Animal Behaviour 122 (2016) 217–225

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Evolutionary stagnation of reciprocators

Shun Kurokawa*

Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto, Japan

A R T I C L E I N F O

Article history:
Received 29 December 2015
Initial acceptance 25 February 2016
Final acceptance 2 August 2016
Available online 13 November 2016
MS. number: 16-00001R

Keywords:
Clutton-Brock (2009)
cooperation
information structure
optimism
reciprocity
repeated prisoner's dilemma

Reciprocity is a leading potential explanatory mechanism for the evolution of cooperation between nonkin. It relies upon individuals possessing information about their opponents' behaviour, but in reality this information is probably often imperfect. Different possible strategies for dealing with imperfect information include optimism (cooperate when information is unavailable) or pessimism (defect when information is unavailable). How do the strategies individuals use to cope with imperfect information when deciding whether to cooperate or defect influence the stability of reciprocity? Our previous work (Kurokawa, 2016, *Letters on Evolutionary Behavioral Science*, 7, 14–16) showed that the conditions under which reciprocity evolves are unaffected by whether reciprocators are optimistic or pessimistic. However, this argument is based on an evolutionarily stable strategy (ESS) analysis against defectors and does not consider the situation where there are heterogeneous reciprocators with different levels of optimism. In this study, by conducting an ESS analysis, I found that optimism evolves when the cost-to-benefit ratio (i.e. the ratio of the cost of cooperating to the benefit of being cooperated with) is low, whereas pessimism evolves when the cost-to-benefit ratio is high, in contrast to the results of the previous study. I also considered the case where unconditional cooperators and defectors exist and found that optimistic reciprocators are invaded by pessimistic reciprocators when the cost-to-benefit ratio is high and by unconditional cooperators when the cost-to-benefit ratio is low, whereas pessimistic reciprocators are invaded by optimistic reciprocators when the cost-to-benefit ratio is low and unconditional defectors when the cost-to-benefit ratio is high. Thus, both optimistic and pessimistic reciprocators are subject to invasion whether the cost-to-benefit ratio is high or low, suggesting that reciprocity is evolutionarily unstable. This result is consistent with a previous empirical study (Clutton-Brock, 2009, *Nature*, 462, 51–57), which reported that firm evidence of reciprocity in animal societies is rare.

Understanding the evolution and maintenance of cooperation is a major topic in evolutionary biology (Hamilton, 1964; Nowak, 2006, 2012; Trivers, 1971). While most of the cooperative behaviour that occurs among animals is between kin, cooperation between nonkin also occurs (Foster, Wenseleers, & Ratnieks, 2006; Frank, 1998; Grafen, 1985; Hamilton, 1964; West, Pen, & Griffin, 2002). The concept of reciprocity (be it direct or indirect) has been essential for explaining why animals sometimes behave cooperatively towards unrelated individuals (Alexander, 1987; Axelrod & Hamilton, 1981; Brembs, 1996; Bshary, 2002; Bshary & Grutter, 2006; Dugatkin, 2002; Fischer, 1988; Hart & Hart, 1992; Kurokawa, 2016a, 2016b; Kurokawa & Ihara, 2009; Kurokawa, Wakano, & Ihara, 2010; Milinski, 1990; Nowak & Sigmund, 1998; Packer, 1977; Pepper & Smuts, 2002; Sella, Premoli, & Turri, 1997; Takezawa & Price, 2010; Trivers, 1971; Wilkinson, 1984). Reciprocity occurs when an actor changes its behaviour towards an opponent based upon information about the opponent's reputation or past behaviour.

Information about an opponent's reputation or past behaviour may be imperfect, either because an actor cannot observe the opponent's behaviour at all times or because an actor has limited cognitive capacity to remember the behaviour of all possible opponents (Akcay, Meirowitz, Ramsay, & Levin, 2012; Bowles & Gintis, 2011; Calvert, 1993; Chong, Camerer, & Ho, 2006; Kurokawa, 2016a, 2016b; Ohtsuki, Iwasa, & Nowak, 2009; Uchida, 2010). For example, gossip is unlikely to be sufficient to provide perfect information to indirect reciprocators unless population size is very small (Brandt & Sigmund, 2005; Ohtsuki et al., 2009). How should actors behave when they have imperfect information about opponents? One

* Correspondence: S. Kurokawa, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan.
E-mail address: kurokawa@kais.kyoto-u.ac.jp.

http://dx.doi.org/10.1016/j.anbehav.2016.09.014
0003-3472/

possible strategy is to cooperate in the absence of information, while another is to defect when information is unavailable. Following Kurokawa (2016a), I call the former ‘optimism’ and the latter ‘pessimism’. Which of these strategies is more conducive to the evolution of reciprocity? Note that some authors call cooperating in the absence of information about the opponent ‘trustful’ and defecting in the absence of information about the opponent ‘suspicious’ (e.g. Nakamura & Masuda, 2011; Panchanathan & Boyd, 2003).

I recently investigated responses to imperfect information under direct reciprocity (Kurokawa, 2016a). When considering direct reciprocity, players have several options to choose from when relevant information is unavailable, including (1) cooperating, (2) defecting, (3) cooperating to some extent (e.g. Frean, 1996; Takezawa & Price, 2010), (4) believing that the opponent's behaviour is unchanged (a type of strong belief), (5) clarifying information and (6) stopping all interactions (Enquist & Leimar, 1993). In a previous study, Kurokawa (2016a) assumed that players only had options (1) and (2) available to them and investigated whether cooperation was more likely to evolve when reciprocators cooperate (i.e. are optimistic) or defect (i.e. are pessimistic) by examining the strategy of tit-for-tat (TFT), which involves a number of forms of optimism and unconditional defection (ALLD). In TFT, the actor cooperates when the opponent cooperates and defects when the opponent defects, whereas in ALLD, the actor defects regardless of how the opponent behaves. Using an evolutionarily stable strategy (ESS) analysis, Kurokawa (2016a) revealed that the condition under which reciprocity evolves remains unaffected whether reciprocators cooperate (i.e. TFT is optimistic) or defect (i.e. TFT is pessimistic) when information is unavailable, suggesting that optimism does not influence the evolution of TFT.

However, Kurokawa (2016a) did not consider the situation where both optimistic TFT and pessimistic TFT exist at the same time. When considering indirect reciprocity, where a donor, a recipient and an observer are present (Brandt & Sigmund, 2005, 2006; Nakamura & Masuda, 2011; Panchanathan & Boyd, 2003) and the donor has imperfect information, it was found that optimistic reciprocators are likely to evolve when the cost-to-benefit ratio is low, whereas pessimistic reciprocators are likely to evolve when the cost-to-benefit ratio is high (Panchanathan & Boyd, 2003; also see Nakamura and Masuda (2011) for the case where both the donor and the observer have imperfect information). I consider it reasonable to assume that there are interactions among reciprocators with different levels of optimism not only in the context of indirect reciprocity but also in the case of direct reciprocity.

First, let us consider the case where optimistic reciprocators invade a population of pessimistic reciprocators. In this case, cooperation between an optimistic reciprocator and a pessimistic reciprocator will last longer than cooperation between two pessimistic reciprocators, and so there is expected to be more individuals cooperating with and being cooperated with by the optimistic intruder than by the resident pessimists. Therefore, when the cost-to-benefit ratio (i.e. the ratio of the cost of cooperating to the benefit of being cooperated with) is low, invasion by optimistic reciprocators may occur, whereas such an invasion would not be expected when the cost-to-benefit ratio is high.

Second, let us consider the case where pessimistic reciprocators invade a population of optimistic reciprocators. In this case, cooperation between a pessimistic reciprocator and an optimistic reciprocator will last less time than cooperation between two optimistic reciprocators, and so there will be fewer individuals cooperating with and being cooperated with by the pessimistic intruder than by the resident optimists. Thus, when the cost-to-benefit ratio is high, invasion by pessimistic reciprocators may occur, but such an invasion would not be expected when the cost-to-benefit ratio is low, as shown by Panchanathan and Boyd (2003) in the context of indirect reciprocity.

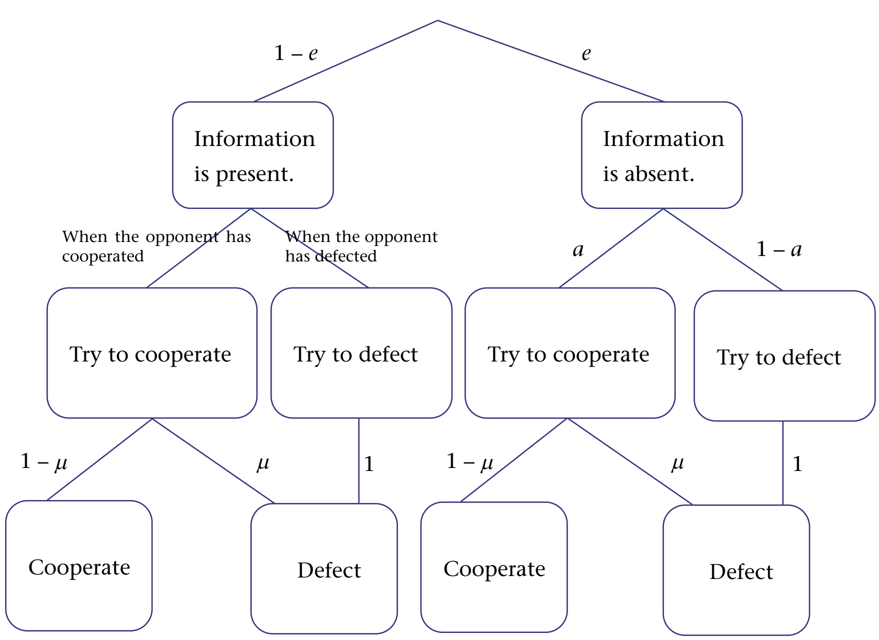

Figure 1. Explanation of the behaviour of the direct reciprocator when information is sometimes absent. Information about whether the player cooperates or defects is transmitted to the opponent with a probability of $1 - e$, while information about whether the player cooperates or defects is not transmitted to the opponent with a probability of e. In the case where the player does not receive information about whether the opponent cooperates or defects and the player is a reciprocator, the player attempts to cooperate with a probability of a and defects with a probability of $1 - a$. Those who attempt to cooperate with the opponent fail to do so with a probability of μ. The range of each parameter is $0 \le e \le 1$, $0 \le a \le 1$ and $0 < \mu < 1$.