



# Coaction versus reciprocity in continuous-time models of cooperation



G. Sander van Doorn<sup>a,b,\*</sup>, Thomas Riebli<sup>a</sup>, Michael Taborsky<sup>a,1</sup>

<sup>a</sup> Institute of Ecology and Evolution, University of Bern, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland

<sup>b</sup> Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

## HIGHLIGHTS

- Coordination and information exchange are prominent in animal social interactions.
- We study how these features affect the evolution of cooperation.
- The ability of players to respond to each other in real time supports cooperation.
- Delays in information exchange (inherent to reciprocal altruism) favour selfishness.
- Cooperative coaction therefore evolves more readily than reciprocal cooperation.

## ARTICLE INFO

### Article history:

Received 2 December 2013

Received in revised form

3 March 2014

Accepted 11 March 2014

Available online 12 April 2014

### Keywords:

Cooperative coordination

Reciprocal altruism

Information transfer

Social dilemmas

Evolutionary game theory

## ABSTRACT

Cooperating animals frequently show closely coordinated behaviours organized by a continuous flow of information between interacting partners. Such real-time coaction is not captured by the iterated prisoner's dilemma and other discrete-time reciprocal cooperation games, which inherently feature a delay in information exchange. Here, we study the evolution of cooperation when individuals can dynamically respond to each other's actions. We develop continuous-time analogues of iterated-game models and describe their dynamics in terms of two variables, the propensity of individuals to initiate cooperation (altruism) and their tendency to mirror their partner's actions (coordination). These components of cooperation stabilize at an evolutionary equilibrium or show oscillations, depending on the chosen payoff parameters. Unlike reciprocal altruism, cooperation by coaction does not require that those willing to initiate cooperation pay in advance for uncertain future benefits. Correspondingly, we show that introducing a delay to information transfer between players is equivalent to increasing the cost of cooperation. Cooperative coaction can therefore evolve much more easily than reciprocal cooperation. When delays entirely prevent coordination, we recover results from the discrete-time alternating prisoner's dilemma, indicating that coaction and reciprocity are connected by a continuum of opportunities for real-time information exchange.

© 2014 Elsevier Ltd. All rights reserved.

## 1. Introduction

The iterated prisoner's dilemma (IPD) (Axelrod and Hamilton, 1981) is the most frequently used game-theoretical paradigm to study the evolution of cooperation among unrelated individuals. It is fundamental to theories of reciprocal altruism based on direct (Trivers, 1971; Axelrod and Hamilton, 1981), indirect (Nowak and Sigmund, 1998) and generalized reciprocity (Pfeiffer et al., 2005).

Yet, among biologists interested in the evolution of animal social behaviour, dissatisfaction with the IPD as a theoretical framework for studying cooperation has grown (Clutton-Brock, 2009), and several reviews have questioned its empirical relevance (Connor, 1995; Hammerstein, 2003; Noë, 2006; Raihani and Bshary, 2011).

One aspect of the IPD that has attracted much criticism is that players are assumed to decide on their actions independently of each other, without having access to information about the choice being made in the same round by the other player (Noë, 2006; Clutton-Brock, 2009). Though natural in the context of the discrete time structure of the IPD, this assumption is problematic for several reasons. First, the lack of information exchange between players can be exploited, posing a danger to the maintenance of cooperation. Second, establishing reciprocal exchange in the IPD is difficult (Stephens et al., 2002), because it requires players to pay in advance for an uncertain future benefit. In fact, all animals tested so far (including humans)

\* Corresponding author at: Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands. Tel.: +31 50 3638097; fax: +31 50 3635205.

E-mail addresses: [g.s.van.doorn@rug.nl](mailto:g.s.van.doorn@rug.nl) (G.S. van Doorn), [thomas.riebli@iee.unibe.ch](mailto:thomas.riebli@iee.unibe.ch) (T. Riebli), [michael.taborsky@iee.unibe.ch](mailto:michael.taborsky@iee.unibe.ch) (M. Taborsky).

<sup>1</sup> Tel.: +41 31 631 9156.

show temporal discounting, which means that they devalue future relative to immediate rewards (Chung and Herrnstein, 1967; Kalenscher and Pennartz, 2008). Moreover, when behavioural decisions are separated in time from the feedback about the consequences of those decisions, the effectiveness of simple associative learning mechanisms will be undermined, forcing players to rely on some sort of memory of past interactions to infer the optimal choice in the current round (Brosnan et al., 2010). Only species with highly advanced cognitive abilities are considered capable of solving decision problems of this kind (Stevens et al., 2005). Still, cooperation is observed in some organisms clearly lacking such abilities (e.g., Milinski et al., 1990; Rutte and Taborsky, 2008; Krams et al., 2008), suggesting that cooperative interactions between animals differ in important aspects from the IPD.

Tellingly, one of the main challenges in designing empirical tests of the IPD is to restrict the flow of information between players such that they make their decisions independently of each other (Noë, 2006). Successful tests have been performed in humans (Milinski and Wedekind, 1998; Gintis et al., 2003) and other animal species (Clements and Stephens 1995; Hauser et al., 2003; Rutte and Taborsky, 2008), but not without forcing subjects to interact under highly artificial conditions. In contrast, natural cooperative behaviours, such as predator inspection (Milinski et al., 1990; Pitcher, 1992), cooperative hunting (Boesch and Boesch, 1989) or joint territory defence (Krams et al., 2008), typically rely on social information exchange. Individuals may observe the current actions of their partners and respond immediately to changes in their behaviour, or they may actively communicate with each other while they establish or maintain cooperation. As a result, cooperation between animals generally involves coaction or more advanced forms of behavioural coordination (Boesch and Boesch, 1989; Schuster, 2002). ‘Acting together’ has in fact been proposed as a simple operational definition of cooperation (Taborsky, 2007) and it has been emphasized that the ‘achievement [of cooperation] requires collective action’ (Dugatkin, 1997, p. 14). In humans, it has been shown experimentally that synchronous action can foster cooperation, partly because it may help to mitigate the free-rider problem (Wiltermuth and Heath, 2009).

The implications of social information exchange and behavioural coordination for the evolution of cooperation are not well understood, because in biology few theoretical models have strayed from the elementary game structure of the IPD. In the present paper, we therefore analyse a continuous-time model of cooperation that allows individuals to respond in real time to the behaviour of their partner. In this model, pairs of players are able to establish cooperation by coordinating current behaviour, as opposed to reciprocating favours that are separated in time. Previous work on dynamic games in economics suggests that the time-structure of interactions is of critical importance for the establishment of cooperation between human players in a public-goods game (e.g., Marx and Matthews, 2000; Duffy et al., 2007). The reason is that information exchange allows for smaller history-contingent contributions to the public good, enabling each of the players to try the other’s good faith for a small price (Schelling, 1960). We show here that this effect also has implications for the evolution of cooperation. In fact, our analysis indicates that restricting the flow of information between players is equivalent to increasing the cost of cooperation. The exchange of social information, which accompanies natural cooperative interactions between animals, therefore creates conditions that are much more favourable for the evolution of cooperation than one would predict from theory based on the IPD.

**2. The model**

The distinguishing feature of our model is that individuals can switch between actions in continuous time rather than in discrete

**Table 1**  
Payoff parameters and model variants.

Payoff to focal	Partner plays	D	D	C
Focal plays		D	P=0	T=b
		C	S=-c	R=b-c+h
Stag-hunt game <sup>a</sup>	$b-c+h > b > 0 > -c$	$\Rightarrow$	$\begin{cases} k_D > 0 \\ k_C < 0 \end{cases}$	
Snowdrift game <sup>b</sup>	$b > b-c+h > -c > 0$	$\Rightarrow$	$\begin{cases} k_C - 1 < k_D < 0 \\ 0 < k_C < 1 \end{cases}$	
Prisoner’s dilemma <sup>c</sup>	$b > b-c+h > 0 > -c$	$\Rightarrow$	$\begin{cases} k_D > 0 \\ 0 < k_C < 1 \end{cases}$	

<sup>a</sup> In the stag-hunt game, players prefer mutual defection over unilateral cooperation, disfavoured the initial establishment of cooperation. However, once cooperation has been established between a pair of players, neither has an incentive to cheat.

<sup>b</sup> In the snowdrift game (also known as the hawk-dove game or the game of chicken), unilateral cooperation is preferred over mutual defection, but players achieve the highest payoff if they defect when their partner cooperates.

<sup>c</sup> The prisoner’s dilemma combines the social dilemmas of the snowdrift and stag-hunt game. Unilateral defection is preferred over mutual cooperation, and mutual defection is preferred over unilateral cooperation, such that D is the dominant strategy in a one-shot game.

<sup>d</sup> The dimensionless parameter combinations  $k_D=c/b$  and  $k_C=(c-h)/b$  measure the relative cost of playing C when the partner defects or cooperates, respectively. These parameters appear in Figs. 2, 3, 5 and S2.

rounds. Other than that, we closely follow the assumptions of standard iterated cooperation games (Macy and Flache, 2002). The results presented here focus almost exclusively on the prisoner’s dilemma game, but our analysis extends to the strategically different situations embodied by the snowdrift and the stag-hunt game (Table 1). Each player interacts with the same partner over an extended period of time, allowing for repeated interactions. During this time, the momentary rate of increase of a player’s payoff is dependent on its own action and that of its partner. Players can choose between two actions, labelled ‘cooperate’ (C) and ‘defect’ (D), such that a pair of two players *i* and *j* can be in one of four discrete states at any moment in time. The state of the pair will be denoted by a combination of two letters, DD, DC, CD or CC, indicating the action currently played by the focal individual *i*, followed by the action currently played by its partner, individual *j*.

**2.1. Pair-state dynamics**

Each player’s strategy is specified by four parameters that determine the rate at which the individual switches between cooperation and defection, depending on the current state of the pair. The four switching rates are assumed to be bounded away from zero by a small constant  $0 < \epsilon \ll 1$  (Selten, 1975). We use  $\sigma_i=(p_i, q_i, r_i, s_i)$  and  $\sigma_j=(p_j, q_j, r_j, s_j)$  to denote the strategies of individual *i* and *j*, respectively, and associate the strategic parameters with transitions between the states of the pair in the following way:

$$\begin{aligned}
 i \text{ changes state : } & \quad DD \xrightleftharpoons[q_i]{p_i} CD \quad DC \xrightleftharpoons[s_i]{r_i} CC \\
 j \text{ changes state : } & \quad DD \xrightleftharpoons[q_j]{p_j} DC \quad CD \xrightleftharpoons[s_j]{r_j} CC
 \end{aligned} \tag{1}$$

From here it is straightforward to derive ordinary differential equations for the probability distribution of pairs over the different states. For example,  $f_{CD}(t)$ , the probability of finding a pair in state CD at time *t*, changes through time according to the equation  $(d/dt) f_{CD}(t) = p_i f_{DD}(t) + s_j f_{CC}(t) - (q_i + r_j) f_{CD}(t)$ . Similar equations for the other pair states give rise to a system of linear ordinary

Download English Version:

<https://daneshyari.com/en/article/6370398>

Download Persian Version:

<https://daneshyari.com/article/6370398>

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