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Variable valuations and voluntarism under group selection: An evolutionary public goods game

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ABSTRACT

In biological systems, as in human society, competing social groups may depend heavily on a small number of volunteers to advance the group's prospects. This phenomenon can be understood as the solution to an evolutionary public goods game, in which a beneficent individual or a small number of individuals may place the highest value on group success and contribute the most to achieving it while profiting very little. Here we demonstrate that this type of solution, recently recognized in the social sciences, is evolutionarily stable and evolves in evolutionary simulations sensitive to alternative ways of gaining fitness beyond the present social group. The public goods mechanism may help explain biological voluntarism in cases like predator inspection and foraging on behalf of non-relatives and may determine the extent of commitment to group welfare at different intensities of group selection.

1. Introduction

Economists, philosophers, and clergymen have long been interested in voluntary contributions by private individuals for public benefit. Though such donations may not always be rational in the economic sense, economists and sociologists have advanced our understanding of this phenomenon through the analysis of public goods games (e.g. Olson, 1965; Diekmann, 1985; Bergstrom et al., 1986). Biologists concerned about the evolution of social behavior can also make effective use of this conceptual framework (Hauert et al., 2002; Semmann et al., 2003).

In public goods games, groups containing more generous donors outperform groups with less generous ones, but donors are disadvantaged relative to others within their groups. The game can be framed as a contest between groups of potential donors, with a prize shared among group members to be awarded with higher probability to a more generous group. Recent work (Baik et al., 2001; Baik, 2008) addresses a type of public goods game with particular biological relevance: individuals within and among groups differ in valuation of the prize and in budget available for making contributions, but all valuations and budgets are public knowledge (see related binary-response games of Diekmann, 1993 and Weesie, 1993). Under these conditions, the Nash equilibrium outcome of the game in the absence of budget constraints is for the individual in each group with the highest personal valuation of the prize to donate most of its expected gain from the contest and for other group members to free-ride by donating nothing. If the highest valuator is constrained by budget, then this budget amount is donated, and the next highest valuator contributes up to her own budget amount, and so on, until the highest remaining valuator cannot benefit from increasing her contributions; lower valuators contribute nothing. Thus high valuators, with a low expected gain from the contest, are exploited by others within the group, who will have positive expected gains that may exceed those of the top evaluator if they have positive valuations of the prize.

But in the present study our perspective is evolutionary, and we focus primarily on evolutionarily stable or non-invasible behavior (ESSs), rather than the Nash equilibria derived from assuming that all individuals engage in perfectly rational and fully informed decision making. The Nash–ESS distinction is important for contests among a finite number of groups, as we illustrate below (see related results in Schaffer, 1988; Leininger, 2003; Hehenkamp et al., 2004). The key difference is that the Nash or "rational" solution is based on each individual's maximizing its *absolute* expected gain, while the ESS solution assumes that each individual maximizes its expected gain *relative* to those of others, consistent with the workings of natural selection in a finite population.

The public goods game of interest here evokes biological analogs in which apparently voluntary donations of effort or acceptance of risk by individuals on behalf of a group have

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puzzled researchers to date. One example is predator inspection (Pitcher et al., 1986; Magurran and Pitcher, 1987; Brown and Dreier, 2002), documented so far in at least seven species of fishes (Dugatkin, 1997). Here usually one or two individuals leave the relative safety of the shoal to approach a nearby predator, seemingly to assess the threat and share this information with the group while perhaps informing the predator that its presence has been detected (Pitcher et al., 1986; Magurran and Higham, 1988). How individuals might inspect cooperatively has been addressed (Dugatkin, 1997; Milinski, 1987; Thomas et al., 2008), but not why those particular individuals would volunteer to accept the risky inspector role (but see Godin and Dugatkin, 1997 on attractiveness of male inspectors to females). A similar acceptance of risk apparently on behalf of a group is the intriguing case of voluntary foraging by a queen in the ant *Acromymex versicolor* (Rissing et al., 1989; Seger, 1989). We address both of these cases in the public goods context.

More generally, we want to know how the balance of opportunity to accrue fitness through group success vs. as an independent individual should influence commitments to the group, when individuals differ in their expected gains from group success. These expectations or valuations are assumed to be non-genetic, as in the predator inspection and voluntary foraging examples, and thus do not evolve themselves. Our analysis largely ignores the role of genetics—not to deny its importance in group facilitation and other altruistic phenomena (e.g. Axelrod and Hamilton, 1981) but to focus on a potentially complementary mechanism necessarily linked more strongly to group selection than to kin selection (e.g. see Wilson and Hölldobler, 2005 on the dominance of group selection in the evolution of eusociality). Competing social groups may differ in overall reproductive success and thus in selection on traits that influence group function, implying group selection (Wilson, 1980). Because the theory is not as well developed for public goods games from an evolutionary perspective, we first demonstrate that strategies closely related to but generally different from Nash equilibria are ESSs. We then use a genetic algorithm to evolve ESS solutions and address how group contributions by individuals reflect group vs. non-group opportunities.

We envision a population subdivided into trait groups, subsets of populations in which traits are expressed (Wilson, 1980). Trait groups compete with each other for some fitness benefit, such as surviving brood-raiding exchanges with neighboring colony groups and thereafter exporting the most dispersers (Rissing et al., 1989). Individuals within these groups are assumed to differ in the amount or value that group success contributes to their fitness (i.e. they differ in valuation). The question then becomes: how much should each individual contribute to the group effort, given its expected gain from the group contest as a function of its contribution and those of others? The answer must hinge in part on what other opportunities an individual has to accumulate fitness outside the context of group competition, as we note below. Thus both individuals and their groups are targets of selection (Hölldobler and Wilson, 2009), a view consistent with both trait group selection models and inclusive fitness models (Dugatkin and Reeve, 1994; Traulsen and Nowak, 2006; Lehmann et al., 2007).

We can invoke and adapt the previously described theory (Baik, 2008) in an attempt to account for cases of interest here. For predator inspection, we postulate that the inspector (or inspectors—but expressed hereafter as singular) is the most vulnerable to predator attack by proximity or social position or by being least able to sacrifice foraging for continual vigilance. As may be recognized by the whole shoal of fish, this individual should benefit most from the inspection, though perhaps only slightly more than others in the group. Similarly, of several queens in a newly formed pleiometrotic *A. versicolor* colony, we postulate that the one taking the considerable risk of foraging outside the nest to feed the entire colony is likely to be the largest and most fecund, with the most to gain from the colony's success.

In each of these cases, we expect the volunteer to have the most to gain or least to lose from volunteering. In the next section, we show how this solution can be evolutionarily stable. We also show how in some situations another individual of slightly lower valuation or multiple volunteers can be an ESS. Then we conduct some evolutionary simulations using a genetic algorithm to illustrate the Nash–ESS distinction and to indicate how contributions by individuals to the group reflect the relative extent of extra-group opportunities. Finally, we interpret our results, emphasize the testability of key predictions, contrast our use of the public goods game with previous biological studies, and note the ongoing convergence of game theoretic thinking in economics and biology.

2. Finding ESSs analytically

Suppose there are G competing, non-empty groups that may differ in numbers of members, but for clarity and notational convenience we assume they all have m members. It emerges from the analysis to follow that the numbers of members among groups do not matter as long as there are enough members in each to avoid constraining individual commitments to group success. By convention, the valuations within each group are ordered such that $v_{i1} > v_{i2} > \cdots > v_{im}$ for each group. With valuations assumed to be continuous, we ignore special cases with two or more equal within-group valuations and thus avoid the mixed-strategy solutions arising with discrete valuation (e.g. see Diekmann, 1993; Weesie, 1993). Assuming equality of valuations may often be difficult to defend empirically, just as the mathematical complexities arising from this assumption may obscure rather than illuminate the biological implications (see Weesie, 1993).

Now let the fitness F_{ir} for an individual in group i at valuation rank r be

$$F_{ir} = v_{ir} p_i - x_{ir}, \tag{1}$$

where v_{ir} is the valuation of group success by the individual at rank r in group i, x_{ir} is the corresponding effort or cost paid by this individual on behalf of the group, and the chance that group i succeeds in group competition is $p_i = \frac{\sum_{r=1}^{m} x_{ir}}{\sum_{j=1}^{G}\sum_{r=1}^{m} x_{jr}} = \frac{X_i}{Y}$. (This is a Tullock game in economics terminology—see Tullock, 1980.) Thus, each group's chance of competing successfully is proportional to the group's total effort committed to the contest. Suppose that each individual in the population of interest (which may be of infinite size, since groups may have infinite numbers of members) is a member of one of the G groups. Assume that each individual has a rank-dependent conditional strategy, which means that selection acts on an individual's ability to compete effectively at each rank. For example, a rank 1 competitor should increase effort as long as this increases its payoff *relative* to its effect on the average of the other rank 1 competitors (Hehenkamp et al., 2004). This simply expresses the standard criterion for evolutionary advantage, implying that a strategy will increase in frequency relative to alternative strategies taken together (Schaffer, 1988). Thus the rank-1 competitor converges on the limit at which

$$\frac{\partial F_{i1}}{\partial x_{i1}} = \frac{\partial \sum\limits_{\substack{j=1 \\ j \neq i}}^{G} F_{j1}/(G-1)}{\partial x_{i1}}. \tag{2}$$

When all rank 1 competitors reach this limit, these partial derivatives must all be equal.