}\boldsymbol{g}_{CD} = x^2 + x(1-x) = x$. Thus,

$\Delta = \boldsymbol{g}_{CC}\,\boldsymbol{d}_{CC} + \boldsymbol{g}_{CD}\,\boldsymbol{d}_{CD} + \boldsymbol{g}_{DD}\,\boldsymbol{d}_{DD} = \boldsymbol{g}_{CC}\left((1-v)x + v\right) + \boldsymbol{g}_{CD}\left((1-v)x + \dfrac{v}{2}\right) + \boldsymbol{g}_{DD}(1-v)x$

$= (\boldsymbol{g}_{CC} + \boldsymbol{g}_{CD} + \boldsymbol{g}_{DD})(1-v)x + \left(\boldsymbol{g}_{CC} + \dfrac{1}{2}\boldsymbol{g}_{CD}\right)v = (1-v)x + xv = x$.

Similar equations can be written for $\boldsymbol{e}_{CD}$ and $\boldsymbol{e}_{DD}$.

For a given pair of siblings, G and H, the conditional probability that H is of type C given that G is of type C is

$$(9) \quad \Lambda(x,m,v) = \boldsymbol{e}_{CC}\boldsymbol{d}_{CC} + \boldsymbol{e}_{CD}\boldsymbol{d}_{CD} + \boldsymbol{e}_{DD}\boldsymbol{d}_{DD}$$

or (for any arbitrary value of x)

$$(10) \quad \Lambda(x,m,v) = x + (1-x)k = k + (1-k)x$$

where $k = (1+m)v^2/2$. Hence,

$$(10') \quad \Lambda(x,m,v) \underset{x\to 0}{=} (1+m)v^2/2. \quad \square$$

Claim 3: When cooperators are rare, the difference between the expected payoff of a rare cooperator and that of a normal defector (that is, a defector child born to a two-defector couple) is $\boldsymbol{b} = (1+m)(v^2/2)(R-S) - (P-S)$.

Proof: When cooperators are rare, the expected payoff to a cooperator from the game played with a sibling is determined by the probability that the cooperator has a cooperator sibling, which is $(1+m)v^2/2$, by the probability that the cooperator has a defector sibling, which is $\left[1-(1+m)v^2/2\right]$, and by the respective payoffs. The expected payoff is therefore $(1+m)(v^2/2)R + \left[1-(1+m)v^2/2\right]S$. When cooperators are rare, the expected payoff to a normal defector from the game the defector plays with a sibling is P. We ignore the possible case in which a defector child interacts with a cooperator sibling because when cooperators are rare, that is, $x \to 0$, the conditional probability that a sibling of a child of type D is of type C, which is $(1-k)x$ where $k = (1+m)v^2/2$, approaches zero. Conversely, when cooperators are rare, the conditional probability that a sibling of a child of type D is of type D, which is $k + (1-k)(1-x)$, approaches 1.[5] The difference between the

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[5] From equations (1) through (10), the conditional probability that a sibling of a child of type C is of type D is

$$(11) \quad 1 - [k + (1-k)x] = (1-k)(1-x).$$

expected payoff

of a rare cooperator and that of a normal defector is thus

$$(1+m)(v^2/2)R+[1-(1+m)v^2/2]S-P=(1+m)(v^2/2)(R-S)-(P-S)=\boldsymbol{b}.\ \square$$

A similar procedure shows that when defectors are rare, the difference between the expected payoff of a normal cooperator and the expected payoff of a rare defector is $\boldsymbol{a}=(1+m)(v^2/2)(T-P)-(T-R)$.

Claim 4: When $\boldsymbol{b}$ and $\boldsymbol{a}$ are both positive, the population will consist entirely of cooperators.

The assumption that a small group of cooperators will continue to grow when it has already gotten bigger and will, in the end, take over the entire population requires examination of intermediate cases, that is, of cases other than the ones in which cooperators are rare $(x \to 0)$ or defectors are rare $(x \to 1)$. However, when the structure of the model is linear in such a way that we can infer about the intermediate cases from the extreme cases, a study of the intermediate cases is not necessary. The proof that this applies in the case of the current model is as follows. For any arbitrary value of x, by using (10) and (11) we calculate first the expected payoff of a child of type C from interacting with a sibling. This payoff is $[k+(1-k)x]R+(1-k)(1-x)S$. Next, by using (12) and (13) we calculate the expected payoff of a child of type D from interacting with a sibling. This payoff is $[k+(1-k)(1-x)]P+(1-k)xT$. Therefore, the difference between these two numbers is $x\{R-[kP+(1-k)T]\}+(1-x)\{[kR+(1-k)S]-P\}=x\boldsymbol{a}+(1-x)\boldsymbol{b}$. The expression $\boldsymbol{a}x+\boldsymbol{b}(1-x)$ is positive for *any* x (that is, not only for $x \to 0$ or $x \to 1$) if and only if $\boldsymbol{a}$ and $\boldsymbol{b}$ are both positive.

The conditional probability that a sibling of a child of type D is of type D is given simply by substituting $1-x$ for x in (10). We thus get,

(12) $k+(1-k)(1-x)$

and similarly, the conditional probability that a sibling of a child of type D is of type C is given by substituting x for 1-x in (11). We thus get,

(13) $(1-k)x$.

We cannot, of course, say that $\boldsymbol{b}$ and $\boldsymbol{a}$ must be positive. But we can find prisoner's dilemma games with payoff parameters S,P,R,T such that both $\boldsymbol{b}>0$ and $\boldsymbol{a}>0$.[6]

6. Explaining the outcome

The likelihood that cooperative behavior will prevail depends on $(1+m)\,v^2/2$. If children are likely to imitate their parents rather than a random role model, v is high; and parents are likely to be cooperators when m is high. The higher is $(1+m)\,v^2/2$, the greater the set of payoff parameters for which both $\boldsymbol{b}$ and $\boldsymbol{a}$ are positive, in which case the population will consist of cooperators only. That is, the greater is $(1+m)\,v^2/2$, the more likely it is that cooperative behavior will prevail. In particular, in the extreme case $m=v=1$, we get $\boldsymbol{b}=\boldsymbol{a}=R-P>0$ and the population will consist of only cooperators for any set of payoff parameters. While random mating $(m=0)$ does not exclude the "cooperators only" outcome as both $\boldsymbol{b}$ and $\boldsymbol{a}$ can still be positive, imitation of parents $(v>0)$ is necessary to get the "cooperators only" outcome.

7. Bringing in strangers

We extend the analysis to incorporate the possibility that the game is played not only with a sibling but also with a stranger. To this end we add a parameter u such that with probability u the single-shot prisoner's dilemma game is played with a sibling, and with probability $1-u$ the game is played with a randomly selected individual.

We first calculate the expected payoff to a cooperator from playing the game when cooperators are rare. As before, the expected payoff from playing with a sibling is

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(We can also derive this last probability from (12) by writing $1-[k+(1-k)(1-x)]=(1-k)\,x$.)

[6] Note that $(1+m)v^2/2$ lies in the closed interval $[0,1]$. It is an increasing function of both m and v. We have $(1+m)v^2/2=0$ if and only if $v=0$, and $(1+m)v^2/2=1$ if and only if $m=v=1$. We have that $\boldsymbol{b}>0$ if and only if $(1+m)v^2/2>(P-S)/(R-S)=k_1$, and that $\boldsymbol{a}>0$ if and only if

$(1+m)(v^2/2)R+[1-(1+m)v^2/2]S$. The payoff to a cooperator from playing with a randomly selected individual is S. Therefore, the expected payoff to a cooperator is $u\{(1+m)(v^2/2)R+[1-(1+m)v^2/2]S\}+(1-u)S$. Similarly, the expected payoff to a normal defector from the game the defector plays is $uP+(1-u)P=P$.

Claim 3': When cooperators are rare, the difference between the expected payoff of a rare cooperator and that of a normal defector is

$$\tilde{b}=u(1+m)(v^2/2)(R-S)+uS+(1-u)S-P=u(1+m)(v^2/2)(R-S)-(P-S).^7$$

A similar procedure shows that when defectors are rare, the difference between the expected payoff of a normal cooperator and that of a rare defector is

$$\tilde{a}=u(1+m)(v^2/2)(T-P)-(T-R).$$

Claim 4': When $\tilde{b}$ and $\tilde{a}$ are both positive, the population will consist entirely of cooperators.

For this result to hold, we require that u is not too small. Clearly, if $u=0$, both $\tilde{b}$ and $\tilde{a}$ will be negative, and the population will consist entirely of defectors. When $u=1$, we have shown that if b and a are both positive the population will consist entirely of cooperators. By continuity it follows that when $u<1$, we will have prisoner's dilemma games with payoff parameters S, P, R, T such that both $\tilde{b}>0$ and $\tilde{a}>0$.

8. Conclusion

The likelihood that a population will consist of cooperators only depends on $(1+m)(v^2/2)$ when individuals interact only with siblings, and on $u(1+m)v^2/2$ when individuals interact with siblings with probability $u<1$. In the latter case, if $(1+m)(v^2/2)$ is

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$(1+m)v^2/2>(T-R)/(T-P)=k_2$. The numbers k_1 and k_2 lie strictly between zero and 1 since $S<P<R<T$.

[7] Note that b is a special case of $\tilde{b}$ where $u=1$.

high but u is low, cooperation will not prevail. Yet a probable play with a randomly selected individual need not wipe out the edge that cooperation reaps from individuals' playing with their siblings. Even if a stranger is the co-player in the prisoner's dilemma single-shot game, cooperative behavior can still surge to become the exclusive population trait.

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