Strong Reciprocity May Evolve With or Without Group Selection

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We would like to thank Clara Jones for inviting us to respond to her comment on Fehr and Fischbacher (2003) and Bowles and Gintis (2004) that our views on the evolution of strong reciprocity are not consistent with the assumptions of evolutionary biology.[1] Her comment raises two questions: First, is it correct to that strong reciprocity cannot evolve except by group selection? Second, does recent research justify the rejection of group selection as a possible mechanism supporting the evolution of strong reciprocity and other human altruistic traits?

We will show that the empirical evidence for strong reciprocity as a common human behavior is compelling, and that Jones' concerns about our evolutionary thinking are misplaced. Concerning the second question, we will show that, given the capacity of humans to construct institutional, cultural and other environments that reduce the force of individual selection against altruistic traits, a genetic predisposition to behave in ways that reduce the fitness of the altruist relative to other members of their group could have evolved by group selection. Concerning the first, we argue that that there may be compensating fitness advantages that offset the net costs of behaving as a strong reciprocator. To avoid misunderstanding we should add that the models we use to show that group selection might support the evolution of strong reciprocity and other forms of altruism among humans do not depend on these compensating fitness advantages.

Strong Reciprocity

Strong reciprocity is a combination of altruistic rewarding, which is a predisposition to reward others for cooperative, norm-abiding, behaviors, and altruistic punishment, which is a propensity to sanction others for norm violations. Strong reciprocators bear the cost of rewarding or punishing but gain no individual economic net benefit from their acts. In contrast, reciprocal altruists, as they have been defined in the biological literature (Trivers 1971, Axelrod and Hamilton 1981), reward and punish only if this is contributes to their reproductive success or some other measure of self interest. Strong reciprocity thus constitutes a powerful incentive for cooperation even in non-repeated interactions and when reputation gains are absent because strong reciprocators will reward those who cooperate and punish those who defect.

There is a large amount of evidence supporting the widespread existence of strong reciprocity among humans. This experimental and field based evidence has recently been summarized in Fehr, Fischbacher and Gächter (2002) and Gintis et al. (2003). Strong reciprocity shows up in a vast variety of social and economic exchanges as well as in multilateral human

interactions.

Other-Regarding Behavior in Primates

Models of animal interaction with non-kin generally assume individuals are *self-regarding*: they care only about their personal payoffs from an interaction. Strong reciprocity is an example of *other regarding behavior*: strong reciprocators' contributions are not contingent upon personal reward, and their punishing of defectors is based on the other's behavior, not the punisher's expected net gain from punishing. It would be surprising if other-regarding behavior were limited to humans alone, and although there has been little systematic investigation of other-regarding behavior in non-human primates, a few studies indicate its existence.

Marc Hauser (1992) showed that rhesus monkeys in capitivity punish those who do not vocalize to advertise food discovery. Monkeys who remain silent, thereby enjoying exclusive access to a desirable food source for a longer period of time before others compete for a share, do indeed attract fewer conspecifics to the site, but those who do detect the food source are sufficiently punitive toward the original discoverer that the latter manages to consume only a fraction of what a vocalizer is permitted to consume by a larger group of conspecifics (2.8 pieces of coconut for the silent discoverer, compared with 4.9 for the vocalizer). In a more recent study Hauser (2003) shows that Cotton-top Tamarin monkeys can distinguish between altruistic and selfish (mutualistic) sharing of food, and that they systematically reward altruistic acts with reciprocal acts of kindness. Finally, Brosnan and de Waal (2003) show that brown capuchin monkeys compare payoffs to themselves with payoffs to other monkeys, and reject valuable food resources and opportunities for profitable exchange when they perceive conspecifics who are getting better deals.

Group Selection

In populations composed of groups characterized by a higher rate of interaction among members than between insiders and outsiders, evolutionary processes may be decomposed into between-group and within-group selection effects (Lewontin 1965, Price 1972, Crow and Kimura 1970, Uyenoyama and Feldman 1980). Where the rate of replication of a trait depends on the frequency of the trait in the group, and where group differences in trait frequencies are substantial and persistent, group selection contributes to the pace and direction of evolutionary change. Thus an altruistic trait that confers fitness advantages on other members of a group while imposing fitness costs on its bearer could evolve if the positive between-group selection effects are sufficiently strong to outweigh the negative within-group selection effects. Group selection works by exactly the same process as kin selection: altruism may evolve if the level of assortative pairing is sufficiently high. It does not matter whether assortative pairing occurs because individuals are more likely to be paired with relatives, or because individuals interact in groups and group compositions differ.

However, most who have modeled evolutionary processes under the joint influence of group and individual selection have concluded that, as an empirical matter, between-group selection pressures cannot override individual within-group selection pressures, save where

special circumstances, such as small group size and/or limited migration, magnify differences between groups relative to within-group differences (Eshel 1972, Boorman and Levitt 1973, Maynard Smith 1976).

But are humans a special case? Beginning with Darwin (for example Darwin (1873):156 and other passages), a number of evolutionary theorists have suggested that human evolution might provide an exception to this negative assessment of the force of multi-level selection. J.B.S.Haldane (1932) suggested that in population of small endogamous Atribes,@ an altruistic trait might evolve because the Atribe splitting@ that occurs when successful groups reach a certain size would create a few successor groups with a very high frequency of altruists, reducing within-group variance and increasing between-group variance. Bowles, Choi and Hopfensitz (2003) provide an analytical model and agent-based simulation of this process.

William Hamilton (1975) embraced Haldane's suggestion, adding that if the allocation of members to successor groups following tribe splitting was Aassociative@ (p.137), group selection pressures would be further enhanced. Subsequently, a number of writers have pointed out that group selection may be of considerably greater importance among humans than among other animals given the advanced level of human cognitive and linguistic capabilities and consequent capacity to maintain group boundaries and to formulate general rules of behavior for large groups, and the resulting substantial influence of cultural inheritance on human behavior (Alexander 1987, Cavalli-Sforza and Feldman 1973,, Boyd, Robert and Richerson 1985,, Boyd,and Richerson 1990, Sober and Wilson 1994, Boehm 1997, Gintis 2000).

While it is well known and widely accepted that the evolution of culture may be strongly influenced by group selection (Boyd, Robert and Richerson(2002, Soltis, Boyd, and Richerson 1995), many doubt the importance of group selection for traits governed by genetic transmission. Whether they are right is an empirical question: could a genetically transmitted altruistic trait evolve under the influence of group selection in an environment approximating past human social and ecological interactions? The models and simulations presented in Gintis (2000,2003), Bowles, Choi, and Hopfensitz (2003), Boyd, Gintis, Bowles, and Richerson (2003) and Bowles and Gintis (2004) suggest a positive answer. Human cultural capacities thus allow the construction of environments affecting the process of selection of both culturally and genetically transmitted traits. Gene culture coevolution thus provides another example of niche construction (Laland, Odling-Smee and Feldman 1999, Bowles 2000), The latter paper shows, for example, that culturally transmitted institutions (niches) can dampen the within group selection process sufficiently so that the positive effects of between group selection sustain high levels of altruism in the population.

These models capture distinctive human characteristics which may support group selection by attenuating within-group selection against an altruistic trait and thus enhancing group selection effects operating on genetic variation. Included is the human capacity for the suppression of within-group phenotypic differences in reproductive or material success, our patterns of social differentiation supporting positive assortation (non-random pairing), and the frequency of intergroup conflict. These observations suggest the limited applicability of the model and simulations to most other animals. However, for species in which neighboring groups including unrelated members compete for resources or in which group extinctions are common, a

similar model might apply.

In these cases, individually costly group-beneficial behaviors may contribute via group size or in other ways to the success of the group in avoiding extinctions or in gaining resources from neighboring groups. Examples include social mammals such as the cooperative mongoose *Suricata suricatta*, for which group extinction rates are inversely correlated with group size and in some years exceed half the groups under observation (Clutton-Brock, Gaynor, McIlrath, Maccoll, Kansky, Chadwick, Manser, Skinner, and Brotherton(1999). Similarly, fire ants (*Solenopsis invicta*) and a large number of other ant species form breeding groups with multiple unrelated queens and practice brood raiding and other forms of hostility toward neighboring groups, with success positively related to group size (Bernasconi and Strassmann 1999). Whether the levels of cooperation observed in these and other species might be explained in part by the causal mechanisms at work in our model is an interesting question which we have not explored.

Whether the gene-culture coevolution perspective advanced in the papers we have cited provides a sufficient explanation of the experimentally observed forms of human altruism is very much an open question and one that should be an active focus of research. The once fashionable dismissal, Abiologists have shown that group selection does not work@ is a generalization that currently hides more than it reveals.

Strong Reciprocity without Group Selection?

The definition of altruism in biology measures costs and benefits in fitness units. The *Stanford Encyclopedia of Philosophy*, for instance, defines "biological altruism" as follows: "In evolutionary biology, an organism is said to behave altruistically when its behaviour benefits other organisms, at a cost to itself. The costs and benefits are measured in terms of *reproductive fitness*, or expected number of offspring." (Okasha 2003). If those who bear the altruistic trait have lower fitness by comparison with the rest of the population of that species, then altruism cannot evolve. If the comparison is with the (smaller) reference group of agents within which all altruistic acts take place—so that altruists have lower fitness than non altruists within their group - - then altruism requires group selection.

But why must strong reciprocators have lower fitness than the other members of their group? Those behaving as strong reciprocators may enjoy compensating fitness advantages. For example strong reciprocity may be pleitropically linked to other behaviors which enhance the individual's fitness (Simon (1990), Caporeal (1989)). Or strong reciprocity might proliferate because it is an honest signal of some unobservable quality as a mate, coalition partner, and competitor, resulting in fitness benefits to those behaving altruistically (Gintis, Smith and Bowles (2001)). In these cases, the behavior is not altruistic (by the conventional definition) because relative to other members of the individuals group, the strong reciprocator does not have lower fitness.

Consider, for instance, the following scenario, which we hold to be rather common in human societies. A behavior, say "abide by the norms of ones group and punish those who violate norms" bears costs (forgone opportunities for extra pair copulations, risk of injury while

punishing norm violators) and confers benefits on others (generalized norm compliance has fitness benefits for group members.) We call this form of strong reciprocity altruistic punishment.

Will this class of strong reciprocators experience lower fitness than others in his group? Not if strong reciprocators are favored by some social mechanism, say sexual selection, so that the net costs of being a norm upholder will be just offset by their advantage in finding a mate. Now suppose there are many groups like the one just described, except that in some, sexual selection favors the norm violators. In the miscreant-loving society, upholding norms will not proliferate and will be eliminated if it is present. Individual selection in both societies will not alter the fraction of the norm upholders. But societies with more strong reciprocators may prevail in bouts with other groups or periodic environmental challenges, resulting in the diffusion of strong reciprocity in the population.

The group selection process in this case would favor strong reciprocity by proliferating the biases in sexual selection that compensate the reciprocator's fitness costs with superior reproductive success in other realms. Notice that because individual selection is not working against the strong reciprocators (they are absent in one group and maintaining their share of the other group) even weak group selection will support the proliferation of strong reciprocity. We use the term weak group selection to distinguish it from cases of strong group selection modeled in the works cited above in which group selection offsets individual (within group) selection working against the altruists.

Gintis (2002) provides an analytical model of weak group selection for human altruism. The model is premised on the fact that the capacity to internalize cultural norms is fitness enhancing because it allows individuals to control their impulses, to maintain prudent standards of personal hygiene and interpersonal relations, and to plan for the future. But the same capacity for internalization of norms can be deployed to produce strong reciprocators, brave soldiers, suicide bombers, and fighters for civil liberties.

Thus, strong reciprocity may be a basic human behavior that under conditions prevailing in recent history generally confers fitness advantages on its bearers in comparison with their self-interested compatriots. It is thus challenge of constitution building and public policy to develop social institutions that transform forms of altruism that require strong group selection in order to proliferate into more robust forms that may diffuse through weak group selection.

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