

- (2004). Dynamics of centromere and kinetochore proteins; implications for checkpoint signaling and silencing. *Curr. Biol.* *14*, 942–952.
13. Sprague, B.L., and McNally, J.G. (2005). FRAP analysis of binding: proper and fitting. *Trends Cell Biol.* *15*, 84–91.
14. Bacia, K., and Schwille, P. (2003). A dynamic view of cellular processes by in vivo fluorescence auto- and cross-correlation spectroscopy. *Methods* *29*, 74–85.
15. Habu, T., Kim, S.H., Weinstein, J., and Matsumoto, T. (2002). Identification of a MAD2-binding protein, CMT2, and its role in mitosis. *EMBO J.* *21*, 6419–6428.
16. Xia, G., Luo, X., Habu, T., Rizo, J., Matsumoto, T., and Yu, H. (2004). Conformation-specific binding of p31(comet) antagonizes the function of Mad2 in the spindle checkpoint. *EMBO J.* *23*, 3133–3143.
17. Peters, J.M. (2002). The anaphase-promoting complex: proteolysis in mitosis and beyond. *Mol. Cell* *9*, 931–943.
18. Vanoosthuysse, V., and Hardwick, K.G. (2005). Bub1 and the multilayered inhibition of Cdc20-APC/C in mitosis. *Trends Cell Biol.* *15*, 231–233.
19. Sudakin, V., Chan, G.K., and Yen, T.J. (2001). Checkpoint inhibition of the APC/C in HeLa cells is mediated by a complex of BUBR1, BUB3, CDC20, and MAD2. *J. Cell Biol.* *154*, 925–936.

Research Institute of Molecular Pathology (IMP), Dr. Bohr-Gasse 7, A-1030 Vienna, Austria.  
E-mail: [peters@imp.univie.ac.at](mailto:peters@imp.univie.ac.at); [lenart@imp.univie.ac.at](mailto:lenart@imp.univie.ac.at)

DOI: 10.1016/j.cub.2006.05.008

## Cooperation: Close Friends and Common Enemies

The Prisoner's dilemma game has been a key conceptual tool for analyzing social behavior for over 50 years. A recent study shows how the spatial scale of competition in this game critically determines when cooperation can emerge.

Bernard Crespi

*A hydrogen bomb is an example of mankind's enormous capacity for friendly cooperation. Its construction requires an intricate network of human teams, all working with single-minded devotion toward a common goal. Let us pause and savor the glow of self-congratulation we deserve for belonging to such an intelligent and sociable species.*

— Robert S. Bigelow, 1969,  
The Dawn Warriors

We are indeed a social and cooperative species. Throughout life we help to generate social resources, from freeways to journals to the internet, via collective endeavors and divisions of labor. But such cooperation is always permeated by conflicts of interest, because resources create opportunities to compete, and to cheat. One of the primary unresolved questions in biology, psychology, philosophy and economics is understanding the ecological and social circumstances that favor and sustain cooperation — especially when cheating can often yield a higher payoff.

Evolutionary biology has provided some clues to solving

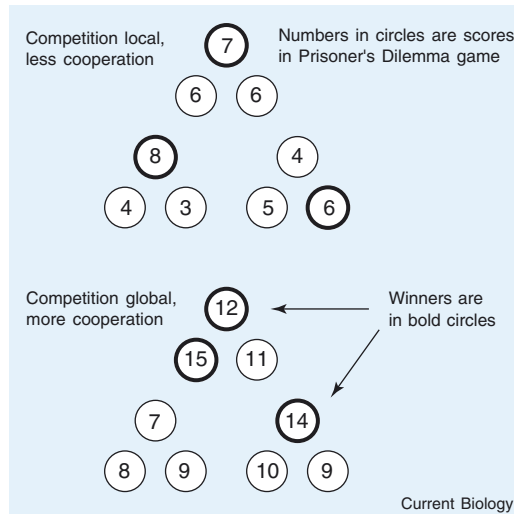
the apparent paradox of cooperation, with myriad studies demonstrating how kinship, mutualism, direct and indirect reciprocity, and threat of punishment can often keep selfishness at bay [1–4]. But we have missed something crucial, perhaps because like the theory of evolution itself, it is so obvious and pervasive. We cooperate and compete in groups, at scales from local to global. In this issue of *Current Biology*, West *et al.* [5] demonstrate that the spatial scale of competition can drive the evolutionary dynamics of social interaction among non-relatives. In particular they show that sociality is favored when cooperation is more local and competition more global — precisely the circumstances under which we first so-cooperatively developed nuclear weapons. This is a key insight because it integrates the theory of cooperation with the real-world structures of human grouping, and the real world now needs all the cooperation it can get.

The tension between conflict and confluence of interest is captured in a classic method to study cooperation, a game first developed by Merrill Flood and Melvin Dresher in 1950 as

a component of the RAND corporation's studies of global nuclear war [6]. Two parties may either cooperate or defect. The highest joint payoff is achieved via mutual cooperation, but each player could achieve an even higher reward if they defected while their opponent cooperates. In the 1950s, 'cooperation' represented the restraint motivated by mutual assured destruction. Albert Tucker resituated this game of terror as the familiar 'Prisoner's Dilemma' of whether two criminals held separately should either cooperate (remain silent about a joint crime) or 'defect' (incriminate the other). The Prisoner's Dilemma game has become a touchstone for analyzing the evolution of cooperation, especially since Axelrod and Hamilton [7] held a computer tournament won by the strategy 'Tit for Tat': cooperate on the first play, then mirror your opponent's previous choice. This strategy is initially nice, forgiving of reformed defection, and provokable to defect, but it can only sustain cooperation under special circumstances and it departs from realism in various ways [7,8].

West *et al.* [5] are the first to extend the structure of the Prisoner's Dilemma game in space, by adding a parameter representing the proportion of competition that occurs locally (in a small group of social partners) versus globally (in the population of players as a whole) (Figure 1). They have shown with an analytic model that as competition becomes more local, cooperation is selected against. This result

Figure 1. Players in the Prisoner's Dilemma game cooperate more, and achieve higher joint pay-offs, when competition is global (across the whole population) rather than local (in small groups, here with three players in each).



makes intuitive sense in that, at the local extreme, two players compete only against each other, and fitness (the payoff) is relative only to one's opponent. As cooperation never leads to higher *relative* payoff, the best option is always to defect. This is Darwin's inexorable machinery of natural selection at work, with fitness always relative to others in the population, no matter how small that population may be. Or how large — inevitable world dominion of one political ideology also provides an example, with memes instead of genes or strategies competing to increase their frequency.

The upshot of West *et al.*'s [5] model is that it predicts what circumstances best enhance cooperativeness. Cooperation is favored under local repeated interactions, with potential gains from local helpfulness, but with competition occurring at a much larger spatial scale, across the population at large or between groups. The researchers tested this prediction using undergraduate students naïve to the Prisoner's Dilemma, playing an iterated game in small groups. Cash rewards were given as fitness payoffs under global competition (rewards given only for top scores across all players) and under local competition (rewards given only for the top score within each of the multiple small groups). As predicted by the model, the students were much more cooperative when

competition was global. The proximate mechanism? One suspects that, under global competition, a group-against-group dynamic took hold, as students cooperated locally in hopes of ultimately scoring higher than students in enemy groups. But under local competition it was every undergraduate for himself or herself.

Like natural selection itself, this theory and experiment are deceptively simple, but the implications are profound. The social behavior of non-human animals often involves cooperation among non-relatives, and natural selection should have led to evolved strategies that reflect the scales of competition and cooperation. For example, in some desert ants, unrelated queens cooperate in incipient colonies, driven by severe competition between nearby nests [9]. However, once a colony is well-established, cooperators turn killers until only one queen remains. Other cases of animal cooperation among non-relatives should be revisited with spatial structure in mind.

In humans, strategic responses to the scales of social costs and benefits can be truly facultative. We can therefore exploit them. As West *et al.* [5] suggest, engineering the spatial structure of human groups in business and academia may provide new means of harnessing the societal benefits possible

from both competition and cooperation. More generally, the Prisoner's Dilemma represents a binary version of the 'public goods' game — the game that famously generates the tragedy of the commons [10,11]. Here, benefits accrue to oneself, or one's local group, but costs are burdened more globally. Cooperation requires restraint and prudent, long-term resource use, but defection destroys the resource for all. Fisheries, forestry, climate change, and the collapse of civilizations form a familiar litany reminding us of the rules and consequences.

Game theory was birthed in the crucible of global conflict, and fostered by John von Neumann, architect of the modern computer and the hydrogen bomb. Can it help us now?

#### References

- Alexander, R.D. (1987). *The Biology of Moral Systems* (Hawthorne, New York: A. de Gruyter Press.).
- Frank, S.A. (2003). Repression of competition and the evolution of cooperation. *Evolution* 57, 693–705.
- Connor, R.C. (1995). The benefits of mutualism: a conceptual framework. *Biol. Rev.* 70, 427–457.
- Clutton-Brock, T.H., and Parker, G.A. (1995). Punishment in animal societies. *Nature* 373, 209–216.
- West, S.A., Gardner, A., Shuker, D.M., Reynolds, T., Burton, M., Sykes, E.M., Guinness, M.A., and Griffin, A.S. (2006). Cooperation and the scale of competition in humans. *Curr. Biol.* 16, 1103–1106.
- Poundstone, W. (1992). *Prisoner's Dilemma* (New York: Anchor Books).
- Axelrod, R., and Hamilton, W.D. (1981). The evolution of cooperation. *Science* 211, 1390–1396.
- Nowak, M.A., Sasaki, A., Taylor, C., and Fudenberg, D. (2004). Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428, 646–650.
- Bernasconi, G., and Strassmann, J.E. (1999). Cooperation among unrelated individuals: the ant foundress case. *Trends Ecol. Evol.* 14, 477–482.
- Hardin, G. (1968). The tragedy of the commons. *Science* 162, 1243–1248.
- Milinski, M., Semmann, D., Krambeck, H.J., and Marotzke, J. (2006). Stabilizing the earth's climate is not a losing game: supporting evidence from public goods experiments. *Proc. Natl. Acad. Sci. USA* 103, 3994–3998.

Behavioural Ecology Research Group,  
Department of Biosciences, Simon  
Fraser University, Burnaby, British  
Columbia V5A 1S6, Canada.  
E-mail: [crespi@sfu.ca](mailto:crespi@sfu.ca)