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Evolutionary games of cooperation: Insights through integration of theory and data

Hannah M. Lewis [a,*], Alex J. Dumbrell [b]

[a] Department of Anthropology, University College London, 14 Taviton Street, London WC1H 0BW, UK
[b] School of Biological Sciences, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, UK

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ABSTRACT

Cooperation is central to the regulation of many ecological processes and the persistence of ecosystems and their associated functions. However, the evolution of cooperation amongst non-kin appears paradoxical. Games such as the prisoner's dilemma, snowdrift and stag hunt have been borrowed from game theory and used extensively to investigate cooperation. Advances in this area have been numerous and have been provided by both empirical and theoretical studies. We outline some of the common games used and review some of the major findings and recent advancements made in this area. We show a clear link between data and theory, and how this link has been key to our understanding of cooperation.

1. Introduction

The evolution of cooperation between unrelated individuals seems to be a paradox; how can something costly to the actor but beneficial to the recipient evolve and be maintained, especially when cheats could prosper? This problem is not limited to within-species interactions, but also extends to mutualisms where individuals of different species cooperate (West et al., 2007). Yet cooperation (intra- and inter-specific) underpins many of the processes regulating the fundamental ecological interactions supporting the world's ecosystems. For example, cooperation is central to various types of plant-microbe mutualisms (Kiers et al., 2003; Verbruggen et al., 2012), is vital to the major transitions in evolution (see Michod and Herron, 2006) and is critical to human sociality (Fehr and Fischbacher, 2004). Thus, it is of no surprise that it has been studied extensively using theoretical (reviewed in Hoeksema and Bruna (2000), Nowak (2006) and West et al. (2011)) and empirical approaches (e.g. Axelrod, 1980a,b; Kiers et al., 2003; Kümmerli et al., 2007; Verbruggen et al., 2012). Moreover, the major advances in our understanding of cooperation are due to the integration of these two approaches, with empirical evidence informing theory, theory in turn being tested and modified or extended in reference to data, and the cycle continuing. This interdisciplinary approach, merging theory and empirical data, where each discipline informs and directs the other, is increasingly highlighted as central to advancing ecological and evolutionary research (Codling and Dumbrell, 2012). Yet, few examples exist of research questions being consistently tackled in this manner and perhaps this approach to the study of cooperation can provide a philosophical model which other researchers may follow?

Nowhere is this integrative approach more evident than in the use of games such as the prisoner's dilemma borrowed from game theory, which have been embraced by both theoreticians and empiricists as we explore in this review. Game theory was first applied to the evolution of animal conflict, an idea associated with cooperation, by Maynard Smith and Price (1973), but games investigating the cooperative nature of human behaviour had already been played with human subjects for decades by this point (reviewed in Rapoport and Orwant, 1962). Evolutionary games are now widely used in studying evolution of behaviour such as signalling in animals (e.g. Lachmann et al., 2001; Maynard Smith, 1979) including human language (e.g. Lachmann et al., 2001; Nowak et al., 1999), and sex ratio evolution (e.g. Abe et al., 2003; Hamilton, 1967). However, this present review is limited to the application of evolutionary games and game theory to the evolution and maintenance of cooperation and mutualisms. This is because their use in this area has been prolific and productive, offering a clear example of the way theory and empirical data can, and should be used together to better understand natural systems.

* Corresponding author. Tel.: +44 20 7679 8645.
E-mail addresses: h.lewis@ucl.ac.uk, hannah.m.lewis.evolution@gmail.com (H.M. Lewis), adumbrell@essex.ac.uk (A.J. Dumbrell).

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We begin by describing a commonly used set of evolutionary games and summarise some of the major discoveries for which they are responsible. As these games continue to be popular tools we try to focus on recent advances, and pay particular attention to the tangible link between theory and data that these games offer and illustrate.

This review is part of a special issue of Ecological Complexity associated with the Mathematical and Theoretical Ecology (MATE) 2011 conference, which focussed on the link between theory and data in ecological/biological research. We believe this philosophy is articulated throughout the evolutionary games literature and we will explore how this has been achieved and what lessons can be learnt from this approach in this article.

2. Evolutionary games

2.1. An overview

In evolutionary game theory, a game is an interaction between two or more individuals (the "players") each with a strategy where the payoff of playing that strategy also depends on the strategy of the other player(s) (Nowak and Sigmund, 2004). Evolutionary game theory considers how the frequencies of these strategies will change over time when the fitness of each strategy (as measured by the payoffs received) depends on the frequencies of the strategies within the population (Maynard Smith, 1982). With this basis, the long term population of strategies can be determined through consideration of mutual invasibility of strategies (e.g. Axelrod and Hamilton, 1981), through considering the rate of change of the frequency of a strategy as a differential equation (e.g. Roca et al., 2009; Santos et al., 2012), through simulations (e.g. Nowak and May, 1992) or even through simulating learning as individuals change their strategies within their lifetimes (e.g. Sandholm and Crites, 1996). When studying the evolution of cooperation the term "strategy" refers to the particular behaviour of interest i.e. "cooperate" (C) and "defect" (D) (or "conventional" and "dangerous" tactics in the evolution of conflict; see Maynard Smith and Price, 1973), although evolutionary games have been used much more widely looking at the evolution of phenotypes (see Maynard Smith, 1982) or even genotypes (e.g. Huang et al., 2012). When being used in relation to mutualisms the term "cooperate" is sometimes replaced with a more biologically plausible term such as "invest" (I), and in models of cooperation and mutualism alike, terms such as "generous" and "selfish" are often used to describe the strategies (e.g. Bergstrom and Lachmann, 2003; Gokhale and Traulsen, 2012). In this review, for simplicity we predominantly use "C" and "D" to represent the strategies, even when discussing mutualisms although we mean them to apply more generally.

When considering humans, the behaviours associated with "cooperate" and "defect" are intuitively obvious, which is perhaps one of the reasons that these games have proved so popular. For example, participation in hunting is to cooperate, while free riding by sharing the spoils of the hunt without paying the associated costs is to defect or cheat (Alvard, 2001). In economic games with human participants, C can represent the strategy of investing in a public good while D is to enjoy the public good without contributing (Archetti, 2009). Such ideas can also be applied to animals quite easily (Dugatkin, 1997). Initially it might be more difficult to imagine plants playing these "games", but there are many examples of plant interactions that can be, and have been considered in this way. In a leguminous plant-*Rhizobia* interaction the microbe's strategy could be the amount of nitrogen to fix, while the plant's strategy is how much carbon to provide; for example, microbes that receive carbon but return little or no nitrogen can be considered as playing defect (Kiers et al., 2006) and some plants can respond to such cheating by cutting off oxygen supply to root nodules (Kiers et al., 2003). Another example is an interaction between plants and ants, where ants provide protection against herbivory and plants provide housing in the form of stem swellings known as domatia (Edwards et al., 2006). Ant colonies that defect do not patrol (and therefore offer little or no protection for the plant) and it has been shown that some plants can adjust their strategy in response to cheating ants through lack of growth of, or even mortality of domatia (Edwards et al., 2006) or through growth of domatia entrances that only permit certain cooperative ant species (Brouat et al., 2001). This is not always the case, for example epiphytic bird's nest ferns (*Asplenium* spp.) do not select for more cooperative ant species, instead the protection offered through housing is a non-excludable public good open to cheats (Fayle et al., 2012).

A general framework for describing two-person (or two-species) games can be given in the form of a payoff matrix. The (i,j)th entry of the matrix gives the payoff received (after subtracting costs associated with playing the strategy) by the focal individual who plays strategy i (row i) against their fellow player playing strategy j (column j). The payoff matrix in its general form is given by

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

where R is the payoff when both players cooperate (C, C) (the reward for cooperation), T is the payoff to an individual who defects while their fellow player cooperates (D, C) (the temptation to defect), S is the payoff for a cooperating player against a defecting player (C, D) (the payoff for being a sucker), and P is the payoff received by both players if both players play defect (D, D) (the punishment for mutual defection). Explicitly, playing cooperate incurs a cost c, which for example represents the cost of a plant giving up carbon (that could otherwise be used for growth) to *Rhizobia*, and defect costs d, which is often assumed to be zero, for example it represents *Rhizobia* contributing nothing to the plant (see Axelrod and Hamilton, 1981). If both players cooperate then they both receive x, if only one cooperates they both receive y and if both defect then they receive z. Hence, $R = x-c$, $S = y-c$, $T = y-d$ and $P = z-d$. The above matrix describes symmetric payoffs (and costs and returns), but there is no reason to restrict the games to have this structure. This is particularly important in the study of mutualisms as it is unlikely that the two-species will experience the costs and benefits in the same way. To represent two species interacting, the scenario can be extended to two payoff matrices, one for each species (e.g. Gokhale and Traulsen, 2012).

The nature of the evolutionary game depends on the sizes of the payoffs in relation to each other, as does the long-term behaviour of the players e.g. if all will cooperate or defect, or if cooperators and defectors will coexist. Different rankings of the payoffs give rise to different outcomes and there are three particularly famous formats that these games can take. We outline the most basic form that these games take in Sections 2.2–2.4 along with suggested biological examples of when these "games" take place. The very simple games are motivated by simple scenarios that humans might face, but these toy models result in interesting behaviours and clearly apply more widely.

2.2. Prisoner's dilemma

The first of the games we describe is the Prisoner's dilemma (PD), which is by far the most frequently used game in both theoretical and empirical investigations into cooperation between rational or selfish individuals (Doebeli and Hauert, 2005; Nowak