

VARIABLE VALUATIONS AND VOLUNTARISM UNDER GROUP SELECTION:  
AN EVOLUTIONARY PUBLIC GOODS GAME

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Running Head: An Evolutionary Public Goods Game

## 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.

Key Words: ESS, game theory, Nash equilibria, pleiotropism, predator inspection

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 valuations contribute nothing. Thus high valuations, 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 (ESS's), 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, and 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 analogues in which apparently voluntary donations of effort or acceptance of risk by individuals on behalf of a group have 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 *Acromyrmex 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 ESS's. 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 pleiomorphic *Acromyrmex 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.

## Finding ESS's 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  $v_{i1} > v_{i2} > \dots > v_{im}$  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 and 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

$$F_{ir} = v_{ir}p_i - x_{ir}, \quad (1)$$

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

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

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

Now

$$\frac{\partial F_{i1}}{\partial x_{i1}} = v_{i1} \left( \frac{Y - X_i}{Y^2} \right) - 1, \quad (3)$$

and (simplifying the notation slightly)

$$\frac{\partial \sum_{j \neq i} F_{j1} / (G-1)}{\partial x_{i1}} = \frac{-\sum_{j \neq i} v_{j1} X_j / (G-1)}{Y^2}. \quad (4)$$

Setting (3) and (4) equal yields

$$\sum_{j \neq i} (v_{i1} (G-1) + v_{j1}) X_j = (G-1) Y^2. \quad (5)$$

At this point, following the lead of a previous study that focused on Nash equilibria (Baik 2008), we conjecture that only the  $x_{i1}$  can be positive in the ESS. We test this below after first finding the ESS effort  $\hat{x}_{i1}$ , given that  $\hat{x}_{ir} = 0$  for  $r > 1$ . This conjecture means that (5) can be written

$$\sum_{j \neq i} (v_{i1}(G-1) + v_{j1}) \hat{x}_{j1} = (G-1)G^2 \bar{x}_1^2, \quad (6)$$

which represents a set of  $G$  equations (one for each of the  $i$  values) in  $G$  unknowns. If we add both sides of all  $i$  equations and simplify, the result is

$$\bar{x}_1 = \frac{\bar{v}_1}{G}. \quad (7)$$

This implies that the average effort by rank 1 individuals equals their average expected gain from the contest at the ESS, assuming no individuals of lower rank commit any effort. In other words, there is an expected net gain of zero across all rank-1 valutors taken together.

Result (7) can now be substituted into (6) so that we have  $G$  *linear* equations in  $G$  unknowns:

$$\sum_{j \neq i} (v_{i1}(G-1) + v_{j1}) \hat{x}_{j1} = (G-1)\bar{v}_1^2. \quad (8)$$

Note that if the  $v_{i1}$  are all the same ( $= \bar{v}_1$ ), then

$$\begin{aligned} G\bar{v}_1(G\bar{x}_1 - \hat{x}_{11}) &= (G-1)\bar{v}_1^2, \\ G\bar{v}_1(G\bar{x}_1 - \hat{x}_{21}) &= (G-1)\bar{v}_1^2, \\ &\vdots \\ G\bar{v}_1(G\bar{x}_1 - \hat{x}_{G1}) &= (G-1)\bar{v}_1^2, \end{aligned} \quad (9)$$

which clearly requires that  $\hat{x}_{11} = \hat{x}_{21} = \dots = \hat{x}_{G1} = \bar{x}_1 = \bar{X}$ , an equal-effort outcome consistent with equation (7).

When the  $v_{i1}$  are not all the same, things are more complex. When  $v_{11} \neq v_{21}$  with two groups, it is easy to show from (8) that  $\hat{x}_{11} = \hat{x}_{21} = \bar{x}_1$ , which results in an expected net loss (i.e. in overdissipation of rent in the terminology of economics) by the high valuator of one group and an expected net gain (i.e. in underdissipation of rent) by the other. Supposing without loss of

generality that  $v_{11} > v_{21}$  means that the high valuator of group 1 gains in fitness, while the high valuator of group 2 suffers a fitness loss, based on evaluating equation (1). But for three or more groups, different valuations generally lead to different effort levels. For example, if  $v_{11} = 3$ ,  $v_{21} = 2$ , and  $v_{31} = 1$ , then  $\hat{x}_{11}^1 = 0.9697$ ,  $x_{21} = 0.7879$ ,  $\hat{x}_{31} = 0.2424$ , and  $\bar{x}_1 = 0.6667$ . Here again there is a net fitness gain at high valuation and a net fitness loss at low valuation; the intermediate valuator in this case expects to break even.

Note in the example for  $G = 3$  that effort level increases with valuation, as might be generally expected. The proof that this is generally true for  $G \geq 3$  when all  $\hat{x}_{i1} > 0$  is as follows.

Expand equation (8) and arrange the terms of the  $n$  equations to leave gaps where  $i = j$  in (8):

$$\begin{array}{ccccccc}
(v_{11}(G-1) + v_{21})\hat{x}_{21}^1 + (v_{11}(G-1) + v_{31})x_{31} + \dots + (v_{11}(G-1) + v_{G1})\hat{x}_{G1} & = & (G-1)\bar{v}_1^2 & & & & \\
(v_{21}(G-1) + v_{11})\hat{x}_{11} & & + (v_{21}(G-1) + v_{31})\hat{x}_{31}^1 + \dots + (v_{21}(G-1) + v_{G1})x_{G1} & = & (G-1)\bar{v}_1^2 & & \\
(v_{31}(G-1) + v_{11})\hat{x}_{11}^1 + (v_{31}(G-1) + v_{21})x_{21} & & & & + \dots + (v_{31}(G-1) + v_{G1})\hat{x}_{G1} & = & (G-1)\bar{v}_1^2 \\
\vdots & & \vdots & & \vdots & & \vdots \\
\vdots & & \vdots & & \vdots & & \vdots
\end{array} \tag{10}$$

Without loss of generality let  $v_{11} > v_{21} > \dots > v_{G1}$ , and notice that the right-hand sides of the  $G$  individual equations are all the same. Now consider the first two equations within (10). All terms in the first equation immediately above a term in the second equation are necessarily larger than the term below. This implies that the remaining term in the second equation must be larger than the remaining term in the first equation. But because what is within the outer parentheses in that second-equation term is smaller than what is within the corresponding parentheses of the remaining first-equation term, it follows that  $\hat{x}_{21}^1 > x_{21}$ . Using the same procedure with the second and third equations and focusing on the terms not immediately above or below another term then yields  $\hat{x}_{21}^1 > x_{31}$ . For any number of groups  $G$ , these pairwise comparisons obviously

imply that  $\hat{x}_{i1} > x_{21} > \dots > x_{G1}$ , and thus that the stable effort level of the highest valuator across the  $G$  groups increases with its valuation for  $G \geq 3$ .

Now we turn to the issue of individuals other than the highest valutors within groups, so far assumed to contribute no effort. If zero effort is evolutionarily stable for the second-highest valutors, then an increase in effort level would be less advantageous to the group containing that individual than to the average of the other groups. Much as before,

$$\frac{\partial F_{i2}}{\partial x_{i2}} = v_{2i} \left( \frac{Y - X_i}{Y^2} \right) - 1, \text{ and} \quad (11)$$

$$\frac{\partial \sum_{j \neq i} F_{j2} / (G-1)}{\partial x_{i2}} = \frac{-\sum_{j \neq i} v_{j2} X_j / (G-1)}{Y^2}, \quad (12)$$

but for zero effort to be an ESS we now need

$$\frac{\partial \sum_{j \neq i} F_{j2} / (G-1)}{\partial x_{i2}} < \frac{-\sum_{j \neq i} v_{j2} X_j / (G-1)}{Y^2}, \quad (13)$$

or

$$\sum_{j \neq i} (v_{i2} (G-1) + v_{j2}) \hat{x}_{j1} < (G-1) \bar{v}_1^2, \quad (14)$$

representing  $G$  inequalities closely resembling the equations in (8). In fact, using (8) we can readily demonstrate that (14) must hold, since each term in the summation of the inequality must be smaller than the corresponding term in the summation of the equation, while the right-hand sides are obviously the same. This is because  $v_{i1} > v_{i2}$  for all  $i$ .

The same argument as in (11) to (14) can be advanced to show that the third-highest valutors will also be unable to increase from zero effort, and so on for still lower valutors.

This means that (8) and  $\hat{x}_{ir} = 0$  for  $r > 1$  is an ESS. Because all group members at or below the second valuation rank exert zero effort, differences in group size have no effect on the outcome. But note the exceptions to the highest valuator providing all of the group's effort below, since these results could be altered if some of the groups are very small.

Now focus on the special case with all  $v_{ir}$  for each rank  $r$  the same ( $=v_r$  in simplified notation). The Nash equilibrium is  $\hat{x}_1 = v_1(G-1)/G^2$  and  $\hat{x}_r = 0$  for  $r > 1$  (Baik 2008), which is lower effort than the ESS (equation (7) with all  $\hat{x}_{i1}$  the same and  $\hat{x}_{ir} = 0$  for  $r > 1$ ) except when the number of groups gets very large. Unlike the ESS, which generates an expected payoff of zero for the top valuator in each group and a positive expected payoff for all others, the Nash equilibrium for a finite number of groups generates a positive expected payoff for all group members. (This is because the solution arises from setting equation (3) equal to zero instead of equal to equation (4), yielding the maximal absolute expected gain for the group rather than the maximal relative expected gain.)

There can be additional ESS's of the same form as above but with a valuation rank other than the first providing all of the effort, as long as this lower valuation is not too low and the number of groups is not too large. For example, in the equal valuation case, if  $v_2 > v_1 \left( \frac{G-1}{G} \right)$ , then there is also an ESS with only the second-highest valutors contributing positive effort (ignoring budget restrictions here); and if  $v_3 > v_1 \left( \frac{G-1}{G} \right)$ , then there is also an ESS with only third-highest valutors contributing, and so on. (The same steps to demonstrate the ESS apply, except with this other rank substituted for 1 in the equations (2)-(8).) In fact, when

$v_i > v_1 \left( \frac{G-1}{G} \right)$  for  $i = \{2, 3, \dots, k\}$ , where  $k \geq 2$ , the individuals contributing positive effort

across the groups need not all have the same valuation rank. This can lead to a large number of ESS's, including, in addition to the valuation-rank-1 individuals having the only positive effort, one or more groups with the rank-2 individual providing the positive effort (when  $k \geq 2$ ), one or more groups with the rank-3 individual providing the positive effort (when  $k \geq 3$ ), and so on.

This implies that the number of ESS's in the equal valuation case, based on the possible combinations of individuals across groups contributing positive effort, is  $k^G$ . When differences in valuation among all individuals within groups are negligible, then *any* individual could assume the role of sole contributor of positive effort. But with greater differences in valuation among members of a finite number of groups, the positive-effort role within groups may be taken by only a subset of individuals. When  $k = 1$  for all groups, only the highest valuers exert positive effort.

It is also straightforward to show for this equal valuation case that when there are budgets  $B_r$  identical by valuation rank, the ESS becomes

$$\begin{aligned}
\hat{x}_1 &= \min \left\{ \frac{v_1}{G}, B_1 \right\}, \\
\hat{x}_2 &= 0 \text{ for } \frac{v_2}{G} \leq B_1 \\
&= \min \left\{ \frac{v_2}{G} - B_1, B_2 \right\} \text{ for } \frac{v_2}{G} > B_1, \\
&\vdots \\
\hat{x}_{ir} &= 0 \text{ for } \frac{v_r}{G} \leq B_1 + B_2 + \dots + B_{r-1} \\
&= \min \left\{ \frac{v_r}{G} - B_1 - B_2 - \dots - B_{r-1}, B_r \right\} \text{ for } \frac{v_r}{G} > B_1 + B_2 + \dots + B_{r-1}.
\end{aligned} \tag{15}$$

This result can be readily generalized beyond the equal valuation case following the Nash analysis of Baik (2008). Thus budget restrictions can cause any number from 1 to  $m$  of the highest valuers in the group to contribute positive effort, depending on budgets and valuations.

### Evolutionary Simulations

To illustrate differences between Nash and ESS solutions for the public goods game and show how these results depend on extra-group opportunities, we formulated a genetic algorithm model tracking an evolving population of individuals across multiple generations. In each generation, the individuals were assigned randomly to groups of equal size, and the groups competed for a public goods prize, with the chance of group success being the group's total contributions divided by the total contributions across all groups (Tullock 1980).

The expected fitness gain  $F_{ir}$  for individual  $r$  (of  $m$  individuals per group) in group  $i$  (of  $G$  groups) was

$$F_{ir} = v_{ir} \left( \frac{\sum_{r=1}^m x_{ir}}{\sum_{j=1}^G \sum_{r=1}^m x_{jr}} \right) - cx_{ir}, \quad (16)$$

where  $v_{ir}$  was the valuation of the prize by individual  $r$  in group  $i$ ,  $x_{ir}$  was that individual's part of the group  $i$ 's total contribution in the contest, and  $c$  was the opportunity coefficient—the expected amount of fitness that could be gained outside of the group per amount of fitness contributed on behalf of the group (cf. the payoff function for equation (1)). The problem for each individual in the population was to set its contribution  $x_{ir}$  to maximize  $F_{ir}$ , subject to the contributions of the other  $mG - 1$  individuals in the population, and subject to its opportunities outside vs inside the group. Previous theoretical analysis (Baik 2008) with  $c = 1$  showed that this solution depends on the valuations within an individual's group (where by convention  $v_{i1} > v_{i2} > \dots > v_{im}$ , ignoring possible ties) and on the highest valuations in the  $G$  groups (i.e. on  $v_{11}, v_{21},$

...,  $v_{G1}$ ); if there are any budget limits constraining the magnitudes of the contributions, these must be known, and in this case also the rest of the valuations across the other  $m - 1$  individuals in each of the remaining  $G - 1$  groups. (Valuations and budget limits in an individual's own group may be the best available indication of the corresponding values in other groups, as assumed in Figure 1.)

In the genetic algorithm, each individual consisted of  $m$  loci, where each locus corresponded to a valuation rank  $r$  and contains the magnitude of  $x_{ir}$ . In an initial simulation, we assumed for simplicity that all individuals had the same budget limit for contributions  $B$ . In each generation, we assumed that each individual in a group was equally likely to be at any of the  $m$  valuation ranks, and we therefore averaged the fitnesses across ranks to obtain  $F_{ir}$ ; to obtain relatively balanced selection on the contribution to an individual's fitness from each rank without otherwise affecting the outcome, we normalized the fitness for each rank, dividing by the corresponding valuation, before averaging.

Once fitnesses were determined for all individuals in the population, individuals were ranked by fitness. Note that the mating group was the entire population, while the trait groups in which fitnesses were determined were the groups designated by subscript. The probability of an individual's becoming the parent of a particular member of the next generation's population was then proportional to  $mG - R + 1$ , where  $R$  is its fitness rank in the entire population, with the restriction that each offspring must have two different parents. The parents were equally likely to become the "template parent"; this individual provided the  $x_{ir}$  at each locus except when these values were modified by crossover and mutation events that occurred independently at each locus with probabilities 0.21 and 0.002, respectively. For each crossover event, the locus value of  $x_{ir}$  obtained from the template parent was replaced by the corresponding value from the other

parent. For each mutation, the locus value of  $x_{ir}$  was increased or decreased with equal likelihood and with a magnitude drawn from a negative exponential frequency distribution with a mean of  $0.05B$ . Following this procedure, the new population was established, completely replacing the parents, and the next generation began (see Crowley (1995) on the use of these methods and parameter values in a similar evolutionary algorithm).

Starting with randomly assigned magnitudes of the  $x_{ir}$  at all loci of all individuals, each run of the model continued for 10,000 generations, with 10 replicate runs. We assessed variability of the results by calculating the mean square error among individuals within groups, among groups within runs, and among runs. To examine the effect of the opportunity coefficient  $c$  on the results, we conducted the analysis at 101 values of  $c$  ranging from  $c = 0$  to  $c = 2$ , presenting the results graphically.

We found the ESS and Nash patterns as follows. The contribution of an individual at rank  $r$  will increase until this just fails to improve its ability to compete for fitness with those at the same rank in other groups. For an individual at rank  $r$  in group  $a$ , this is when  $\partial F_{ar}/\partial x_{ar} = \partial F_{br}/\partial x_{ar}$ , where  $b$  designates the average of the other groups. This amounts to spiteful behavior (Hehenkamp et al. 2004), because effort by the highest valuator in a group will increase beyond the point of maximal expected fitness gain (the Nash equilibrium); and though this individual thereby suffers a lower payoff, its competitors in the other groups fare still worse.  $F_{ar} = F_{br} = 0$  at this evolutionarily stable point (see equation (7)). (Hereafter we drop the group subscript for this special case, because  $v$ ,  $F$ , and  $x$  depend only on rank.) To obtain the  $x_r$ , we therefore set  $F_1 = 0$  and solve for  $x_1$ . If the result exceeds the budget  $B$ , then  $x_1 = B$  and we set  $F_2 = 0$ , solving for  $x_2$ , and so on. This continues until a  $x_r$  fails to exceed  $B$ ; the  $x_j$  for  $j > r$  are zero. We define two

limiting values of  $c$  for each individual's contribution function,  $C_{rL}$  and  $C_{rH}$ , between which  $x_r$  ranges from  $B$  to 0. The resulting functions of  $c$  are

$$\begin{aligned} x_r &= B, & \text{when } c \leq C_{rL}, \\ x_r &= \frac{v_r}{cG} - (r-1)B, & \text{when } C_{rL} \leq c \leq C_{rH}, \text{ and} \\ x_r &= 0, & \text{when } c \geq C_{rH}, \end{aligned} \quad (17)$$

where  $C_{rH} = \infty$  and otherwise  $C_{rH} = \frac{v_r}{(r-1)BG}$ , and  $C_{rL} = \frac{v_r}{rBG}$ . The Nash equilibria are similar except that the first term of  $x_r$ , along with  $C_{rH}$  and  $C_{rL}$ , are multiplied by  $(G-1)/G$ . ESS and Nash equilibria converge as the number of groups becomes very large.

Results from our genetic algorithm model were consistent with these interpretations and with ESS rather than Nash solutions (Figure 1; Hehenkamp et al. 2004). We expressed the fitness value of a unit of contribution outside the group relative to the same contribution inside the group using the opportunity coefficient  $c$ . (Opportunities outside the group include joining other groups as a queen or as a helper of relatives, founding another group, or reproducing independently.) Since shoaling provides some predator protection, and moving between shoals may carry a cost, we expect a value of  $c$  less than one, resulting in the one or two inspectors usually observed, unless the upper limit of an individual contribution is very low. For *A. versicolor* (Rissing et al. 1989, Seger 1989), queens ordinarily found colonies in groups of 2-4 unrelated individuals, and alternative opportunities are fairly high at this stage of colony formation; thus a single foraging queen is plausible, though additional foragers cannot be ruled out without information about physiological constraints.

## Discussion

This line of reasoning provides a useful perspective on individual contributions to social groups in nature. Consider a gradient of conditions along which the magnitude of the opportunity coefficient  $c$  declines. As local competition for defensible nesting sites and food resources intensifies, forming collaborative groups or colonies becomes increasingly attractive, particularly since the highest valuers are willing to make the initial investments needed to establish and maintain the colony.

What determines an individual's expected gain (and thus its valuation) through group success? Its dominance rank or body size may influence an individual's access to gains by group foraging, security through group defense, and reproductive potential via the pattern of reproductive skew. Differences in experience, shelter ownership, disease status, or fat reserves could shift the balance between potential gains inside vs outside the group. Random situations like being the most proximal individual in a shoal to a possible predator may also influence valuation. Though the model does not explicitly incorporate genetics or relatedness, such effects could be crudely expressed as differences in valuation, depending on an individual's relatedness to other group members, particularly those more likely to reproduce.

The public goods game arising from colonial competition thus can yield investment in the group by a single individual or a small number of individuals out of all group members. While opportunities outside the group still remain, this outcome amounts to “exploitation of the great by the small” (Olson 1965). These chief contributors may surround themselves with close relatives that may benefit as much or more in terms of inclusive fitness from assisting the colony in specialized roles as they would from reproducing themselves, especially since established

colonies are such formidable competitors (Hamilton 1972). As opportunities elsewhere diminish with evolutionary specialization and intense intergroup competition,  $c$  approaches zero, and all members become fully invested in the colony.

Pleiomertotic (multi-queen) systems seem to follow this general theme. Pleiomertosis is often linked to brood raiding, which puts heavy selection pressure on colonies to produce large numbers of workers quickly. In *Messor pergandei*, colonies are founded by multiple queens that collaborate in brood rearing until workers begin foraging, when the several queens begin fighting to the death (Rissing and Pollock 1987). But in some cases, competition from other colonies may be intense enough that unrelated queens must tolerate each other indefinitely within a colony. This may be considered a situation in which the contribution of the highest valuator is limited (perhaps because of physiological constraints on reproduction), thus requiring major reproductive donations from other queens to accumulate the evolutionarily stable group contribution.

As shown in (11)-(14), fitness maximization by the highest valuator in a group raises the group's total contribution to the point where all lower valutors benefit from reducing their own contributions to zero. This is the evolutionarily stable group contribution. But if the highest valuator is unable to provide this entire amount because of budgetary constraints, then successively lower valutors do increase their own fitness by contributing up to their own budgetary limits until the stable total contribution is reached. Reducing  $c$  with  $B = 1$  in Figure 1 forces exactly this cascade of additional contributors and contributions.

For situations in which valuations can be quantitatively determined, it may be possible to identify which individuals are "eligible" to serve as a group's chief or sole contributor by having a valuation  $v_i > v_1 \left( \frac{G-1}{G} \right)$ , allowing for the possibility of more than one ESS solution to the

public goods game (also see Myatt and Wallace 2008). Where relative valuations are clear to group members, efficient mechanisms for encouraging the highest valuator to contribute may arise under group selection (see Weesie 1993); these mechanisms should be even more important where valuations can only be assessed with considerable uncertainty. Responsibility for volunteering could become linked to social rank (high or low), body size, or age; or a more sophisticated turn-taking system could arise in species with adequate memory and individual recognition.

This game in which groups compete through contributions by group members applies to biological situations that fit the following four requirements:

- (1) Individuals fare better within groups than separately.
- (2) All group members benefit from group success, but in general they benefit unequally, with differences determined by environmental circumstances rather than by genetics.
- (3) Information about relative valuations within groups and among high valutors between groups is widely available.
- (4) Helping within the group contributes to group success but trades off against opportunities outside the group.

As for the cases addressed in this article and potentially many others, whether these requirements are met should generally be ascertainable via empirical tests. The game represents a mechanism to focus contributions to group establishment and maintenance on a single primary contributor or a small subset of the group, helping to create the conditions in which strong social units or colonies could evolve through group selection. The analysis shows how environments that favor group effectiveness over independent gains by individuals (i.e. environments with lower  $c$ ) draw greater contributions from group members that benefit less from group success.

Eusociality is the consummate social system, with all group members fully invested in the group (i.e.  $c = 0$ , thus violating requirement (3) above). Here intense group selection apparently overwhelmed individual selection and kin selection to elaborate group-benefitting specialization, leading to overlapping generations with distinct division of labor and extreme reproductive skew (Wilson and Hölldobler 2005, Hölldobler and Wilson 2009). The central role of group selection in binding social groups together extends to many other social systems where the public goods game may encourage voluntarism. Experimental work could address public goods games in social species that are not eusocial (Michener 1969) or are primitively eusocial (Gadagkar 2001) by manipulating the contribution budget through the food supply or the opportunity coefficient  $c$  through habitat characteristics and intensity of competition. The numbers of substantial contributors within groups should rise with decreasing  $c$  or increasingly limited budget availability per individual.

Volunteers are expected to be high valuers, having the most to gain or least to lose from volunteering—a testable hypothesis whenever valuations can be reliably determined in advance. Predictions can be based on quantifiable morphological, physiological, ecological, behavioral, or social traits. Alternatively, the volunteer may routinely be self-identified by conventional means—the individual closest to the predator or the most fecund—whether or not this individual has the highest valuation of group success in a given case. The convention could become established through even a weak correlation between trait and valuation, along with all individuals' need to minimize costly conflict in selecting a volunteer (see Maynard Smith 1982 and Weesie 1993).

Previous analyses of public goods games by biologists have focused on the frequencies of cooperators, defectors, and loners (group dropouts) within a single group, all assumed to value

and gain from group success equally (Hauert et al. 2002, Semmann et al. 2003). This scenario resulted in an unstable “rock-paper-scissors” type of frequency dependence. A recent modeling analysis (Reeve and Hölldobler 2007) addressed the emergence of degrees of eusociality under different intensities of between-group and within group competition. Their nested tug-of-war formulation (see Reeve et al. 1998) amounts to a public goods game but without allowing for differences in valuation, resulting in identical evolutionarily stable contributions to the group by all group members. In contrast, our approach incorporating valuation differences shows that voluntarism within such groups provided by only one or a small number of individuals may often be evolutionarily stable under comparably intense group selection. Interestingly, the nested tug-of-war analysis indicates that per capita group output generally declines as colony size increases (Reeve and Hölldobler 2007), corresponding to our finding of a small number of group contributors independent of group size. In other words, increasing group size in our model simply increases the number of free-riders, reducing the average contribution over the group.

While evolutionary thinking began to influence modern theoretical economics as early as the mid twentieth century (Alchian 1950), the Nash or rational-solution framework remains widespread. Yet some convergence of basic assumptions and approaches may be underway, with biologists using economic concepts like contest theory and public vs private goods, and economists beginning to ground economic theory in a more biologically defensible view of human behavior (Hammerstein and Hagen 2005).

The ESS framework in particular has been widely accepted by economists, notably including those studying competition between groups, by virtue of shedding new light on the free-rider problem (Leininger 2002, Hehenkamp et al. 2004). An ESS is known to exist for circumstances in Tullock competitive games that admit a pure strategy Nash equilibrium

(Hehenkamp et al. 2004), and the ESS and Nash equilibrium solutions in such games always differ (Leininger 2003). Our analysis demonstrates the existence of one or more ESS solutions when individual strategies may be conditional on differing within-group valuations of group success.

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## Figure Legends

Figure 1 Contribution  $x_{ir}$  to group  $i$  by individual  $r$  vs opportunity coefficient  $c$  for 5 groups ( $G = 5$ ) of size 5 ( $I = 5$ ), based on 10 replicate simulations. There were 10 replicate runs of 10,000 generations each; mean square errors at  $c = 1$  were all  $\ll 0.001$ .

A. Solid lines indicate simulation results for  $v_{ir} = 5 - r + 1$ , where  $r$  is within-group valuation rank and  $i$  designates the group. For these results, the budget limit or upper bound on contributions  $B = 1$ , independent of valuation. Note that for  $c \geq 0.8$ , only the highest valuator invested in the group, consistent with previous Nash-equilibrium results (Baik 2008) for  $c = 1$ . For  $c < 0.8$ , decreasing  $c$  and thus decreasing opportunities for fitness gain outside the group produced increasing numbers of contributors and larger contributions. The dashed lines mostly covered by the solid lines of the results indicate the ESS expectation; dotted lines are the Nash equilibria for comparison.

B. This is an identical scenario to the one depicted in panel A, except that budgets are proportional to valuation ( $B_i = v_i/5$ ), on the grounds that individuals with more to gain from group success might be those with more potential to contribute. The terms  $(r-1)B$  and  $rB$  in equations (16) are replaced by  $\sum_{j=1}^{r-1} B_j$  and  $\sum_{j=1}^r B_j$ , respectively. Nash solutions are not shown but are shifted along the  $c$  axis by the multiplicative factor  $(G-1)/G$ , as in panel A.

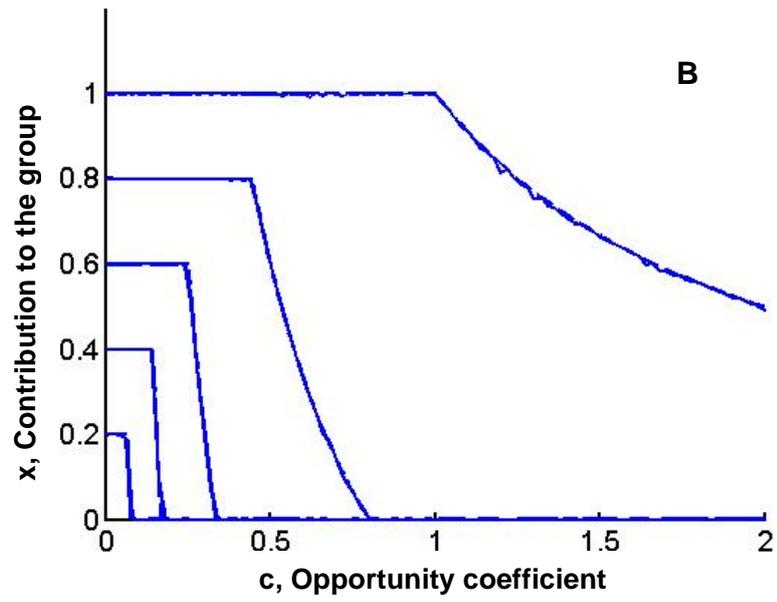
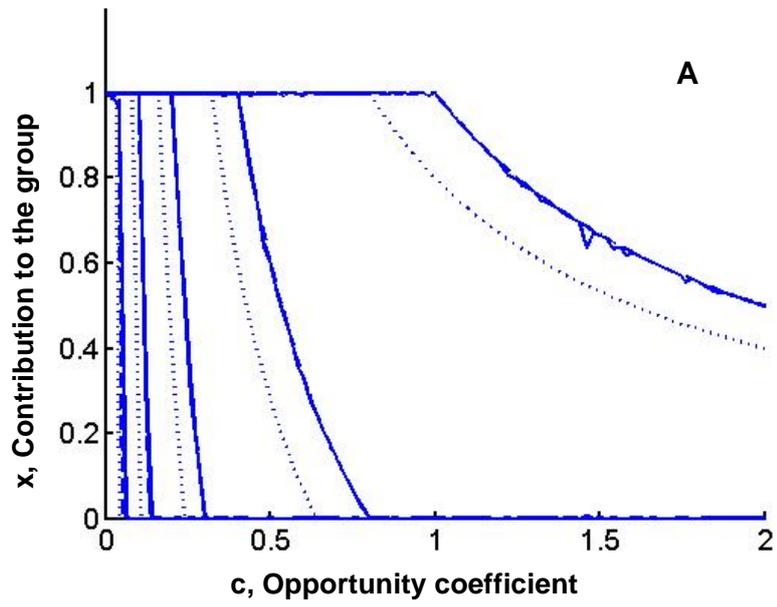


FIGURE 1