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Do asymmetries destabilize the Prisoner's Dilemma and make reciprocal altruism unlikely?

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Ever since the publication of the seminal papers by Trivers (1971) and Axelrod & Hamilton (1981) on the evolution of cooperation, there has been great theoretical interest in the idea that animals might show reciprocal altruism, that is, perform an apparently altruistic act to another unrelated animal and then gain from being repaid later. The shadow of the future (the future consequences of failing to reciprocate) can make reciprocal altruism the selfishly best strategy for both participants (Axelrod & Hamilton 1981; Dawkins 1989). However, what has characterized the years since the publication of these original papers is both the number of different theoretical models that have appeared (e.g. Lehmann & Keller 2006; Nowak 2006) and also the relative rarity of good empirical evidence that real animals do what any of the models say they should (Dugatkin 1997; Clutton-Brock 2009). Time and time again what looked like reciprocal altruism has turned out to be an immediate benefit to self (e.g. Clutton-Brock et al. 1999), kin selection, the animal having a selfish stake in the other animal (Roberts 2005) or by-product mutualism (Brown 1983; Grinnell et al. 1995; Dugatkin 1997; Clutton-Brock 2009).

One reason that has been put forward to explain the apparent rarity of reciprocal altruism among animals is that it is too cognitively demanding for most species, requiring feats of memory and other cognitive abilities that are beyond all but a few (Hauser et al. 2003; Stevens & Hauser 2004; Melis et al. 2006). Clutton-Brock (2009) even argued that without language to make bargains about the future, nonhuman species are largely restricted to forms of cooperation that give immediate selfish or kin benefits. But while a cognitive limit may be one reason for the rarity of reciprocity in other species, it may not be the only explanation. Other phenomena that are also strongly affected by the shadow of the future and also seem to depend as much, if not more, on apparent cognitive abilities are widespread in the animal kingdom.

During the formation of dominance hierarchies or peck orders, for example, animals often inflict damage on each other with little or no initial benefit and possibly considerable cost to themselves. Mutual attacks may initially be frequent but the benefit comes later from reduced costs of subsequent interactions with the same individual. In settling their peck orders, chickens are aggressive to each other as strangers, but as they become familiar with each other in subsequent interactions some individuals give way to others without any signs of overt aggression (Guhl 1968; Rushen 1982). Just as in the case of reciprocal altruism, the advantages of paying the initial costs depend on meeting the same individual again in the future so that the rewards of having been aggressive initially can be recouped through the subsequent submissive behaviour of the other. If chickens are kept in groups that are too large for repeated encounters with the same individuals to be likely, peck orders are not expected on theoretical grounds (Pagel & Dawkins 1997) and chickens kept in large high-density flocks do

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not form peck orders at all. Instead they adopt nonsocial, nonaggressive strategies (Nicol et al. 1999). Aggressive pecking and hierarchy formation are features of small flocks (Nicol et al. 1999).

The maintenance of dominance hierarchies where each animal knows its place with respect to the others would seem to be at least as cognitively demanding as keeping track of which animals cooperated on the last encounter. So why should dominance hierarchies be common throughout the animal kingdom (Barnard & Burk 1979; Syme & Syme 1979; Broom et al. 2009) and reciprocity so rare it is hard to find many convincing real-life examples? Could the answer lie not so much in cognitive limits as in the very assumptions of the Prisoner's Dilemma model that is so often used as the basis for explaining reciprocal altruism?

The Prisoner's Dilemma arises when two prisoners are being interrogated separately by the police (Fig. 1a). Each has to decide whether to cooperate (tell the police the other is innocent) or defect (tell the police the other is guilty). The consequences of cooperating and defecting depend on whether the other person cooperates or defects (Axelrod & Hamilton 1981). The model shows that if the two prisoners are never to meet again, the best strategy is to defect, but with repeated interactions, cooperation leaves them both better off. The best strategy for increasing the likelihood of cooperation in a partner in the future is cooperation now. In predicting this outcome, however, the model makes a number of assumptions, including the assumption that the roles of the two prisoners are identical and can be switched. But what if this symmetry is broken? What if real animals cannot be represented as identical prisoners playing interchangeable roles with identical costs and benefits?

Consider a simple situation in which one animal is a much better hunter than another and much more likely to be able to find food on its own. The good hunter gains something from being given food, but gains less than a poor hunter, because its chances of being able to go and get its own food are higher. The good hunter also pays fewer costs, since giving away food is less costly if the chances of being able to find food elsewhere are higher. Figure 1b shows a case in which there are differential costs and benefits for the two types of hunter. In both cases, 'defecting' (being given food without giving anything back) is the best option for a one-off encounter. In both cases giving without receiving (being a sucker) is worse than mutual defection or refusing to cooperate at all. But whereas the poor hunter finds mutual cooperation the best long-term outcome, the good hunter gains so little from cooperating that defection becomes the best long-term policy.

The fact that cooperation can be bettered by such simple changes in the model parameters raises the further question: are such asymmetries (e.g. of need, ability, etc.) between real animals usually so large that cooperation is almost never favoured? Has too much reliance on the Prisoner's Dilemma overestimated the likelihood that reciprocal altruism will occur precisely because it has not embraced the effects of introducing asymmetries? Do asymmetries mean that defection, rather than cooperation, is the best policy, even with repeated interactions between the same animals? By contrast, social hierarchies thrive on asymmetry. Where there are marked differences between individuals, both dominant and subordinate animals benefit from using their experience of previous outcomes with the same individual and continuing to observe their place in the hierarchy (not defecting). For example, a hen that has been beaten by another bird as the peck order was taking shape is unlikely to be able to win against the same individual a week later, and so benefits from not even trying to do so. The bigger the differences between animals, the more mutual benefit there is in a stable hierarchy. Individual differences thus appear to stabilize dominance hierarchies (Broom et al. 2009) whereas they destabilize reciprocity. Dominance hierarchies become destabilized when individual differences become less, for example when a dominant animal ages or is wounded and a subordinate challenges the old order.

It may not, therefore, just be cognitive ability that limits the occurrence of reciprocity and makes it relatively rare. It may be the assumption of the Prisoner's Dilemma game that there should be more symmetry between the participants than is generally the case. Animals, unlike theoretical prisoners, are not equal and their roles are not perfectly exchangeable. The asymmetries between them may favour initial aggression with a time lag before benefits are recouped, resulting in animals learning and sticking to their place in a dominance hierarchy. But these same inequalities may also limit the evolution of cooperation to immediate benefit or benefit to kin. The kind of cooperation that involves giving now and only being repaid at a later date may be limited to conditions that, in nature, are almost never fulfilled.

Player 2

(a)

	Cooperate	Defect
Cooperate	R 1 year in prison	S 5 years in prison
Defect	T 0 years in prison	P 3 years in prison

Player 1

Player 2 (poor hunter)

(b)

	Cooperate	Defect
Cooperate (rich hunter)	$C_g = -2$ $B_g = +1$ **Net = −1**	$C_g = -2$ $B_g = 0$ **Net = −2**
Defect	$C_g = 0$ $B_g = +1$ **Net = +1**	$C_g = 0$ $B_g = 0$ **Net = 0**

Player 1

Player 2 (good hunter)

	Cooperate	Defect
Cooperate (poor hunter)	$C_p = +10$ $B_p = -3$ **Net = +7**	$C_p = -3$ $B_p = 0$ **Net = −3**
Defect	$C_p = 0$ $B_p = +10$ **Net = +10**	$C_p = 0$ $B_p = 0$ **Net = 0**

Player 1

Figure 1. (a) The Prisoner's Dilemma game. The game is defined in the following way: T is a better outcome than R which is better than P which is better than S, and 2R is better than T + S. The game is assumed to be symmetrical in that the roles of Player 1 and Player 2 can be reversed. (b) The effect on the Prisoner's Dilemma of letting the costs and benefits for the two players differ. Player 1 is a better hunter than Player 2. The cost of giving a unit of food is C_g for the good hunter and C_p for the poor hunter. The benefit to the good hunter of being given the food is B_g and that to the poor hunter is B_p.

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