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Variability in group size and the evolution of collective action

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HIGHLIGHTS

- We study collective action problems with variable group sizes.
- Group-size variability may promote or inhibit the evolution of cooperation.
- We obtain conditions under which the sign of such variability effects is determined.
- Distinguishing between group sizes and experienced group sizes is important.
- We make use of stochastic orders and Bernstein polynomials.

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ABSTRACT

Models of the evolution of collective action typically assume that interactions occur in groups of identical size. In contrast, social interactions between animals occur in groups of widely dispersed size. This paper models collective action problems as two-strategy multiplayer games and studies the effect of variability in group size on the evolution of cooperative behavior under the replicator dynamics. The analysis identifies elementary conditions on the payoff structure of the game implying that the evolution of cooperative behavior is promoted or inhibited when the group size experienced by a focal player is more or less variable. Similar but more stringent conditions are applicable when the confounding effect of size-biased sampling, which causes the group-size distribution experienced by a focal player to differ from the statistical distribution of group sizes, is taken into account.

1. Introduction

Fish schools, wolf packs, bird flocks, and insect colonies exemplify the inherent tendency of animals to aggregate and live in groups (Krause and Ruxton, 2002; Sumpter, 2010). Within these groups, animals engage in a vast array of collective actions such as foraging (Giraldeau and Caraco, 2000), hunting (Packer and Ruttan, 1988), vigilance (Ward et al., 2011), defense (Hartbauer, 2010), and navigation (Simons, 2004). These social interactions are not without conflict, as individual and collective interests can oppose each other to the point of discouraging joint action and the pursuit of common goals.

Here we follow the game-theoretic approach of modelling such social dilemmas involved in collective action as multiplayer matrix games in which payoffs for individuals are determined by their own action, namely whether to cooperate or not, and the number of other individuals within their group who choose to cooperate (Broom et al., 1997; Peña et al., 2014). As shown in the vast literature on nonlinear public goods games (e.g., Dugatkin, 1990; Motro, 1991; Bach et al., 2006; Hauert et al., 2006; Cuesta et al., 2008; Pacheco et al., 2009; Archetti and Scheuring, 2011) cooperative behavior may arise in the evolutionary solution of such games even when other mechanisms potentially promoting cooperation such as relatedness (Eshel and Motro, 1988; Archetti, 2009; Peña et al., 2015) and reciprocity in repeated interactions (Boyd and Richerson, 1988; Hilbe et al., 2014) are absent.

Evolutionary models of collective action, including the ones cited above, typically assume that social interactions occur in groups of identical size. In contrast, empirical studies of animal group sizes show large variation in group size (Bonabeau et al., 1999; Gerard et al., 2002; Jovani and Tella, 2007; Griesser et al., 2011; Hayakawa and Furuhashi, 2012). This paper studies how this intrinsic variability in group size affects the evolution of cooperative behavior. We do so by modeling the evolutionary dynamics with the replicator dynamics (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998) and under the assumptions that the group-size distribution is exogenous, the population is well-mixed, and individuals express one of the two possible pure strategies. This is

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the same setting as the one used in Peña (2012) to investigate the effects of group-size diversity in public goods, that is, without any frequency-dependent or assortment bias in group composition. Although real group formation processes will certainly lead to such biases, we stick to this setting as it allows us to infer the consequences of relaxing the assumption of fixed group sizes without introducing the confounding effect of strategy assortment.

We identify general conditions, both on the class of group-size distributions and on the payoff structure of the collective action problem, which allow us to conclude whether more or less variation in group size promotes or inhibits cooperation. We thus go beyond Peña (2012) in not limiting us to the comparison of a deterministic group size with a variable group size (resp. the comparison of three particular group-size distributions) and by going beyond particular examples for collective action problems such as the volunteer's dilemma (Diekmann, 1985) and public goods game with synergy or discounting (Hauert et al., 2006).

To obtain our results, we combine three different kinds of insights. First, we build on results obtained in Motro (1991) and Peña et al. (2014) to identify conditions on the payoff structure of the game which are sufficient to infer those shape properties of the gain function that are required to identify the variability effects we are interested in (Lemmas 1 and 2). These results dispense with the need to explicitly calculate the gain function (i.e., the difference in expected payoff between the two strategies) whenever the payoff structure of the game satisfies the relevant conditions.

Second, we use the theory of stochastic orders (Shaked and Shanthikumar, 2007) to give precise meaning to the notion that one distribution is more ore less variable than another. This allows us to extend the comparison between a deterministic group size and a variable group size considered in Peña (2012) to the comparison of different group-size distributions. In particular, the very same condition on the shape of the gain function (when viewed as a function of group size) which Peña (2012) identified as being sufficient for group-size variability to promote cooperation relative to the benchmark of a deterministic group size yields the same conclusion for any two group-size distributions that can be compared in the convex order (Shaked and Shanthikumar, 2007). Many commonly considered group-size distributions with the same expected value can be compared in this way and often this is easy to check graphically.

Third, we demonstrate that focusing on the variability of the group-size distribution *per se* confounds two effects that are better understood when viewed separately. The issue is that the proportion of groups with a given size s is not identical to the proportion of individuals in groups with size s because a randomly chosen individual is more likely to find itself in a large rather than a small group. Whereas the former proportions are described by the group-size distribution, the latter are described by the so-called size-biased sampling distribution (Patil and Rao, 1978) that, for convenience, we refer to as the experienced group-size distribution. The empirical importance of distinguishing the group-size distribution and the experienced group-size distribution is well-understood in the statistical literature; a recent discussion in a biological context can be found in Jovani and Mavor (2011). The theoretical importance of distinguishing between the two distributions in our setting arises because an increase in the variability of the experienced group-size distribution may have different evolutionary consequences than an increase in the variability of the group-size distribution. This is because more variability in group size does not simply induces more variability in experienced group size but also increases average experienced group size.

Our main results are summarized in Propositions 1 and 2. These propositions are stated in terms of the gain sequence of the game, which collects the gains from switching (Peña et al., 2014), i.e., the difference in payoff a focal player obtains from switching its strategy as a function of the number of other cooperating players in the focal player's group. Proposition 1 shows that more variation in experienced group size promotes the evolution of cooperative behavior whenever the payoff structure of the game is such that the gain sequence is convex, whereas with concave gains from switching more variation in experienced group size inhibits the evolution of cooperative behavior.[1] Because more variation in group size not only implies more variation in experienced group size but also an upward shift in the experienced group-size distribution, these conditions do not suffice to imply that more variation in group size (rather than in experienced group-size) promotes or inhibits cooperative behavior. Proposition 2 takes this confounding effect into account and shows that more variation in group size promotes cooperative behavior whenever the gain sequence is convex and increasing, whereas cooperative behavior is inhibited when the gain sequence is concave and decreasing.

The difference between the sufficient conditions in Propositions 1 and 2 is significant as there are interesting collective action problems for which the gains from switching are convex or concave but fail the additional monotonicity properties required to determine whether more variation in group size promotes or inhibits cooperation. We illustrate this and other features of our analysis by using the volunteer's dilemma (Diekmann, 1985) and the public goods game with synergy or discounting (Hauert et al., 2006, Section 2.3.2) as examples. Further examples will be provided in Section 4, where we also discuss classes of collective action problems for which our approach is not applicable because the gain sequences are neither convex nor concave. Finally, we investigate the consequences of our main results for the number and location of stable rest points of the replicator dynamics, demonstrating that an increase or decrease in experienced group-size variability can induce transcritical and saddle-node bifurcations by which rest points can be created, destroyed, and their stability changed.

2. Methods

2.1. Group size and experienced group size

We consider an infinitely large and well-mixed population subdivided into groups consisting of a finite number of individuals. We assume that group size is given by a random variable S with support in the non-negative integers, probability distribution $p=(p_0, p_1, \ldots)$, and finite expected value $\mathrm{E}_p[S]=\sum_s p_s \cdot s$. We refer to p as the group-size distribution and assume throughout that $p_0+p_1<1$ holds, so that the fraction of groups with at least two individuals is not zero.[2]

Given a group-size distribution p, the fraction $\hat{p}_s$ of individuals who find themselves in a group of size $s \geq 1$ is

$$\hat{p}_s=\frac{p_s \cdot s}{\mathrm{E}_p[S]}. \tag{1}$$

We refer to the probability distribution $\hat{p}=(\hat{p}_1, \hat{p}_2, \ldots)$ defined by (1) as the experienced group-size distribution and to its associated

[1] Here and throughout our formal analysis we focus on the effects of an increase in (experienced) variability as the corresponding results for the effects of a decrease in (experienced) variability are easily inferred as they are simply opposite in sign. For instance, Proposition 1 can be read as the statement that less variation in experienced group size inhibits cooperation when the gain sequence is convex and promotes cooperation when the gain sequence is concave.

[2] We refrain from making stronger assumptions on the support of the group-size distribution – such as imposing a lower and/or upper bound – to accommodate commonly considered models for group-size distributions that we use for illustrative purposes.