



Game theoretic treatments for the differentiation of functional roles in the transition to multicellularity



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HIGHLIGHTS

- We demonstrate the shortcoming of conventional “Dawesian” cooperative dilemmas.
- We define a new type of evolutionary game called division of labour games.
- We show that assortment is insufficient for cooperation to evolve in such cases.
- We show that there exist two increasing levels of fitness in such games.
- We argue that these models shed valuable light on important biological processes.

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ABSTRACT

Multicellular organisms are characterised by role specialisation, brought about by the epigenetic differentiation of their constituent parts. Conventional game theoretic studies of cooperation do not account for this division of labour, nor do they allow for the possibility of the plastic expression of phenotype. We address these issues by extending the notion of cooperative dilemmas to account for such interaction in which heterogeneous roles are advantageous and present an extended dynamical model of selection that allows for the possibility of conditional expression of phenotype. We use these models to investigate systematically when selection will favour an adaptive diversification of roles. We argue that such extensions to models and concepts are necessary to understand the origins of multicellularity and development.

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1. Introduction

The evolution of cooperation has been a central theme of research within evolutionary biology (Axelrod and Hamilton, 1981; Fletcher and Doebeli, 2009; Lehmann and Keller, 2006). In nearly all such formal studies cooperation is modelled by Dawesian dilemmas, most commonly the Prisoner's dilemma and closely related games (Doebeli and Hauert, 2005). A Dawesian dilemma (Dawes, 1980; Macy and Flache, 2002) is one which satisfies two conditions:

- Dawes I* There exists a single cooperative strategy whereby mean fitness is maximised if all individuals perform this action.
Dawes II There exists an individual incentive not to perform this action.

Hence, evolution in a freely mixed population will not lead to a cooperative state that maximises mean fitness.

The biological systems in which Dawesian dilemmas are usually applied have, in recent years, greatly expanded from the study of eusocial insects and social vertebrates to a vast number of different cases (Queller, 1997; Bourke, 2011). Of particular interest is the extension of the notion of cooperation to the origin of multicellularity and hence development (Buss, 1987; Maynard Smith and Szathmary, 1997; Michod and Herron, 2006; Grosberg and Strathmann, 2007). The cells of a multicellular organism are often colloquially described as cooperating with one another (Queller, 2000; Lehmann and Keller, 2006; Michod and Roze, 2001). However, the cells cannot be thought of as being engaged in a Dawesian cooperative dilemma as there is no one phenotype that can be considered as *the* cooperator. Instead the multicellular organism is characterised by having multiple complementary cell types (Bonner, 1993). This diversification of roles is an important detail that conventional studies of the evolution of cooperation do not adequately model. Whilst games such as the snow drift game

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are polymorphic at equilibrium, this does not represent a diversification of roles, as the two behaviours do not complement one another, but instead defectors simply exploit cooperators. Protomulticellular organisms, such as slime moulds (Strassmann et al., 2000) and volvocine algae (Michod, 2007), often have two distinct cell types; both of which are important for the function of the organism; thus no one type should be thought of as the cooperator. To avoid semantic confusion we re-label cooperate as A and defect as B. To reflect better the adaptive nature of role diversification we define a Division Of Labour (DOL) game to be any game that has the property of mean individual fitness being maximised by a polymorphic state. We call the state that maximises fitness the Socially Efficient State (SES).

In cooperative dilemmas freely mixed populations will not reach the SES. This, in general, will also be the case for DOL games. We thus retain the label of cooperative dilemmas in such cases; whilst not adhering to Dawes I. Structuring of interactions, and specifically positive assortment on cooperative phenotypes, is often claimed to be the central resolution to cooperative dilemmas (Eshel and Cavalli-Sforza, 1983; Fletcher and Zwick, 2006; Godfrey-Smith, 2008). However, in the limit, positive assortment of cooperators removes heterogeneity and thus cannot maximise fitness in a DOL game. Complete positive assortment can only ever lead to interaction between individuals of the same type, whereas fitness in DOL games is maximised if all interactions are between unlike types. This apparent paradox, between the need for heterogeneity of roles to gain from specialisation/complementary functions and homogeneity to resolve the cooperative dilemma can only be overcome if the individuals can express a phenotype conditionally upon their social environment (including, potentially, a phenotype conditioned on the phenotype of their parent (s)). This is so that individuals can have a positive assortment on genotype, i.e. relatedness, whilst simultaneously creating a negative assortment on phenotype. These are features of biological systems that conventional game theoretic models do not account for. They are, however, crucial for understanding the origins of development and multicellularity; in which the epigenetic determination of phenotype plays a key role (Lachmann and Sella, 2003; Jablonka and Lamb, 2006).

Stark (2010) studies *dilemmas of partial cooperation*, which are mathematically equivalent to DOL games, and concludes that partial levels of cooperation maximise fitness in certain types of dilemma. However, as we shall show, this mixture of strategies is not optimal if one takes into account the structuring of interactions, as fitness can be increased further if one allows for a complete negative assortment on phenotype. Furthermore, Stark concludes that an intermediate level of assortment will allow the population to reach the SES, which we show is not the case (see Section 3), as his argument does not account for how the SES is altered by assortment. Other authors (Neill, 2003; Browning and Colman, 2004; Tanimoto and Sagara, 2007) have analysed the *turn-taking* solution to DOL games. They conclude that if individuals alternate sequentially between strategies then the dilemma can be resolved. En route to multicellularity it may be the case that unicellular organisms employ life cycle stages that alternate between roles, but true multicellular organisms have cells that remain specialised for the entirety of their life, as the alternation of cell type is either costly or unfeasible (Michod, 2007). Therefore, we study solutions in which individual cells are constrained to stick to a single phenotype after development.

Previous studies have taken the evolution of specialisation and the evolution of cooperation as separate problems, the latter often modelled via cooperative dilemmas such as the prisoner's dilemma (Doebeli and Hauert, 2005; Fletcher and Doebeli, 2009; Traulsen and Nowak, 2006). These two problems have therefore previously been studied largely in isolation. This paper formulates

the issue of specialisation via a simple extension of existing cooperative dilemmas. We thereby relate the relatively understudied problem of specialisation, to a problem that has been studied extensively: cooperation.

A number of papers have looked at models in which individual components can potentially specialise in a number of set tasks and further investigate the conditions under which specialisation may occur. In particular both Gavrillets (2010) and Michod and Herron (2006) look at a model in which individual cells can specialise in one of two tasks relating to fecundity and viability, or alternatively remain as generalists. In these models the groups benefit from having both tasks performed together, but there is an inefficiency cost for individual cells to perform both. If the inefficiency is large enough then specialisation may evolve. Ispolatov et al. (2012) analyse a model in which group structure is not presupposed and is itself an endogenous parameter of evolution. This is embodied through a stickiness parameter. Again they conclude that specialisation and group structure can evolve in a certain region of parameter space, where here the important parameters are the cost of stickiness and the inefficiency cost for a single cell to perform both actions together. Willensdorfer (2009) presents a similar study, but formulates the model in terms of the fitness of a pre-existing group on which selection acts. The model is phrased in terms of three key parameters: the cost of somatic function, the cost of size (i.e. number of cells) and the benefit of group living. Whilst the authors derive some mathematical results about when specialisation will evolve, and to what extent, they do not address the problem of cooperation *per se* as selection at the colony level is presupposed. Rueffler et al. (2011) present a model, in which pre-existing colonies begin in an entirely undifferentiated state and then subsequently can evolve specialisation. As in other studies, whether or not this will happen depends upon the detailed relationship between a number of parameters involving the costs and benefits of specialisation. All of these studies are reviewed in more detail in Hanschen et al. (2015).

Whereas in all previous studies (summarised above) groups are essentially undifferentiated bags of cells performing one of two tasks, our model properly considers the internal structure of interactions. We thereby consider an additional step towards the evolution of new levels of individuality. In addition to group formation and specialisation we recognise that a more detailed and controlled structuring of interaction is necessary for the evolution of multicellularity. Furthermore, we claim that this can only come about through phenotypic plasticity and that mixed strategies that have no context-sensitive expression are insufficient.

In the following section we give a full categorisation of two-player symmetric DOL games and in Section 3 discuss two different notions of social efficiency and how these are effected by population structure. In Section 4 we briefly study some biological examples of DOL games from a number of different fields. In Section 5 we extend traditional models of evolutionary game theory in order to allow for the possibility of conditional expression of phenotype.

2. Categorisation of DOL games

We restrict our attention to symmetric two-player cooperative dilemmas, as all our key points can be understood from within this simple framework. All symmetric two-player cooperative dilemmas can be represented via a two-by-two payoff matrix, M , with four parameters: R, S, T, P (Rapoport and Guyer, 1967) (see Eq. (1)). M can be simplified due to the fact that payoff is relative. One can multiply all payoffs by a positive constant without qualitatively changing the features of the game (although this alters the speed of selection). Likewise, one may also add a constant to every payoff

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