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Geometry of 'standoffs' in lattice models of the spatial Prisoner's Dilemma and Snowdrift games

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HIGHLIGHTS

- Prisoner's Dilemma (PD) and Snowdrift (SD) are games used to study cooperation.
- Spatial interactions affect cooperation frequency in PD and SD.
- Certain cost–benefit ratios potentially lead to static spatial patterns (standoffs).
- Standoffs can only occur where aperiodic static patterns are possible.
- Standoffs can emerge spontaneously from non-standoff conditions.

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ABSTRACT

The Prisoner's Dilemma and Snowdrift games are the main theoretical constructs used to study the evolutionary dynamics of cooperation. In large, well-mixed populations, mean-field models predict a stable equilibrium abundance of all defectors in the Prisoner's Dilemma and a stable mixed-equilibrium of cooperators and defectors in the Snowdrift game. In the spatial extensions of these games, which can greatly modify the fates of populations (including allowing cooperators to persist in the Prisoner's Dilemma, for example), lattice models are typically used to represent space, individuals play only with their nearest neighbours, and strategy replacement is a function of the differences in payoffs between neighbours. Interestingly, certain values of the cost–benefit ratio of cooperation, coupled with particular spatial configurations of cooperators and defectors, can lead to 'global standoffs', a situation in which all cooperator–defector neighbours have identical payoffs, leading to the development of static spatial patterns. We start by investigating the conditions that can lead to 'local standoffs' (i.e., in which isolated pairs of neighbouring cooperators and defectors cannot overtake one another), and then use exhaustive searches of small square lattices (4×4 and 6×6) of degree $k = 3$, $k = 4$, and $k = 6$, to show that two main types of global standoff patterns – 'periodic' and 'aperiodic' – are possible by tiling local standoffs across entire spatially structured populations. Of these two types, we argue that only aperiodic global standoffs are likely to be potentially attracting, i.e., capable of emerging spontaneously from non-standoff conditions. Finally, we use stochastic simulation models with comparatively large lattices (100×100) to show that global standoffs in the Prisoner's Dilemma and Snowdrift games do indeed only (but not always) emerge under the conditions predicted by the small-lattice analysis.

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1. Introduction

Cooperation occurs when individuals provide a benefit to each other at a cost to themselves [1]. Cooperation among non-kin is a long-standing issue in evolutionary biology, because cooperators are vulnerable to invasion by defectors, those that accept the benefits of cooperation *from* others yet fail to provide benefits *to* others (and, in doing so, avoid the costs). Nevertheless, cooperation is both common and important in natural systems—most spectacularly in the eusocial insects and in human societies [2].

Evolutionary game theory is the main theoretical framework used to explore the evolution of cooperation [3–9]. Typically, individual cooperators and defectors interact amongst themselves and receive 'payoffs' from these interactions that influence their fitness. Payoffs depend on who interacts with whom. In the Prisoner's Dilemma, the prototypical game in cooperation studies, defection against a cooperator yields the highest payoff, followed by mutual cooperation, mutual defection, and cooperation with a defector. Regardless of what one's co-player does, it is always better to defect rather than cooperate; defection is an evolutionarily stable strategy that dominates cooperation, even though a group of cooperators has a higher mean fitness than a group of defectors [3]. Thus, the Prisoner's Dilemma is an abstraction of cooperation that evokes the inherent conflict between the interests of individuals and the interests of the populations to which they belong.

Another game with relevance to the evolutionary dynamics of cooperation is the Snowdrift game (sometimes referred to as 'hawk–dove' or 'chicken' [3,10–12]). Like the Prisoner's Dilemma, in the Snowdrift game, defection against a cooperator and mutual cooperation represent the first- and second-highest payoffs, respectively. However, in contrast to the Prisoner's Dilemma, cooperation against a defector is the third-highest payoff, with mutual defection being the worst possible outcome. This reflects the fact that in some potentially cooperative interactions, the benefit provided by a cooperator accrues not only to its co-player, but also to itself (e.g., the production of enzymes for extracellular digestion [13]). If the co-player fails to cooperate, the cooperator is stuck with paying the entire cost to receive a benefit, but so long as the value of the benefit of cooperating exceeds its cost, it is still a better outcome than mutual defection [8].

Interestingly, and counter to the Prisoner's Dilemma, in the Snowdrift game, the best strategy against a cooperator is defection and the best strategy against a defector is cooperation. Thus, in large, well-mixed populations playing the Snowdrift game, there is a stable equilibrium composed of a mixture of cooperators and defectors, with their frequencies determined by the relative costs and benefits of cooperation [4,5,11]. (In the Prisoner's Dilemma, the stable equilibrium in large, well-mixed populations is the fixation of defectors at the expense of cooperators [5].)

Several mechanisms have been proposed to explain the existence of cooperation in the Prisoner's Dilemma; to a lesser extent, the effects of these mechanisms on the prospects of cooperators and defectors in the Snowdrift game have also been examined. These mechanisms, which rely on assortative interactions among cooperators, include kin selection [14], iterated interactions [15], reputational effects [16], recognition effects (a.k.a. 'green-beard' effects [17–22]), group selection [23], and network selection [11,24–28] (see recent reviews by Nowak [1,5] and Sherratt and Wilkinson [2]). The last of these, network selection, is generalised by evolutionary graph theory [6,29], in which individuals interact with only a small subset of the entire population. In turn, this occurs due to limited social contacts or localised spatial interactions. Certain effects of localised spatial interactions (i.e., 'spatial selection') are the focus of the current study.

Spatially local interactions are most typically studied using lattice models [30]. Individual cooperators and defectors are arrayed as lattice cells with $k = 3$, 4, or 6 nearest neighbours, corresponding to the three types of regular tessellations on a plane in the context of two-dimensional geometry (i.e., those composed of tiled equilateral triangles, squares, and regular hexagons, respectively), and corresponding to regular graphs with nodes of varying degree in the context of evolutionary graph theory. Although the geometric and graph-theoretical interpretations are equivalent, here we focus on the geometrical interpretation for consistency with most previous examinations of the effects of space on the evolution of cooperation. Thus, individuals situated at a given focal cell interact with all the other individuals whose cells share a border with this focal cell; in addition, these bordering cells compose the focal cell's local neighbourhood. Furthermore, the rate of strategy replacement is proportional to the difference in payoffs between individuals situated at bordering cells.

As an aside, note that $k = 8$ lattices are also sometimes considered in studies using lattice models. In this case, space is represented by a tiled-square lattice in which cells that share a common *corner* are considered neighbours, in addition to cells that share a common *border* (i.e., the 'Moore neighbourhood' [30]). However, these are not considered here for two main reasons: First, common-corner neighbours in tiled-square lattices have a centre-to-centre distance that is greater than that of common-border neighbours by a factor of $\sqrt{2}$; in two dimensions, it is not possible for all members of an entire population to have exactly $k = 8$ equally close nearest neighbours (geometrically, this is equivalent to the fact that it is not possible to create a regular tessellation using octagons). Second, common-corner neighbours have two neighbours in common, whereas common-border neighbours have four neighbours in common. The presence of two fundamentally different types of spatial interactions greatly complicates the analyses, and also seems rather arbitrary, given that such types are not commonly considered for the other lattice types. For these two reasons, we omitted the $k = 8$ case and stuck with $k = 3$, 4, or 6.

Spatially local interactions have contrasting effects in lattice models of the Prisoner's Dilemma and Snowdrift games [26]. In the Prisoner's Dilemma, local interactions allow cooperators to persist – at least when the cost–benefit ratio of cooperation is relatively low – because, by forming clusters, cooperators interact with other cooperators more than would be expected based on their relative abundance in the population alone (thereby skewing the effective payoffs associated with the different interaction outcomes [31]). In the Snowdrift game, local interactions can cause the frequency of cooperators to be greater or less than that of the mean-field predictions (with the latter outcome occurring over a wider range of cost–benefit