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Cheating is evolutionarily assimilated with cooperation in the continuous snowdrift game

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ABSTRACT

It is well known that in contrast to the Prisoner's Dilemma, the snowdrift game can lead to a stable coexistence of cooperators and cheaters. Recent theoretical evidence on the snowdrift game suggests that gradual evolution for individuals choosing to contribute in continuous degrees can result in the social diversification to a 100% contribution and 0% contribution through so-called evolutionary branching. Until now, however, game-theoretical studies have shed little light on the evolutionary dynamics and consequences of the loss of diversity in strategy. Here, we analyze continuous snowdrift games with quadratic payoff functions in dimorphic populations. Subsequently, conditions are clarified under which gradual evolution can lead a population consisting of those with 100% contribution and those with 0% contribution to merge into one species with an intermediate contribution level. The key finding is that the continuous snowdrift game is more likely to lead to assimilation of different cooperation levels rather than maintenance of diversity. Importantly, this implies that allowing the gradual evolution of cooperative behavior can facilitate social inequity aversion in joint ventures that otherwise could cause conflicts that are based on commonly accepted notions of fairness.
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1. Introduction

In daily life, cooperative behavior in joint ventures is a fundamental index that represents the real state of human sociality and is often a matter of degree that can continuously vary and diverge within a wide range. In general, understanding the origin and dynamics of diversity or heterogeneity has been one of the most challenging hot topics in biology and the social sciences (Axelrod, 1997; McCann, 2000; Valori et al., 2012). However, most traditional game-theoretical studies on cooperation have described the degree of cooperation in terms of discrete strategies, such as cooperators who contribute all and cheaters who do nothing. Compared with matrix games for finite discrete strategies, games for infinite continuous strategies have been relatively little studied (Brännström et al., 2011; Cressman et al., 2012; Le Galliard et al., 2005; Hilbe et al., 2013; Killingback and Doebeli, 2002; Killingback et al., 1999; McNamara et al., 2008; Nakamaru and Dieckmann, 2009; Roberts and Sherratt, 1998,b; Wahl and Nowak, 1999a,b). We should note that a common motivation among previous game-theoretical models with continuous strategies was to resolve the fundamental question, "How altruistic should one be?" (Roberts and Sherratt, 1998).

Crucially, in the last decade it has been clarified that even without specific assortment, very small, occasional mutations on the degree of cooperation can lead subpopulations of the cooperators and cheaters to gradually dissimilate each other out of a uniform population ("evolutionary branching") (Brännström and Dieckmann, 2005; Brown and Vincent, 2014; Doebeli et al., 2004; Parvinen, 2010). This divergence scenario for the cooperation level has been termed the "tragedy of the commune" (Doebeli et al., 2004). Gradual evolution can favor such a state in which a sense of fairness may be minimized, rather than a state in which all adopt the same cooperation level. To date, theoretical and numerical investigations have shown the conditions under which evolutionary branching occurs at the cooperation level, and by also considering ecological dynamics, where even extinction at the population level can follow (Parvinen, 2010, 2011).

Importantly, previous studies implicitly indicated that a heterogeneous population of cooperators and cheaters may be unstable when considering a small mutation (Brown and Vincent, 2014; Doebeli et al., 2004 Doebeli et al., 2004). To the best of our

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knowledge, this issue has never been seriously tackled, despite the fact that the coexistence of cooperators and cheaters is one of most elementary equilibria in classical 2×2 matrix games as described in Eq. (1) and is also common in nature and human societies. Indeed, little is known about how continuous investment in joint ventures affects what the traditional framework of a two-person symmetric game with two strategies has so far predicted (Doebeli et al., 2013; Shutters, 2013; Tanimoto, 2007; W. Zhong et al., 2012).

To address this issue, we consider the snowdrift game (Chen and Wang, 2010; Doebeli and Hauert, 2005; Gore et al., 2009; Hauert and Doebeli, 2004; Kun et al., 2006; Maynard Smith, 1982; Sugden, 1986), which has traditionally been a mathematical metaphor to understand the evolution of cooperation, and in particular, it can result in the coexistence of cooperation and cheating or inter-species mutualism (Fujita et al., 2014; Gore et al., 2009; Kun et al., 2006). (The snowdrift game is also well recognized as the chicken or hawk-dove game (Maynard Smith, 1982)). The classical snowdrift game for cooperators and cheaters has been featured by the rank ordering of the four payoff values: $T > R > S > P$ (Doebeli and Hauert, 2005; Sugden, 1986), which are given in the 2×2 payoff matrix for cooperation (C) and cheating (or defection) (D),

$$\begin{array}{cc} & \begin{array}{cc} \mathrm{C} & \mathrm{D} \end{array} \\ \begin{array}{c} \mathrm{C} \\ \mathrm{D} \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}. \tag{1}$$

We note that if P and S have the other order: $P > S$, then this matrix represents the well-known Prisoner's Dilemma, leading to mutual cheating (D–D) (Axelrod and Hamilton, 1981). The rank ordering for the snowdrift game indicates that when starting with the D–D state where both cheat, for one cheater to switch to cooperation is beneficial to both, yet not so is then for the other to switch to cooperation. The following situation may be useful as an example: the front porch of an apartment has been covered by a snowdrift, such that getting out requires someone to shovel the snowdrift. The situation becomes a sort of snowdrift game if a resident is willing to shovel snow and how much snow (C), and a best response for the other resident(s) is to shovel less (or nothing) (D). Considering that shoveling time and effort can vary continuously, this would naturally evoke a question of "How much would high- and low-contributors differ from each other in the snowdrift game?"

In Section 2, we extend the discrete snowdrift game to continuous cooperation. Fig. 1 presents an overview encompassing evolutionary scenarios in the classical and continuous snowdrift games. In Section 3, we then investigate the gradual evolution of cooperation with small mutations. In the continuous extension we consider quadratic payoff functions for interpolating these four payoff values in Eq. (1). It is known that the continuous model with quadratic payoff functions is at minimum, required for full coverage of basic adaptive dynamics for a population monomorphic with the same level of cooperation (Brown and Vincent, 2008; Doebeli et al., 2004) (see also (Boza and Számadó, 2010; Chen et al., 2012; Zhang et al., 2013) for effects of more generalized payoff functions). We show that adaptive dynamics in the snowdrift game analytically provides a solution whether a population is monomorphic or dimorphic. Finally, in Section 4 we provide a summary and discuss the model, results, and future work.

2. Models and methods

2.1. Replicator dynamics for cooperators and cheaters

We consider the 2×2 matrix game in Eq. (1) in infinitely large populations without any assortment. We denote by $P_\mathrm{C}(n)$ and $P_\mathrm{D}(n)$ the expected payoffs for a cooperator (C) and cheater (D), respectively, in the population with the frequency of cooperators n. Clearly,

$$\begin{aligned} P_\mathrm{C}(n) &= nR + (1-n)S, \\ P_\mathrm{D}(n) &= nT + (1-n)P. \end{aligned} \tag{2}$$

we analyze the replicator equation for the frequency of cooperators n (Cressman and Tao, 2014; Hofbauer and Sigmund, 1998),

$$\frac{\mathrm{d}n}{\mathrm{d}t} = n(P_\mathrm{C}(n) - \overline{P}(n)), \tag{3}$$

where $\overline{P}(n) = nP_\mathrm{C}(n) + (1-n)P_\mathrm{D}(n)$ denotes the average payoff over the population. Eq. (3) can be rewritten as

$$\begin{aligned} \frac{\mathrm{d}n}{\mathrm{d}t} &= n(1-n)(P_\mathrm{C}(n) - P_\mathrm{D}(n)) \\ &= n(1-n)[n(R-T) + (1-n)(S-P)]. \end{aligned} \tag{4}$$

Therefore, the replicator dynamics in the 2×2 matrix game in Eq. (1) are classified into four types by the sign combination of $S-P$ and $R-T$ (Table 1 and Fig. 2(x)) (Lambert et al., 2014; Santos et al., 2012; Shutters, 2013). In particular, if and only if $S-P>0$ and $R-T<0$ hold, the dynamics have a stable interior equilibrium with

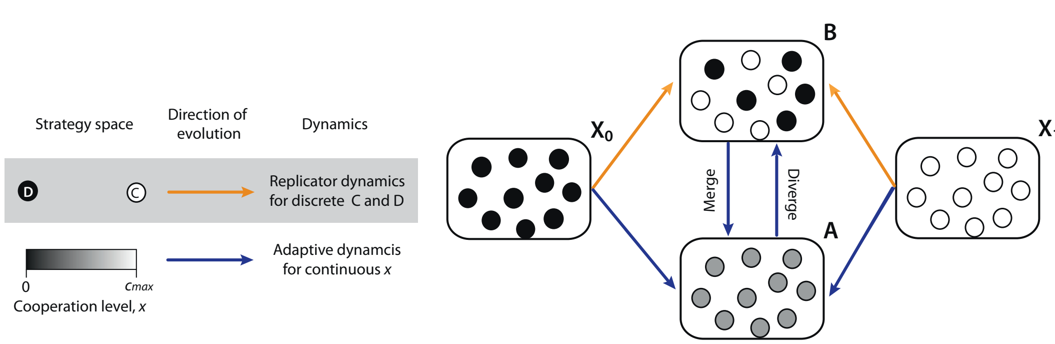

Fig. 1. Evolution of cooperation in snowdrift games. For discrete strategies, on the one hand, the evolution of the strategy frequencies can lead to the coexistence of cooperators and cheaters (upper arrows, X_0 to B and X_1 to B), yet do not help in understanding whether or not the resultant mixture is stable against continuously small mutations. For continuous strategies, on the other hand, the population converges to an intermediate level of cooperation (lower arrows, X_0 to A and X_1 to A) and can further undergo evolutionary branching (vertical arrow, A to B). In this case, the population splits into diverging clusters across an evolutionary-branching point $x = \hat{x}$ and eventually evolves to an evolutionarily stable mixture of full- and non-contributors (B). Otherwise, it is possible that a point where $x = \hat{x}$ has already become evolutionarily stable. In this case, the initially dimorphic population across a point $x = \hat{x}$ can be evolutionarily unstable, and thus the population will approach each other and finally merge into one cluster at the point ("evolutionary merging"; vertical arrow, B to A).

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