Current Biology *16*, 1103–1106, June 6, 2006 ©2006 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2006.03.069

Report

Cooperation and the Scale of Competition in Humans

Stuart A. West,[1,*] Andy Gardner,[1,2,3] David M. Shuker,[1]
Tracy Reynolds,[1] Max Burton-Chellow,[1]
Edward M. Sykes,[1] Meghan A. Guinnee,[1]
and Ashleigh S. Griffin[1]
[1] Institute of Evolutionary Biology
School of Biological Sciences
University of Edinburgh
King's Buildings
Edinburgh, EH9 3JT
United Kingdom
[2] Department of Biology
[3] Department of Mathematics and Statistics
Queen's University
Kingston, ON, K7L 3N6
Canada

Summary

Explaining cooperation is one of the greatest challenges for evolutionary biology [1–3]. It is particularly a problem in species such as humans, where there is cooperation between nonrelatives. Numerous possible solutions have been suggested for the problem of cooperation between nonrelatives, including punishment, policing, and various forms of reciprocity [3–14]. Here, we suggest that local competition for resources can pose a problem for these hypotheses, analogous to how it can select against cooperation between relatives [15–21]. We extend the prisoner's dilemma (PD) game to show that local competition between interacting individuals can reduce selection for cooperation between nonrelatives. This is because, with local competition, fitness is relative to social partners, and cooperation benefits social partners. We then test whether nonrelated humans adjust their level of cooperation facultatively in response to the scale of competition when playing the PD for cash prizes. As predicted, we found that individuals were less likely to cooperate when competition was relatively local. Cooperation between humans will therefore be most likely when repeated interactions take place on a local scale between small numbers of people, and competition for resources takes place on a more global scale among large numbers of people.

Results

Incorporating Local Competition into the PD

In the PD game, two individuals interact with each other and choose whether to cooperate or not cooperate (defect or cheat) [22]. The payoffs assumed for different strategies lead to the focal player doing better if they defect, irrespective of whether the other player cooperates or defects, but both parties defecting gives a lower payoff than if both had cooperated (Table 1). The dilemma is that from a selfish perspective each will decide that the best course is defect, thus making both worse off than if they had both cooperated. The most famous solution to this problem occurs when players interact a number of times (multiple rounds), termed the iterated PD [22]. In this case, cooperation can be favored by a "Tit-For-Tat" (TFT) strategy, which is to cooperate in the first round and in every subsequent round copy the partner's play from the previous round [22]. TFT is a strategy of facultative (reciprocal) cooperation, which punishes defectors by not cooperating with them.

We introduced the possibility of local competition for resources into the PD (Supplemental Data available with this article online). Specifically, we introduced a scale of competition parameter, *a*, that denotes the proportion of competition that occurs locally (i.e., at the level of the pair of social partners engaged in an evolutionary game) as opposed to globally (i.e., at the level of the whole population). Our results showed that as competition became more local, cooperation was selected against (Figure 1). Specifically, the expected number of interactions between players (rounds per game), required for TFT to be stable against invasion by always defect, increased with more local competition (higher *a*). Higher numbers of interactions favor altruism because they allow greater opportunities for reciprocal altruism [4, 22].

As competition becomes more local, the payoff of the focal individual relative to their partner becomes more important. With global competition ($a = 0$), fitness is determined by the classical payoff structure (absolute values). However, as competition becomes more local, the relative payoff becomes more important, and the absolute payoff becomes less important. In the extreme, with completely local competition ($a = 1$), the focal individual is competing only with their partner, and so fitness is determined by how the focal individual does relative to their partner. Cooperation never results in an increase in relative payoff, whereas defection does (Table 1). Consequently, the dilemma disappears, as defection always leads to a higher payoff, and both players cooperating does not lead to a higher payoff than both players defecting (Table 1).

Testing with Humans

We then tested our model by examining whether nonrelated humans adjust their level of cooperation in response to the scale of competition. We made students play the PD game in groups of three. Each student played each of the other two students for an unknown number of repeated interactions (an average of seven rounds). We varied the scale of competition by having five groups play at a time (a class) and giving cash rewards to the top five scores in the class for relatively global competition or the top score in each group for relatively local competition. Each student played once with

---

*Correspondence: stu.west@ed.ac.uk

Table 1. The Payoffs for Player A with Different Strategies in the Prisoner's Dilemma

		Player B	
		Cooperation	Defection
Player A	Cooperation	R = 3 (1), rewards for mutual cooperation	S = 0 (0), sucker's payoff
	Defection	T = 5 (∞), temptation to defect	P = 1 (1), punishment for mutual defection

The dilemma is that defection always leads to a higher payoff ($T > R$ and $P > S$) but that both cooperating leads to a higher payoff than both defecting ($R > P$). Exact values given are for illustration. Given in parentheses are the relative payoffs, which is the payoff for player A divided by the payoff for player B. Local competition leads to the relative payoffs being the crucial score, in which case both cooperating does not lead to a higher payoff than both defecting ($R = P$).

relatively local competition and once with relatively global competition.

We found that students showed higher levels of cooperation when competition was relatively global than when competition was relatively local (Figure 2). This result held irrespective of whether analysis was carried out at the level of the individual ($t = 7.34$, $n = 57$, $p < 0.0001$; 52/57 individuals showed higher levels of cooperation with relatively global competition), group ($t = 7.80$, $n = 9$, $p < 0.0001$; 9/9 groups), or class ($t = 10.97$, $n = 4$, $p = 0.002$; 4/4 classes). Overall, students were more than twice as likely to cooperate with relatively global competition (44% of the time) than they were with relatively local competition (18%; Figure 2).

Discussion

Theoretical Explanations for Cooperation

We have shown that local competition for resources between nonrelatives selects against cooperation (Figure 1). As competition becomes more local, the fitness of an individual becomes more dependent upon how they do relative to the partners that they interact and potentially cooperate with. In this case, cooperation is selected against because it never leads to an increase in payoff relative to the beneficiary of cooperation (Table 1). Another way of conceptualizing this is that local competition leads to the increased fitness of the beneficiary of altruism coming at the cost of the provider of the cooperation and so selects against cooperation.

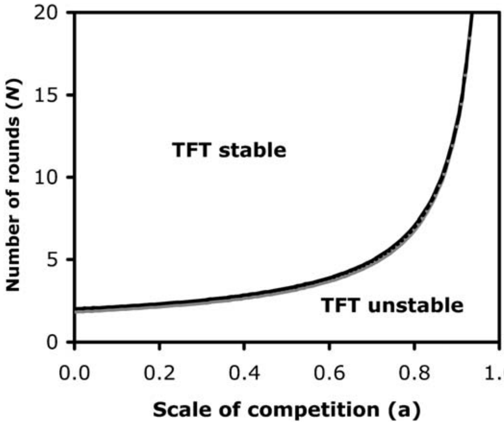

Figure 1. Local Competition Selects against Cooperation in the Iterated PD

The threshold expected number of rounds per game (N^*) required for Tit-For-Tat (TFT) to be evolutionarily stable is a monotonically increasing function of the scale of competition (a). Assuming the payoffs $T = 5$, $R = 3$, $P = 1$, and $S = 0$, then when competition is global ($a = 0$) TFT is stable when $N^* > 2$, and this threshold increases to infinity as competition becomes increasingly local (higher a).

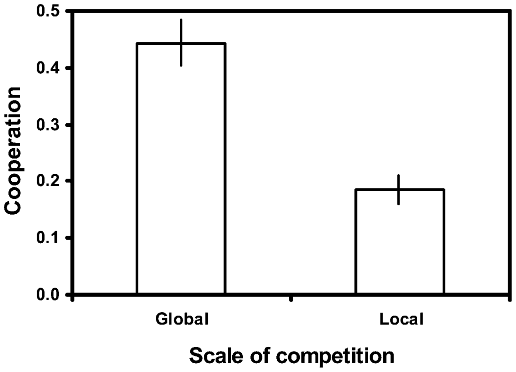

Figure 2. Human Cooperation and the Scale of Competition

The mean proportion of cooperative decisions made by students with respect to the scale of competition. Error bars are back-transformed 95% confidence intervals with individual students as independent data points. As predicted (see Figure 1), individuals were less likely to cooperate when competition was relatively local.

We used the framework provided by the PD, because it is a commonly used tool for demonstrating the problem of cooperation between nonrelatives [4, 22], and because we were able to test these predictions experimentally with humans. Several authors have argued that the PD, and the ability of reciprocal altruism to solve the problem of cooperation, require a large number of very specific assumptions and are likely to be of limited importance outside of humans [8, 23]. However, reciprocal altruism is just one of many mechanisms that can provide a direct fitness benefit to cooperation—alternatives include group augmentation, policing, sanctions, and punishment [7–14, 24]. We suggest that the consequences of local competition for these different mechanisms will depend upon how cooperation is favored. Although local competition makes relative fitness more important and, hence, selects against cooperation, it can also increase the advantage of punishing or spiteful behaviors [25, 26], which can be used to enforce cooperation.

Our results also illustrate a problem that needs to be solved in the theoretical literature. Several simulation studies, based on the PD, have suggested that limited dispersal favors cooperation [27, 28]. In contrast, analytical studies have suggested this will not necessarily be true because limited dispersal can also increase local competition. In the simplest case, the effect of increased competition exactly negates any benefit of limited dispersal [17, 29]. More complex analytical models can be constructed in which limited dispersal does not lead to such an increase in local competition, and hence, cooperation can be favored, depending upon biological details [3, 16–19, 29–35]. This raises the question of what assumptions have removed this problem in the simulation studies and allowed the benefits of limited dispersal to outweigh the cost of increased competition.

Cooperation in Humans and Other Animals

Our results showed that humans were more likely to cooperate in the PD when competition was more global. This will happen when individuals tend to have repeated interactions (with the potential for cooperation) with a small number of other individuals (or within groups), but competition for resources occurs with a larger number of people (or between groups). Humans are a useful study organism for testing this hypothesis, as their cognitive abilities could allow the scale of competition to be assessed. In addition, determining the cognitive tools involved in cooperation between humans is key to resolving the debate over how the data from experimental games are to be interpreted [36–39]. We suspect that with most other organisms individuals will not be able to assess variation in the scale of competition, and so the response will be evolutionary rather than behavioral (i.e., fixed not facultative) [20, 21].

An implication of our results is that if the perceived scale of competition is manipulated, then this will alter the level of cooperation among humans. This could occur in numerous ways in all forms of society. One way is to create a common enemy, who must be competed against relatively globally. A famous example of this is in *Nineteen Eighty-Four*, where The Party uses a poster with a "monstrous figure of a Eurasian soldier" to unite the proles into "one of their periodical frenzies of patriotism" [40]. As Hamilton [15, 41] pointed out, the same competitive issues that can favor cooperation within groups, can also favor the evolution of hostility (or war) between groups. An alternative possibility is to reward local cooperation. For example companies (or any form of institution) could provide productivity rewards (or evaluations) to individuals that depend in part upon the performance of the workers that interact with that individual, rather than just the performance of the individual or the company as a whole.

Experimental Procedures

We carried out the following experiment on four undergraduate classes, three containing 15 students and one containing 12 students. Two of these classes were in 2004 and two were in 2005. This class was prior to a course on social evolution theory, which means it was before the students were taught relevant evolutionary biology. Each class was split up into five groups of three students (four groups in the class with 12 students). The PD was then explained to the students, who were then allowed to play approximately seven interactions to familiarize themselves with it.

We then made the students play for cash rewards. Cash rewards were given out anonymously. In two classes, the students played the relatively local competition session first and then the relatively global competition session second. In the other two classes, the students played the relatively global competition session first. For each class, we did the following. Within each group of three students, each student played each other for one game. Each game was for an average of seven repeated interactions of the PD, with the number of interactions unknown to the students (who were only told that there was an equal likelihood of the game finishing after each interaction). For each interaction, both players made their decisions simultaneously, without knowledge of the other's decision. After each interaction, the students were told the strategy that they had each chosen, and the points pay off, before the next interaction.

We varied the scale of competition by how cash prizes were awarded. The details of the cash rewards were given to the students at the start of each session (global or local). For relatively global competition, the five students in the class who scored the most points won £10 (top four students in the class with 12 students). For relatively local competition, the top score in each of the five (or four) groups of three students won £10. This procedure meant that the total amount awarded was the same for both local and global competition. An equally valid way of conceptualizing this is by considering within and between group competition: within group competition is relatively greater with local competition.

Our aim with this experiment was to test whether individuals adjusted their level of cooperation in response to the scale of competition. We tested for this by comparing the average proportion of interactions in which they cooperated, when playing the same two players, with relatively local and global competition. Data were arcsin square root transformed prior to analysis to remove the problem of nonnormal errors that can arise with proportion data. It can be argued that the results from the three individuals in the same group are not independent, because they arise from the same games. Consequently, we examined the robustness of results by analyzing our data at a number of levels: individuals (n = 57), groups (n = 9), and classes (n = 4). We calculated the proportion of times the individual (or group or class) cooperated (arcsin square root transformed) with relatively global competition minus the proportion of times the individual (or group or class) cooperated with relatively local competition. These values were then tested against the null hypothesis that the average value did not differ significantly from zero (i.e., there was no difference in the likelihood of cooperation between relatively local and relatively global competition) with a t test. All analyses were carried out with the package GLMStat 6.0 (http://www.glmstat.com). By comparing the incidence of cooperation in the relatively local and global games, we provide a qualitative test of our theory.

Cooperation in humans has been much investigated, and the importance of a range of other factors has been demonstrated, including sanctions, image scoring, and indirect reciprocity [4–7, 36, 39, 41–44]. In our experiment, the students were split by boards when playing the game and were not allowed to talk or signal at any point. Despite this, we cannot eliminate the possibility that their behavior was influenced by prior knowledge of each other, such as image scoring. However, this would only influence the average level of cooperation between players, at both local and global competition, and so does not alter our ability to test for differences between these two experimental treatments. A possible influence of time or experience (number of games played) was controlled for by making the students play local first in two classes and global first in two classes. Our results therefore show that when all else is equal, variation in the scale of competition leads to different levels of cooperation, suggesting that the importance of these other factors will be mediated by the scale of competition.

Supplemental Data

Supplemental Data include Supplemental Results and Experimental Procedures and can be found with this article online at http://www.current-biology.com/cgi/content/full/16/11/1103/DC1/.

Acknowledgments

The experimental part of this paper was inspired by the Wedekind and Braithwaite (2002) study. We thank all the students who took part in the experiment, S. Frank, K. Foster, and two anonymous referees for comments, and K. Foster for providing the *Nineteen Eighty-Four* quote. We are funded by the Royal Society, Natural Environment Research Council, and Biotechnology and Biological Sciences Research Council.

Received: February 6, 2006
Revised: March 4, 2006
Accepted: March 16, 2006
Published: June 5, 2006

References

1. Hamilton, W.D. (1964). The genetical evolution of social behaviour, I & II. J. Theor. Biol. *7*, 1–52.
2. Maynard Smith, J., and Szathmary, E. (1995). The Major Transitions in Evolution (Oxford: W.H. Freeman).
3. Hamilton, W.D. (1996). Narrow Roads of Gene Land: I Evolution of Social Behaviour (Oxford: W.H. Freeman).
4. Trivers, R.L. (1971). The evolution of reciprocal altruism. Q. Rev. Biol. *46*, 35–57.
5. Nowak, M.A., and Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring. Nature *393*, 573–577.
6. Boyd, R., Gintis, H., Bowles, S., and Richerson, P.J. (2003). The evolution of altruistic punishment. Proc. Natl. Acad. Sci. USA *100*, 3531–3535.
7. Gardner, A., and West, S.A. (2004). Cooperation and punishment, especially in humans. Am. Nat. *164*, 753–764.
8. Clutton-Brock, T.H. (2002). Breeding together: kin selection, reciprocity and mutualism in cooperative animal societies. Science *296*, 69–72.
9. Frank, S.A. (1995). Mutual policing and repression of competition in the evolution of cooperative groups. Nature *377*, 520–522.
10. Frank, S.A. (2003). Repression of competition and the evolution of cooperation. Evolution Int. J. Org. Evolution *57*, 693–705.
11. Kokko, H., Johnstone, R.A., and Clutton-Brock, T.H. (2001). The evolution of cooperative breeding through group augmentation. Proc. R. Soc. Lond. B. Biol. Sci. *268*, 187–196.
12. Panchanathan, K., and Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. Nature *432*, 499–502.
13. Ratnieks, F.L.W., Foster, K.R., and Wenseleers, T. (2006). Conflict resolution in insect societies. Annu. Rev. Entomol. *51*, 581–608.
14. West, S.A., Kiers, E.T., Simms, E.L., and Denison, R.F. (2002). Sanctions and mutualism stability: why do rhizobia fix nitrogen? Proc. R. Soc. Lond. B. Biol. Sci. *269*, 685–694.
15. Hamilton, W.D. (1971). Selection of selfish and altruistic behaviour in some extreme models. In Man and Beast: Comparative Social Behavior, J.F. Eisenberg and W.S. Dillon, eds. (Washington, DC: Smithsonian Press), pp. 57–91.
16. Queller, D.C. (1992). Does population viscosity promote kin selection? Trends Ecol. Evol. *7*, 322–324.
17. Taylor, P.D. (1992). Altruism in viscous populations - an inclusive fitness model. Evol. Ecol. *6*, 352–356.
18. Wilson, D.S., Pollock, G.B., and Dugatkin, L.A. (1992). Can altruism evolve in purely viscous populations. Evol. Ecol. *6*, 331–341.
19. West, S.A., Pen, I., and Griffin, A.S. (2002). Cooperation and competition between relatives. Science *296*, 72–75.
20. West, S.A., Murray, M.G., Machado, C.A., Griffin, A.S., and Herre, E.A. (2001). Testing Hamilton's rule with competition between relatives. Nature *409*, 510–513.
21. Griffin, A.S., West, S.A., and Buckling, A. (2004). Cooperation and competition in pathogenic bacteria. Nature *430*, 1024–1027.
22. Axelrod, R., and Hamilton, W.D. (1981). The evolution of cooperation. Science *211*, 1390–1396.
23. Stevens, J.R., and Hauser, M.D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. Trends Cogn. Sci. *8*, 60–65.
24. Clutton-Brock, T.H., and Parker, G.A. (1995). Punishment in animal societies. Nature *373*, 209–216.
25. Gardner, A., and West, S.A. (2004). Spite and the scale of competition. J. Evol. Biol. *17*, 1195–1203.
26. Gardner, A., West, S.A., and Buckling, A. (2004). Bacteriocins, spite and virulence. Proc. Biol. Sci. *271*, 1529–1535.
27. Nowak, M.A., and May, R.M. (1992). Evolutionary games and spatial chaos. Nature *359*, 826–829.
28. Doebeli, M., and Knowlton, N. (1998). The evolution of interspecific mutualisms. Proc. Natl. Acad. Sci. USA *95*, 8676–8680.
29. Taylor, P.D. (1992). Inclusive fitness in a homogeneous environment. Proc. R. Soc. Lond. B. Biol. Sci. *249*, 299–302.
30. Grafen, A. (1984). Natural selection, kin selection and group selection. In Behavioural Ecology: An Evolutionary Approach, 2nd Edition, J.R. Krebs and N.B. Davies, eds. (Oxford, UK: Blackwell Scientific Publications), pp. 62–84.
31. Queller, D.C. (1994). Genetic relatedness in viscous populations. Evol. Ecol. *8*, 70–73.
32. van Baalen, M., and Rand, D.A. (1998). The unit of selection in viscous populations and the evolution of altruism. J. Theor. Biol. *193*, 631–648.
33. Taylor, P.D., and Irwin, A.J. (2000). Overlapping generations can promote altruistic behaviour. Evolution Int. J. Org. Evolution *54*, 1135–1141.
34. Gardner, A., and West, S.A. (2006). Demography, altruism, and the benefits of budding. J. Evol. Biol., in press.
35. Pen, I., and West, S.A. (2006). Reproductive skew paves the way for altruism. Evolution Int. J. Org. Evolution, in press.
36. Fehr, E., and Fischnacher, U. (2003). The nature of human altruism. Nature *425*, 785–791.
37. Haley, K.J., and Fessler, D.M.T. (2005). Nobody's watching? Subtle cues affect generosity in an anonymous economic game. Evol. Hum. Behav. *26*, 245–256.
38. Hagen, E.H., and Hammerstein, P. (2006). Game theory and human evolution: a critique of some recent interpretations of experimental games. Theor. Popul. Biol. *69*, 339–348.
39. Fehr, E., and Rockenbach, B. (2003). Detrimental effects of sanctions on human altruism. Nature *422*, 137–140.
40. Orwell, G. (1949). Nineteen Eighty-Four (London: Secker & Warburg).
41. Hamilton, W.D. (1975). Innate social aptitudes of man: an approach from evolutionary genetics. In Biosocial Anthropology, R. Fox, ed. (New York: Wiley), pp. 133–155.
42. Wedekind, C., and Milinski, M. (2000). Cooperation through image scoring in humans. Science *288*, 850–852.
43. Wedekind, C., and Braithwaite, V.A. (2002). The long-term benefits of human generosity in indirect reciprocity. Curr. Biol. *12*, 1–4.
44. Nowak, M.A., and Sigmund, K. (1992). Tit for tat in heterogeneous populations. Nature *355*, 250–253.