



Evolutionary dynamics of collective action in spatially structured populations



Jorge Peña^{a,*}, Georg Nöldeke^b, Laurent Lehmann^c

^a Department of Evolutionary Theory, Max Planck Institute for Evolutionary Biology, August-Thienemann-Str. 2, 24306 Plön, Germany

^b Faculty of Business and Economics, University of Basel, Peter Merian-Weg 6, 4002 Basel, Switzerland

^c Department of Ecology and Evolution, University of Lausanne, Le Biophore, 1015 Lausanne, Switzerland

HIGHLIGHTS

- We study n -player games in spatially structured populations.
- Such games are mathematically equivalent to transformed games in well-mixed populations.
- We illustrate our theory with an application to the evolution of collective action.
- Results depend on the kind of collective good, its economies of scale, and scaled relatedness.

ARTICLE INFO

Article history:

Received 24 March 2015

Received in revised form

22 June 2015

Accepted 24 June 2015

Available online 4 July 2015

Keywords:

n -player games

Games between relatives

Relatedness

Inclusive fitness

ABSTRACT

Many models proposed to study the evolution of collective action rely on a formalism that represents social interactions as n -player games between individuals adopting discrete actions such as cooperate and defect. Despite the importance of spatial structure in biological collective action, the analysis of n -player games in spatially structured populations has so far proved elusive. We address this problem by considering mixed strategies and by integrating discrete-action n -player games into the direct fitness approach of social evolution theory. This allows to conveniently identify convergence stable strategies and to capture the effect of population structure by a single structure coefficient, namely, the pairwise (scaled) relatedness among interacting individuals. As an application, we use our mathematical framework to investigate collective action problems associated with the provision of three different kinds of collective goods, paradigmatic of a vast array of helping traits in nature: “public goods” (both providers and shirkers can use the good, e.g., alarm calls), “club goods” (only providers can use the good, e.g., participation in collective hunting), and “charity goods” (only shirkers can use the good, e.g., altruistic sacrifice). We show that relatedness promotes the evolution of collective action in different ways depending on the kind of collective good and its economies of scale. Our findings highlight the importance of explicitly accounting for relatedness, the kind of collective good, and the economies of scale in theoretical and empirical studies of the evolution of collective action.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Collective action occurs when individuals work together to provide a collective good (Olson, 1971). Examples abound in the social and natural sciences: humans collectively build houses, roads, walls, and mobilize armies to make war; bacteria secrete enzymes that benefit other bacteria; sterile ant workers build the nest and raise the brood of the queen; lions work together to catch

large game. Yet cooperation of this kind poses a collective action problem: if individual effort is costly there is an incentive to reduce or withdraw one's effort, but if enough individuals follow this logic the collective good will not be provided.

Much research in the social sciences has identified mechanisms for solving collective action problems, including privatization and property rights, reciprocity in repeated interactions, and institutions (Hardin, 1982; Sugden, 1986; Taylor, 1987; Ostrom, 2003). The principles behind these mechanisms have also been explored in evolutionary biology (Boyd and Richerson, 1988; Noë and Hammerstein, 2001; Strassmann and Queller, 2014) where it has been further emphasized that individual effort in cooperation should also increase as the relatedness between interactants

* Corresponding author.

E-mail addresses: pena@evolbio.mpg.de (J. Peña), georg.noeldeke@unibas.ch (G. Nöldeke), laurent.lehmann@unil.ch (L. Lehmann).

increases (Hamilton, 1964). As social interactions often occur between relatives (because of spatial structure, kin recognition, or both; Rousset, 2004; Bourke, 2011) it is thought that relatedness plays a central role for solving collective action problems in biology. In particular, relatedness has been identified as the main mechanism of conflict resolution in the fraternal major transitions in evolution, i.e., those resulting from associations of relatives, such as the transitions from unicellularity to multicellularity, or from autarky to eusociality (Queller, 2000).

Mathematical models of collective action in spatially structured populations or between relatives often assume that strategies are defined in a continuous action space, such as effort invested into the provision of a public good or level of restraint in resource exploitation (Frank, 1995; Foster, 2004; Lehmann, 2008; Frank, 2010; Cornforth et al., 2012). This allows for a straightforward application of the direct fitness method (Taylor and Frank, 1996; Rousset, 2004) to investigate the effects of relatedness on the evolution of collective action. Contrastingly, many evolutionary models of collective action between unrelated individuals (Boyd and Richerson, 1988; Dugatkin, 1990; Motro, 1991; Bach et al., 2006; Hauert et al., 2006; Pacheco et al., 2009; Archetti and Scheuring, 2011; Sasaki and Uchida, 2014) represent interactions as n -player games in discrete action spaces (e.g., individuals play either “cooperate” or “defect”). These models can be mathematically involved, as identifying polymorphic equilibria might require solving polynomial equations of degree $n - 1$, for which there are no general analytical solutions if $n \geq 6$.

Here we integrate two-action n -player mixed strategy game-theoretic models into the direct fitness method of social evolution theory (Taylor and Frank, 1996; Rousset, 2004), which allows for studying the effect of spatial structure on convergence stability by using pairwise relatedness. Several shape-preserving properties of polynomials in Bernstein form (Farouki, 2012) allow us to characterize convergence stable strategies with a minimum of mathematical effort. Our framework delivers tractable formulas for games between relatives which differ from the corresponding formulas for games between unrelated individuals only in that “inclusive payoffs” (the payoff to self plus relatedness times the sum of payoffs to others) rather than solely standard payoffs must be taken into account. For a large class of games, convergence stable strategies can be identified by a straightforward adaptation of existing results for games between unrelated individuals (Peña et al., 2014).

As an application of our modeling framework, we study the effects of relatedness on the evolution of collective action under different assumptions on the kind of collective good and its economies of scale, thus covering a wide array of biologically meaningful situations. To this aim, we distinguish between three kinds of collective goods: (i) “public goods” where all individuals in the group can use the good, e.g., alarm calls in vertebrates (Searcy and Nowicki, 2005) and the secretion of diffusible beneficial compounds in bacteria (Griffin and West, 2004; Gore et al., 2009; Cordero et al., 2012); (ii) “club goods” where only providers can use the good (Sandler and Tschirhart, 1997), e.g., cooperative hunting (Packer and Rutman, 1988) where the benefits of a successful hunt go to individuals joining collective action but not to solitary individuals; and (iii) “charity goods” where only nonproviders can use the good, e.g., eusociality in Hymenoptera (Bourke and Franks, 1995) where sterile workers provide a good benefiting only queens.

For all three kinds of goods, we consider three classes of production functions giving the amount of good created as a function of the total level of effort and hence describing the associated economies of scale: (i) linear (constant returns to scale), (ii) decelerating (diminishing returns to scale), and (iii) accelerating (increasing returns to scale). Although linear production functions are often assumed because of mathematical simplicity, collective goods can be characterized by either decelerating or accelerating functions, so that the net effect of several individuals behaving

socially is more or less than the sum of individual effects. In other words, social interactions can be characterized by (either positive or negative) synergy. For instance, enzyme production in microbial collective action is likely to be nonlinear, as in the cases of invertase hydrolyzing disaccharides into glucose in the budding yeast *Saccharomyces cerevisiae* (Gore et al., 2009) or virulence factors triggering gut inflammation in the pathogen *Salmonella typhimurium* (Ackermann et al., 2008). In the former case, the relationship between growth rate and glucose concentration in yeast has been reported to be decelerating, i.e., invertase production has diminishing returns to scale (Gore et al., 2009, Fig. 3c); in the latter case, the relationship between the level of expression of virulence factors and inflammation intensity appears to be accelerating, i.e., it exhibits increasing returns to scale (Ackermann et al., 2008, Fig. 2d).

We show that the effect of relatedness on the provision of collective goods, although always positive, critically depends on the kind of good (public, club, or charity) and on its economies of scale (linear, decelerating or accelerating production functions). Moreover, we show that relatedness and economies of scale can interact in nontrivial ways, leading to patterns of frequency dependence and dynamical portraits that cannot arise when considering any of these two factors in isolation. We discuss the predictions of our models, their implications for empirical and theoretical work, and their connections with the broader literature on the evolution of helping.

2. Model

2.1. Population structure

We consider a homogeneous group-structured population with a finite number of groups each containing an identical number of haploid individuals. Spatial structure may follow a variety of schemes, including the island model of dispersal (Wright, 1931), the isolation-by-distance model (Malécot, 1975), the haystack model (Maynard Smith, 1964), models where groups split into daughter groups and compete against each other (Gardner and West, 2006; Traulsen and Nowak, 2006; Lehmann et al., 2007b), and evolutionary graphs (Ohtsuki et al., 2006; Taylor et al., 2007; Lehmann et al., 2007a). We leave particular details of the life history (e.g., whether generations are overlapping or non-overlapping) and population structure (e.g., the dispersal distribution) unspecified as they do not affect our analysis. All that is required is that the “selection gradient” can be written in a form proportional to (4) below. For this, we refer the interested reader to Rousset (2004), Lehmann and Rousset (2010) and Van Cleve (2015).

2.2. Social interactions

Within groups, individuals participate in an n -player game with two available actions: A (e.g., “cooperate”) and B (e.g., “defect”). We denote by a_k the payoff to an A -player when $k = 0, 1, \dots, n - 1$ co-players choose A (and hence $n - 1 - k$ co-players choose B). Likewise, we denote by b_k the payoff to a B -player when k co-players choose A . These payoffs can be represented as a table of the form:

Opposing A -players	0	1	...	k	...	$n - 1$
Payoff to A	a_0	a_1	...	a_k	...	a_{n-1}
Payoff to B	b_0	b_1	...	b_k	...	b_{n-1}

Individuals implement mixed strategies, i.e., they play A with probability z (and B with probability $1 - z$). The set of available

Download English Version:

<https://daneshyari.com/en/article/6369520>

Download Persian Version:

<https://daneshyari.com/article/6369520>

[Daneshyari.com](https://daneshyari.com)