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Comment on Bergstrom

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In his recent *JEP* article, Theodore Bergstrom (Spring 2002, pp. 67–88) joins a small but distinguished group of economists who have seriously considered the implications of group selection for the conduct of economic inquiry and the assumptions we make about human nature. Until recently, this group has essentially been limited to Gary Becker, Friedrich Hayek, Jack Hirshleifer and Paul Samuelson. Each of these has not only acknowledged the possibility of group level selection (uncontroversial among biologists), but more significantly, has written sympathetically about the possibility that this variant of natural selection has left lasting imprints on human behavioral predispositions.

This note is concerned with one specific claim in Bergstrom's article, however, which I think is wrong or, at best, misleading: the claim that in "haystack" models, group composition must be assortative in order for group selection to attain any traction.

The intuition behind Bergstrom's "theorem" is clear. If altruists interact with defectors, they will have relatively fewer offspring than the defectors at any moment in time. Only if group composition is assortative, requiring that altruists have some way of seeking each other out and differentially associating with each other, can they benefit from their shared altruism and gain in a way that would increase the proportion of altruistic offspring in the population.

In haystack models, populations separate into groups or demes for one or several generations before merging and then reassorting. Bergstrom's logic is premised on the assumption of very large numbers in the individual groups. He argues that if the overall population is large and groups are "formed by random sampling without replacement from this population, then matching will be almost nonassortative" (p. 71). My claim is that the assumption of very large numbers is unrealistic if it is intended to apply to any actual demographic situation under which group selection might apply. Why does this matter? If the numbers are small, random variation alone will almost certainly produce variation in the percentages of altruists within each group. Bergstrom, in fact, acknowledges this: "In haystack models, random group formation produces some groups with more cooperators than others" (p. 71). So long as there is some variation in these frequencies, so that altruists are in some cases grouped together, group selection has the potential to act in a manner that causes the frequency of altruists in the general population to rise. This can happen even if the altruists are declining in each and every group at any moment of time—as long as the groups with relatively more altruists have a greater number of total offspring. And it can happen even though there is no mechanism whereby altruists seek out others similarly inclined and try to join groups differentially composed of them.

My point is related to that used to account for genetic drift, and is based on the statistical properties of small samples. If you flip a true coin, there is a 50:50 chance of getting a head or a tail. It does not follow, however, that if you choose groups of 10, you will always end up with five heads and five tails. The larger the size of the group, of course, the smaller will be the variance of the actual population shares around a mean of a fifty-fifty split. But a variance will remain.

Suppose mutation or genetic recombination has created a small number of altruistically inclined individuals. We are concerned with whether natural selection can allow these genes to persist. Suppose these individuals comprise 10 percent of the total population. Let $n = 100$ and have the population assort periodically into 10 equally sized haystacks. It is quite unlikely that each group will end up with nine defectors and one altruist. Perhaps the ten haystacks would include one that contains three altruistic individuals, one that contains two, five that contain one and three haystacks that contain none. Where small numbers are involved, random variation will produce a variation in trait frequency within groups that produces an outcome that to the untrained eye might in fact look *as if* there had been some tendency for altruists to seek each other out and associate with them. But the process is essentially random.

This point matters because as it stands, Bergstrom's logic appears to require as a precondition for any operation of group selection that individuals be armed with machinery for seeking out and differentially assorting with other cooperators. There is some experimental evidence that we have in fact acquired these capabilities, but to make it a precondition for the evolution of altruism raises unnecessarily the hurdles that group selection must overcome to be considered a potentially serious influence on human nature. It faces enough of these as things stand.

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Reference

Field, Alexander J. 2001. *Altruistically Inclined? The Behavioral Sciences, Evolutionary Theory, and the Origins of Reciprocity.* Ann Arbor: University of Michigan Press.