

Partner choice creates competitive altruism in humans

Pat Barclay^{1,*} and Robb Willer²

¹Department of Neurobiology & Behaviour, Cornell University, Ithaca, NY 14853, USA ²Department of Sociology, University of California, Berkeley, CA 94720, USA

Reciprocal altruism has been the backbone of research on the evolution of altruistic behaviour towards non-kin, but recent research has begun to apply costly signalling theory to this problem. In addition to signalling resources or abilities, public generosity could function as a costly signal of cooperative intent, benefiting altruists in terms of (i) better access to cooperative relationships and (ii) greater cooperation within those relationships. When future interaction partners can choose with whom they wish to interact, this could lead to competition to be more generous than others. Little empirical work has tested for the possible existence of this 'competitive altruism'. Using a cooperative monetary game with and without opportunities for partner choice and signalling cooperative intent, we show here that people actively compete to be more generous than others when they can benefit from being chosen for cooperative partnerships, and the most generous people are correspondingly chosen more often as cooperative partners. We also found evidence for increased scepticism of altruistic signals when the potential reputational benefits for dishonest signalling were high. Thus, this work supports the hypothesis that public generosity can be a signal of cooperative intent, which people sometimes 'fake' when conditions permit it.

Keywords: competitive altruism; reputation; trust; cooperation; costly signalling

1. INTRODUCTION

Reciprocal altruism (Trivers 1971; Alexander 1987) has been a backbone for research on the evolution of altruistic behaviour towards non-kin, but recent research has also begun to apply costly signalling theory to this problem (e.g. Zahavi & Zahavi 1997; Bliege Bird et al. 2001; Gintis et al. 2001; Hawkes & Bliege Bird 2002; Lotem et al. 2003). In addition to signalling resources (e.g. Boone 1998; Harbaugh 1998) or abilities (Smith et al. 2003; Smith 2004), public generosity could function as a costly signal of cooperative intent (Bolle 2001; Gintis et al. 2001; McNamara & Houston 2002; Smith 2003; Smith & Bliege Bird 2005), though this has received less theoretical and empirical work. Such a signal could benefit altruists in terms of (i) better access to cooperative relationships and (ii) greater cooperation within those relationships.

Observers benefit from attending to such signals if there is some consistency in individual tendencies towards cooperation (and see Van Lange et al. 1997; Clark 2002; Sefton et al. 2002; Kurzban & Houser 2005), because doing so allows observers to display more trust towards trustworthy individuals and choose more cooperative partners. In behavioural experiments, people usually do not have a choice of partners, but they typically respond to cooperation by trusting and/or cooperating more with highly cooperative individuals than with less cooperative individuals (Albert et al. 2002; Milinski et al. 2002a,b; Wedekind & Braithewaite 2002; Barclay 2004, 2006).

Outside the laboratory, partner preferences and time constraints typically inhibit equal rates of interaction between group members, the result being that people (and other social animals) interact with some individuals

more than others. If more cooperative individuals are preferable as cooperative partners owing to the benefits they confer upon partners, then market forces (Noë & Hammerstein 1995) can create competition to be more altruistic than others in order to interact most often with the best partners (Roberts 1998), and this competition can increase generosity above the level that results from people simply attempting to appear cooperative. Such competition for reputational benefits would be most likely to occur when the highest ranked cooperators receive disproportionate benefits. High variance in reputational benefits could result in high investment in competitive altruism and signalling of altruism, just as high variance in male reproductive success selects for increased investment in courtship signals and male-male competition in polygynous species (Daly & Wilson 1983). However, just as strong sexual selection on males can result in alternative mating strategies such as territoriality versus sneaking (Daly & Wilson 1983), strong selection for cooperative partners could result in individuals adopting alternative cooperative strategies, such as competitive altruism versus outright defection which saves the cost of altruism.

Past research suggests that individuals are more generous when observed (e.g. Milinski et al. 2002a; Barclay 2004; Hardy & Van Vugt 2006), but this type of display is not necessarily competitive, in that individuals may strive for a 'good' reputation without actually competing for a better reputation than others. Competitive altruism occurs when people go beyond attempting to merely appear generous and instead actively try to be more altruistic than one another, and this has yet to be unambiguously demonstrated. Barclay (2004) found that cooperation dropped less in the final round of an experimental cooperative game when reputational benefits

^{*} Author for correspondence (pjb46@cornell.edu).

Table 1. Three experimental conditions and incentives to give money in each. (Each participant experienced all three conditions, with the order of conditions counterbalanced across sessions.)

	player C has knowledge of the contributions of players A and B (i.e. is there a potential incentive to generate a reputation for generosity?)	method of determining player C's partner in part 2 (i.e. is there a potential incentive to compete by giving more in order to be chosen?)
random/anonymous condition (control)	no	randomly selected (competition absent)
random/knowledge condition choice/knowledge condition	yes ves	randomly selected (competition absent) player C chooses (competition present)

were a limited resource that only the most cooperative group members were likely to receive. However, this is best seen as merely suggestive, because it only surfaced in the last round of a five-round cooperative game. Recently, Hardy & Van Vugt (2006) have claimed to show competitive altruism by showing that people are more generous when observed and also rate group members who display generosity in cooperative tasks as having higher status than those who display relatively less generosity, but contrary to their claim, this does not provide evidence for the existence of competitive altruism because there is no evidence that their participants actually competed to be more generous than each other.

The present study sought to provide the first firm experimental evidence for competitive altruism in humans. Participants did a dvadic cooperative task similar to a 'Prisoner's Dilemma' and were later randomly paired with (or chosen as) cooperative partners by other participants who did (or did not) know their decisions in the earlier cooperative task. By contrasting the amounts given by players when their contributions are known to a future interaction partner versus when they are unknown, we can test whether participants give more as a way of signalling cooperativeness to potential partners (e.g. Barclay 2004; Hardy & Van Vugt 2006). Further, by contrasting the amounts given when partners are chosen versus randomly selected, we can test whether participants give more to increase the likelihood of being chosen above and beyond what they would give to 'merely' signal cooperative intent. The former contrast tests for altruistic signalling, whereas the latter tests for competitive altruism. We predicted that donations would be lowest when there were no possible reputational benefits and highest when partnerships were chosen. Furthermore, we predicted that generous players would benefit from their altruistic behaviour by being chosen more often as partners than less generous players. However, as the reputational benefits for altruism increase, the incentives for sending dishonest signals of cooperative intent (i.e. appearing cooperative in order to later defect) also increase (Barclay 2004). Given this, we also predicted that others would be more sceptical of altruism (i.e. trust it less as a signal of cooperative intent) when partnerships are chosen, owing to the potential benefit for dishonestly signalling one's cooperative intent.

2. MATERIAL AND METHODS

(a) Participants and anonymity

Participants were 31 females (average age $=20.5\pm s.d.$ 1.3 years) and 23 males (average age $=21.0\pm s.d.$ 2.8 years) of various ethnic backgrounds from Cornell University, who

were recruited from previous experiments and from an internet site for experimental research. They received \$7 plus their earnings in the cooperative task, which averaged an additional \$7.43 (s.d. \$2.32). Participants were seated in booths and separated by curtains to prevent visual contact during the decision-making component of the experiment, and they received private code names (e.g. A1, B2, etc.), such that they could earn a reputation in certain conditions of the study without anyone knowing their actual identities. All decisions were collected via individual envelopes, and the results of past pairings (and earnings at the end of the experiment) were returned in private envelopes. We used two experimenters to make all decisions strictly anonymous: one experimenter knew the participants' code names but did not know their decisions, whereas the other experimenter knew the decisions but not who had which code name.

(b) Cooperative task

The experiment used a continuous Prisoner's Dilemma (Roberts & Renwick 2003) to measure cooperative behaviour. Each member of a pair of participants was given an endowment of 10 lab dollars and both were simultaneously given the option of sending any number of these dollars to their partner and the amounts sent were doubled. All lab dollars were converted to US dollars at the end of the experiment at the rate of 15 cents to the lab dollar.

(c) Experimental design and conditions

Within each session of nine people, participants were placed into one of three groups of three people. In part 1 of the experiment, two participants within each group ('A' and 'B') completed a one-shot continuous Prisoner's Dilemma with one another while the third member ('C') sat out and received no money. In part 2, that third member was either (i) randomly paired with one of them and not informed about either one's donations ('random/anonymous condition'), (ii) randomly paired with one and informed about their donations ('random/knowledge condition'), or (iii) asked to choose one of them after being informed about their donations ('choice/knowledge condition'). That third member (C) then completed a one-shot continuous Prisoner's Dilemma with one of the first two players (A or B), while the other sat out and received no money. This structure was common knowledge, so the first two members of each group (A and B) could potentially benefit from a good reputation (in part 1) in the latter two conditions, but not in the first condition. Table 1 contrasts these conditions.

There are substantial individual differences in cooperativeness (e.g. Van Lange *et al.* 1997; Kurzban & Houser 2005), and we factored this out using a within-subjects design: each participant went through all three experimental

conditions, each with a completely different group of three players. In other words, each participant was a member of three different groups: one group for each experimental condition. Players kept the same role (A, B or C) for the entire experiment. Order of conditions was counterbalanced across the six sessions. Participants made all of their part 1 decisions before making any part 2 decisions, and they received feedback on other player's part 1 decisions right before the part 2 decisions in each group, so the results of one condition could not affect the part 1 decisions in another condition. To increase the amount of data, we elicited all players' part 2 decisions regarding how much to give to their partner in the event that they were selected to do the continuous Prisoner's Dilemma, only implementing the decision of the selected participant ('strategy method'; Fehr & Fischbacher 2004). When they received their earnings post-experiment, participants found out all of their partners' part 2 decisions.

Participants were made familiar with the procedure by completing a practice round after hearing the instructions and before doing the experiment for money. In the practice round, all participants were instructed to give \$5 to their partners 'because it is an arbitrary halfway between giving everything and giving nothing'. Post-experimental questionnaires indicated that participants understood the procedure. This study was approved by the Cornell University Committee on Human Subjects, and all participants gave informed consent before participating.

3. RESULTS

(a) Part 1 data: using generosity to signal and compete

Part 1 donations differed between the three conditions (Friedman $\chi^2 = 28.27$, p < 0.001; figure 1). Participants gave more when their decisions were observed by a potential future interaction partner than when they were not (random/knowledge versus random/anonymous condition: Wilcoxon z=3.19, p=0.001). Between the two conditions where donations were known, donations were higher when participants could choose their partners than when partners were randomly assigned (choice/knowledge versus random/knowledge condition: Wilcoxon z=2.31, p=0.021). These results support the primary predictions that participants would donate to signal cooperativeness to potential partners, and when donations could affect partner choice, they would give even more to increase the likelihood of being chosen. The latter strategy typically worked, because when participants could choose partners (choice/knowledge condition), the highest contributor was chosen on 17/18 occasions (binomial p < 0.0001). This suggests that competition for social partners may play an important role in the evolution of altruistic behaviour.

(b) Part 2 data: responses to the signals

After being paired with their chosen/assigned partners, participants' subsequent donations could have no further effect on others' decisions. Correspondingly, donations after this re-pairing were near zero and there were no differences among conditions. Among participants who had previously been paired ('A' and 'B'), the median contribution was 0 in all the three conditions and the upper quartile for donations was 0, 1.75 and 1 in the random/anonymous, random/knowledge and choice/knowledge conditions, respectively (Friedman $\chi^2 = 2.23$, p = 0.33). Among participants who

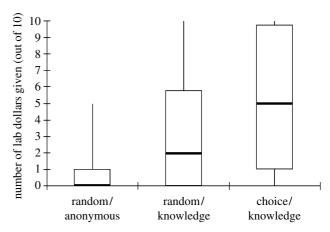


Figure 1. Number of lab dollars given to partners in each condition before partner choice/assignment. At this point, donations could affect future partners' decisions. Bars represent the interquartile range for donations in each condition and lines represent the 10th and 90th percentiles for donations, and much of this variation is between subjects rather than between experimental conditions. Participants gave significantly more when their donations were known than unknown (random/knowledge versus random/anonymous: Wilcoxon z=3.19, p=0.001) and gave still more when donations could affect partner choice than when they could not (choice/knowledge versus random/knowledge: Wilcoxon z=2.31, p=0.021).

had previously observed others ('C'), the median donation was also 0 in all the three conditions and the upper quartile for donations in those conditions was 0, 0 and 0.25, respectively (Friedman $\chi^2 = 2.00$, p = 0.37).

(c) Parts 1 and 2 together: was generosity an honest signal?

We expected to find increased deception as the benefits for signalling increased, because the benefits become more likely to outweigh the signal cost (Barclay 2004), and indeed, we do find significant differences (Friedman $\chi^2=17.60,\ p<0.001$): there is a smaller drop in contributions from part 1 to part 2 when donations would not be known to the partner than when they would (average drop in random/anonymous versus random/knowledge conditions, -\$0.1 \pm s.e. \$0.43 versus \$2.0 \pm s.e. \$0.41, respectively; Wilcoxon $z=2.68,\ p=0.007$), which in turn had a lower drop than when donations could have also influenced partner choice (average drop of \$4.1 \pm s.e. \$0.49, random/knowledge versus choice/knowledge; Wilcoxon $z=2.39,\ p=0.017$). However, this finding is potentially a mere floor effect.

Based on the possibility of deceptive signalling, one would also predict increased scepticism of altruistic signals as the potential benefits for deceptive signalling increase, such as when participants' donations could potentially influence partner choice (Barclay 2004). Consistent with this prediction, when participants could view their partners' past donations, they gave significantly more to high contributors than to low contributors when those partners were assigned randomly (random/knowledge condition: r_{16} =0.50, p=0.036), but not when they got to choose partners (choice/knowledge condition: r_{16} =0.26, p=0.30). This scepticism seems appropriate, given that participants' earlier donations were correlated with their later donations when there was no competition to be chosen (random/knowledge condition: r_{34} =0.40,

p=0.015), but were not significantly correlated with their later decisions when they had been competing to be chosen (choice/knowledge condition: $r_{34}=0.18$, p=0.30).

4. DISCUSSION

These results clearly show that participants were more generous when their behaviour could affect the decisions of future interaction partners; under these circumstances, generous behaviour could be useful for soliciting future cooperation by signalling the participant's cooperative intent (Milinski et al. 2002a,b; Wedekind & Braithewaite 2002; Albert et al. 2002; Barclay 2004, 2006). Results further showed that participants were even more generous when there was competition to be chosen as social partners and generosity could potentially increase one's chance of being chosen. This generosity generated by social competition was above and beyond that generated by a 'mere' incentive to present oneself as cooperative (i.e. the random/knowledge condition). This can justifiably be called competitive altruism, given that competition to be chosen was the only difference between the random/ knowledge and the choice/knowledge conditions, and participants increased their contributions relative to what they themselves gave in the absence of competition. This was not the only possible result; participants could have ignored the presence of competition if they did not value the future interaction or if they assumed that observers would discount greater giving, and they could even have given less on the assumption that other participants would give more. Nevertheless, the partner choice incentive created competition, affecting contributions positively.

Thus, this study provides the only unambiguous evidence to date for the existence of competitive altruism in humans and shows that partner choice is one way to produce competitive altruism. This is consistent with a desire to present oneself favourably, which itself is a probable proximate cause of behaviour that has ultimately been selected for due to selection pressures in social markets. However, our results are more than simple self-presentation effects because participants incurred actual costs to present themselves favourably. Further, they only did so when it could affect partners' decisions and modulated their self-presentation according to the degree and type of reputational benefits.

We predicted two types of reputational benefits for altruistic behaviour: (i) increased access to future cooperative interactions and (ii) higher cooperation elicited from partners within future cooperative interactions. The former was clearly found in this study, in that the future interaction partners almost always chose to interact with the more generous member of a pair. As for the latter, people gave significantly more (albeit still very little) to generous partners when it was not possible to affect access to relationships (i.e. the random/knowledge condition), but not when it was possible (i.e. the choice/knowledge condition). If participants had been choosing partners for repeated interactions instead of a single round, then there is reason to think that the more generous participants would have elicited higher cooperation from their partners in both conditions (see below).

Although participants gave more when their donations could affect future interactions (part 1), they gave next to nothing when this was not the case (part 2). This suggests

that participants gave in order to attract higher donations, but were often deceptive in that they generally did not continue making high donations in subsequent interactions. These near-zero contributions (and the initial low contributions in the random/anonymous condition) are surprising because they are much lower than is typical in anonymous social dilemmas without future interaction (Ledyard 1995; Gintis et al. 2003), and may have potential implications for theories of 'strong reciprocity' which claim that (some) people have a preference for being altruistic and derive pleasure from the well-being of others (e.g. Fehr & Fischbacher 2003; Gintis et al. 2003). The within-subjects nature of the present design may have made especially salient the strategic incentives to give or not give, which could have overwhelmed any such 'other-regarding preferences'. The strict anonymity may have further contributed to low donations after re-pairing. Post-study responses to an open-ended questionnaire suggested that low levels of cooperation were largely due to a desire to increase personal profits and not as much from fear of non-reciprocation. One implication of the near-zero part 2 contributions is that they suggest that experimenter expectations ('demand characteristics') were not a significant factor in participants' behaviour in this experiment, having probably been reduced or eliminated by monetary incentives and the strict anonymity of participants' decisions.

Although participants did use generosity to attract partners, dishonest signalling of cooperative intent was possible in this experiment because the potential gains from being chosen as a cooperative partner outweighed the cost of being generous. This was deliberately made possible in order to test for the possibility of dishonest signalling, although we did not expect it would be as prevalent as it was. Despite the presence of dishonest signalling, participants still chose higher contributors as partners, probably because choosing partners based on a possibly (but not necessarily) dishonest signal is better than choosing randomly so long as there are no consistent opportunity costs or search costs associated with choosing signallers.

Where future interactions are repeated, dishonest signalling would probably be minimized because either member of the partnership could cease cooperating if the other defected. Thus, in repeated interaction, the benefits for defecting on a partner would generally not outweigh the cost of attracting partners via altruistic signals, whereas the long-term benefits of cooperation would (Smith & Bliege Bird 2005; Barclay 2006). Outside the laboratory, repeated interaction may be typical, thus minimizing opportunities for dishonest signalling and allowing for the stability of systems where some individuals signal cooperative intent and attend to such signals in others. Participants tend to bring their expectations and preferences from the outside world into experiments (Henrich et al. 2001), so real-world experience with repeated interactions would probably lead participants to have some expectation that generosity may indicate cooperative intent and that generosity is rewarded at least some of the time (as seen in Albert et al. 2002; Milinski et al. 2002a,b; Barclay 2004; and others). Such expectations could result in participants giving money when it could influence others' decisions and choosing higher contributors as partners, despite the fact that signals of cooperative intent turned out to be often uninformative in this particular experiment.

Anything that decreases the costs of an altruistic signal decreases its effectiveness as a signal of cooperative intent, because dishonest signalling becomes more worthwhile. Anything that increases the potential reputational benefits (including audience size or characteristics, broadcast efficiency, amount of benefits or low fitness if not chosen as a partner) should increase not only individuals' willingness to compete for partners, but also audience scepticism of the signal. Future studies should investigate further the conditions under which signals of cooperative intent are honest, the dynamics of audience discounting of potentially dishonest signals, the strength of the preference for cooperators and the effects of opportunity costs, search costs and assessment costs on preferences for cooperators.

We thank H. Kern Reeve and Brent Simpson for valuable discussions and comments on manuscripts, two anonymous reviewers for additional comments, and Cornell University's Department of Neurobiology and Behaviour and Center for the Study of Inequality for funding.

REFERENCES

- Albert, M., Güth, W., Kirchler, E. & Maciejovsky, B. 2002 Are we nice(r) to nice(r) people? An experimental analysis. Discussion Paper 2002-15, Max Planck Institute for Research into Economics Systems, Strategic Interaction Group, Jena, Germany. ftp://papers.mpiew-jena.mpg.de/ esi/discussionpapers/2002-15.pdf.
- Alexander, R. D. 1987 The biology of moral systems. New York, NY: Aldine de Gruyter.
- Barclay, P. 2004 Trustworthiness and competitive altruism can also solve the "tragedy of the commons". Evol. Hum. Behav. **25**, 209–220. (doi:10.1016/j.evolhumbehav.2004.04.002)
- Barclay, P. 2006 Reputational benefits for altruistic punishment. Evol. Hum. Behav. 27, 344-360. (doi:10.1016/ j.evolhumbehav.2006.01.003)
- Bliege Bird, R., Smith, E. A. & Bird, D. W. 2001 The hunting handicap: costly signalling in human foraging strategies. Behav. *Ecol. Sociobiol.* **50**, 9–19. (doi:10.1007/ s002650100338)
- Bolle, F. 2001 Why to buy your darling flowers: on cooperation and exploitation. Theor. Decis. 50, 1-28. (doi:10.1023/A:1005261400484)
- Boone, J. L. 1998 The evolution of magnanimity: when is it better to give than to receive? *Hum. Nat.* **9**, 1–21.
- Clark, J. 2002 Recognizing large donations to public goods: an experimental test. Manag. Decis. Econ. 23, 33-44. (doi:10.1002/mde.1044)
- Daly, M. & Wilson, M. 1983 Sex, evolution, and behaviour. Boston, MA: Willard Grant Press.
- Fehr, E. & Fischbacher, U. 2003 The nature of human altruism. Nature 425, 785–791. (doi:10.1038/nature02043)
- Fehr, E. & Fischbacher, U. 2004 Third-party punishment and social norms. Evol. Hum. Behav. 25, 63-87. (doi:10. 1016/S1090-5138(04)00005-4)
- Gintis, H., Bowles, S., Boyd, R. & Fehr, E. 2003 Explaining altruistic behaviour in humans. Evol. Hum. Behav. 24, 153-172. (doi:10.1016/S1090-5138(02)00157-5)
- Gintis, H., Smith, E. A. & Bowles, S. 2001 Cooperation and costly signalling. J. Theor. Biol. 213, 103-119. (doi:10. 1006/jtbi.2001.2406)
- Harbaugh, W. T. 1998 What do donations buy? A model of philanthropy based on prestige and warm glow. J. Public Econ. 67, 269–284. (doi:10.1016/S0047-2727(97)00062-5)
- Hardy, C. & Van Vugt, M. 2006 Giving for glory in social dilemmas: the competitive altruism hypothesis. Pers. Soc. Psychol. Bull. 32, 1402-1413. (doi:10.1177/ 0146167206291006)

- Hawkes, K. & Bliege Bird, R. 2002 Showing off, handicap signalling, and the evolution of men's work. Evol. Anthropol. 11, 58-67. (doi:10.1002/evan.20005)
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H. & McElreath, R. 2001 In search of Homo economicus: Behavioral experiments from 15 small-scale societies. Am. Econ. Rev. 91, 73-78.
- Kurzban, R. & Houser, D. 2005 Experiments investigating cooperative types in humans: a complement to evolutionary theory and simulations. Proc. Natl Acad. Sci. USA 102, 1803–1807. (doi:10.1073/pnas.0408759102)
- Ledyard, J. O. 1995 Public goods: a survey of experimental research. In The handbook of experimental economics (ed. J. H. Kagel & A. E. Roth), pp. 111-194. Princeton, NJ: Princeton University Press.
- Lotem, A., Fishman, M. A. & Stone, L. 2003 From reciprocity to unconditional altruism through signalling benefits. Proc. R. Soc. B 270, 199-205. (doi:10.1098/rspb. 2002.2225)
- McNamara, J. M. & Houston, A. I. 2002 Credible threats and promises. Phil. Trans. R. Soc. B 357, 1607-1616. (doi:10. 1098/rstb.2002.1069)
- Milinski, M., Semmann, D. & Krambeck, H.-J. 2002a Reputation helps solve the "tragedy of the commons". Nature 415, 424–426. (doi:10.1038/415424a)
- Milinski, M., Semmann, D. & Krambeck, H.-J. 2002b Donors to charity gain in both indirect reciprocity and political reputation. Proc. R. Soc. B 269, 881-883. (doi:10. 1098/rspb.2002.1964)
- Noë, R. & Hammerstein, P. 1995 Biological markets. Trends Ecol. Evol. 10, 336-339.
- Roberts, G. 1998 Competitive altruism: from reciprocity to the handicap principle. Proc. R. Soc. B 265, 427-431. (doi:10.1098/rspb.1998.0312)
- Roberts, G. & Renwick, J. S. 2003 The development of cooperative relationships: an experiment. Proc. R. Soc. B **270**, 2279–2283. (doi:10.1098/rspb.2003.2491)
- Sefton, M., Shupp, R. & Walker, J. 2002 The effects of rewards and sanctions in provision of public goods. Working Paper W00-16, Centre for Decision Research and Experimental Economics, Nottingham, UK.
- Smith, E. A. 2003 Human cooperation: perspectives from behavioural ecology. In Genetic and cultural evolution of cooperation (ed. P. Hammerstein), pp. 401-428. Cambridge, MA: MIT Press.
- Smith, E. A. 2004 Why do good hunters have higher reproductive success? Hum. Nat. 15, 343-364.
- Smith, E. A. & Bliege Bird, R. 2005 Costly signalling and cooperative behaviour. In Moral sentiment and material interests: the foundations of cooperation in economic life (ed. H. Gintis, S. Bowles, R. Boyd & E. Fehr), pp. 115-148. Cambridge, MA: MIT Press.
- Smith, E. A., Bliege Bird, R. & Bird, D. W. 2003 The benefits of costly signalling: Meriam turtle hunters. Behav. Ecol. 14, 116-126. (doi:10.1093/beheco/14.1.116)
- Trivers, R. L. 1971 The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35–57. (doi:10.1086/406755)
- Van Lange, P. A. M., Otten, W., De Bruin, E. M. & Joireman, J. A. 1997 Development of prosocial, individualistic, and competitive orientations: theory and preliminary evidence. J. Pers. Soc. Psychol. 73, 733-746. (doi:10.1037/0022-3514.73.4.733)
- Wedekind, C. & Braithwaite, V. A. 2002 The long-term benefits of human generosity in indirect reciprocity. Curr. Biol. 12, 1012–1015. (doi:10.1016/S0960-9822 (02)00890-4)
- Zahavi, A. & Zahavi, A. 1997 The handicap principle: a missing piece of Darwin's puzzle. New York, NY: Oxford University Press.