

The Comedy of the Trojans

Reversing the tragedy of the commons, etc.

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Evolution of cooperation reviewed

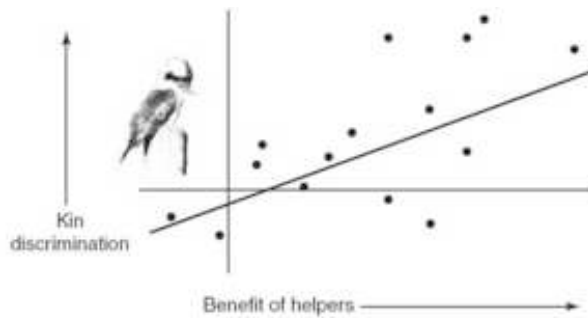
The theme of the latest issue of *Current Biology* is "Biology of Societies." There are reviews on the social life of spiders, crows, hyenas, amoebae, and insects, plus the role of cognition in social interactions among humans. If you are interested in the evolution of cooperation, it might be worth a trip to your nearest university library (if you don't have access via the web) to browse this issue.

I particularly liked "Evolutionary Explanations for Cooperation" by Stuart West, Ashleigh Griffin, and Andy Gardner. Their [review](#) reprints figures from several recent papers, so you can see some of the data upon which their generalizations are based. I won't try to summarize the whole thing, just some points that may have been neglected in other reviews of this topic.

They begin with a definition: "A behaviour is cooperative if it provides a benefit to another individual and if it has evolved at least partially because of this benefit." Plants benefit when soil bacteria breaking down organic matter release nitrogen in the process, but do the bacteria release some of the nitrogen in the organic matter (rather than using it themselves) *because* it benefits plants? Plant growth benefits bacteria near their roots, but do plants selectively benefit those bacteria that release the most nitrogen, relative to other bacteria nearby? If not, then bacteria that let others shoulder the cost of supporting plant growth (by giving up some nitrogen) would out-compete any bacterial "altruists." (If bacteria don't have any use for additional nitrogen, then leaving it in the soil has no cost, but neither would it qualify as cooperation.) Similar Tragedies of the Commons have the potential to undermine cooperation at all levels, from cooperation among cells in a multicellular organism to cooperation in human societies.

Kin selection can favor altruism ("behaviour that is costly to the actor and beneficial to the recipient") towards close relatives. W.D. Hamilton predicted that a gene that leads to altruistic activity will spread when the cost (decrease in reproduction of the actor) is less than the benefit (increased reproduction) to the recipient times their relatedness.

West and coauthors point out that research to test Hamilton's Rule has emphasized relatedness, but benefit and cost are also important. For example, species in which help raising young is most important to the survival of those young are more likely to help closer relatives (kin discrimination) as previously shown by Griffin and West (*Science* 302:634).



Indiscriminate helping may not be the result of kin selection, but rather some individual benefit to the helper, such as being allowed to remain in another's territory.

The authors reiterate an important point they have made previously, related to the effects of migration on kin selection. Animals that don't move around much may end up surrounded by relatives. This may be even more true of plants. This increased relatedness favors altruism, except that it may also increase the cost of altruism or reduce the benefits. If a bunch of relatives are all competing for the same resources, help that lets one sister reproduce more may come at the expense of the altruist's own reproduction (increasing cost) or that of another sister (reducing total benefits).

Cooperation between unrelated individuals, often of different species, can also be favored by enforcement mechanisms that tie individual benefit to cooperative behavior. For example, cleaner fish that bite their hosts get chased and other potential hosts avoid them. Humans (at least Swiss college students) tend to punish noncooperation in "experimental economics" games, even at some expense to themselves.

Enforcement mechanisms need not require conscious intelligence, however. The review mentions research by Toby Kiers in my lab showing that soybean plants punish rhizobium bacteria that fail to provide them with nitrogen. We assume that the soybean plants, in contrast to Swiss college students, obtain some individual benefit, such as saving scarce photosynthate, from doing so. Further work in this area was discussed last week.

The review points out that the mechanisms that prevent "cheaters" from undermining cooperation may be different from the mechanisms by which cooperation arose in the first place.

They make the important point that

we do not need to keep reinventing the wheel with more theoretical models that incorrectly claim to provide a new mechanism for the evolution of cooperation [12,97,98]. This has especially been a problem with models that examine limited dispersal or group structures [99-103] and which are, therefore, just reinventing kin selection. Second, we do not need redefinitions of terms that already have specific and useful meanings.

Instead, they say "we need greater integration between theoretical and empirical work." They suggest that there has been too much emphasis on "birdwatching or the glamour of working with fluffy mammals" while neglecting bacteria and "interplay between mechanistic (proximate) and evolutionary (ultimate or selective value) approaches." I can only hope that scientists reviewing my latest NSF proposal will agree.

Posted by R. Ford Denison on August 22, 2007 12:24 PM | [Permalink](#)

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