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COMMENTARY

Self-serving punishment and the evolution of cooperation

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Lehmann and Keller provide a useful synthesis to bring some order to the plethora of models that have been proposed to account for the evolution of cooperation and altruism in humans and other animals. Their modelling framework reveals that a few key principles underlie the results of a wide variety of models. However, we believe that the classification of mechanisms given by Lehmann and Keller underestimates the role of punishment as a driving force in the origin of cooperation, rather than just a modifier of the costs and benefits of defection. This omission is in some ways understandable, because there are some logical difficulties inherent in the idea that punishment can drive the initial spread of cooperative strategies. Some forms of punishment, however, do not entail such difficulties. Specifically, the option to terminate an interaction as a response to defection can be a powerful force favouring the spread of cooperative mutants in a noncooperative population. This possibility is not considered by Lehmann and Keller because their model, like most models involving repeated interactions, assumes that individuals engage in 'forced play', i.e. players cannot choose to exit the interaction. Exit threats do not require cognitive processes such as memory or reputation to be effective. Moreover, because termination offers an immediate benefit (in the form of an escape from exploitation), it is an inherently credible threat. As we explain below, it can therefore explain the initial evolution of cooperation more easily than can arguments based on other, costly forms of punishment.

The problem of mutually conditional responses

A common problem with invoking the threat of punishment as an effective force in the initial spread of cooperation is that it requires the simultaneous invasion of mutually conditional responses. Punishers must be selected to respond to defectors by punishing, and defectors must be selected to respond to punishment by cooperating. A mutant 'punisher' strategist cannot spread unless a strategy of responding to punishment by cooperating is already common, but there can be no selection for such responsiveness unless the punishment strategy is already established. Thus, we have a 'chicken-and-egg' problem: how do two conditional strategies, each requiring the presence of the other to be effective, get started in the population?

Most models of punishment simply bypass this problem by assuming the prior presence of one or both conditional strategies to provide the necessary selective environment for the other conditional strategy to prosper. Clutton-Brock & Parker (1995) assume that punishment strategists are already present in the population, and examine the evolutionary stability of punishment when defectors learn to respond cooperatively on a behavioural time scale. The models of Bowles & Gintis (2004) and Gardner & West (2005) also get around the difficulty by fixing one side of the problem, although here it is the facultative response to punishment rather than the punishing strategy that is assumed to be resident in the ancestral population. Boyd & Richerson (1992), however, explicitly discuss the problem of the initial spread of mutually conditional punishment and response. They suggest that nonadaptive behavioural error might provide the punishment environment required to favour the initial spread of conditional cooperation. The presence of a small number of individuals who punish defectors by mistake can give conditional cooperators an edge over unresponsive defectors, which in turn favours the spread of conditional punishers, and so on.

Cutting off relations: a self-serving punishment

While behavioural error may offer one way out of the difficulty, there is a simple alternative solution that does not require this ad hoc invocation of nonadaptive variation. A strategy of punishment can invade a population of nonpunishers if it pays regardless of the response of the other player. The most general example of this type of 'self-serving' punishment arises where players are allowed to terminate the interaction in response to defection (Schuessler, 1989; Majeski *et al.*, 1997; Hauk, 2001; West *et al.*, 2002; Frank, 2003; McNamara *et al.*, 2004). Upon termination, both punisher and defector may suffer the penalty of having to find another interactant, but the punishing strategy can be favoured because it affords the punisher protection from further exploitation. This kind of punishment could also be described as a negative form of 'pseudoreciprocity' (Connor, 1986; Leimar & Connor, 2003), as the self-serving response of one party to defection leads the other party to invest in mutually beneficial cooperation. A classic interspecific example of this mechanism is provided by cleaner fish and their clients (Bshary, 2001). Cleaners can cheat by feeding on client tissue rather than parasites, but it often pays to resist this temptation and settle for a lower rate of energy gain because clients respond to defection by terminating the interaction (Johnstone & Bshary, 2002; Bshary &

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Grutter, 2005). A second example is the mutualism between leguminous plants and N_2 fixing bacteria. Here plants can promote good behaviour in bacteria by switching resources from nodules containing 'lazy' bacteria (who fix little or no N_2 for the plant) to those nodules containing bacteria that are more cooperative (West *et al.*, 2002).

Modelling exit threats

The importance of exit options in the evolution of cooperation is illustrated by a simulation of Schuessler (1989). This model is interesting because of the minimal nature of its assumptions: players pair at random and play an iterated prisoner's dilemma with the option to exit at the end of a round if the other player defects. Finding a new partner involves no cost to either party, and the model assumes no memory or reputation. Schuessler simulates the evolutionary success of a range of strategies of the form 'cooperate on the first $n-1$ rounds, then defect', where n varies from 1 (i.e. 'always defect') to infinity (i.e. cooperate until the other player defects, a strategy termed 'conditional cooperation'). To avoid the unrealistic possibility of two conditional cooperators cooperating forever, the model incorporates a small chance of termination at each round due to extrinsic factors. Given these assumptions it might appear that individuals who 'hit and run' while retaining anonymity could flourish. On the other hand, there is also the potential for cooperators to find each other and enjoy the benefits of long interaction. It turns out that for many for reasonable parameter values the strategy of conditional cooperation can spread against strategies that involve defection. It should be noted, however, that Schuessler's results are based on simulations starting from a population with an equal mix of strategies, and the evolutionary stability of strategies of the form 'cooperate up to round n, then defect and exit' is not explored. Such strategies are not ordinarily evolutionarily stable, as a monomorphic population employing a strategy of this type can be invaded by mutants who defect one round earlier. Cooperation can persist, however, if there is behavioural variation due to mutation, errors in decision making or differences in quality (McNamara *et al.*, 2004).

Schuessler's model shows that exit threats can promote cooperation even when players are symmetrical and there are no costs of finding another partner. Exit threats are likely to be even more effective where the costs of finding a new partner are relatively higher for defectors and lower for terminators (Johnstone & Bshary, 2002; Bowles & Gintis, 2004). In asymmetrical interactions, the balance of power between two players will depend on who suffers most from the breakdown of the interaction. Where one party can find partners much more easily than the other, that party may use the threat of terminating the interaction to extract greater cooperation from their partner. Market forces should thus play a central role in the evolution of cooperation (Noe & Hammerstein, 1995; Noe, 2001; Bshary & Noe, 2003).

More generally, there may be many ecological factors that influence the costs of terminating an established interaction, perhaps differently for different players. Exit threats thus tie the resolution of conflict between individuals to the wider biotic and abiotic environment in which their interaction takes place. This link has been missing from models of cooperation based on forced play, such as the standard iterated Prisoner's Dilemma. However, this link to the external setting of an interaction is an integral part of other approaches to intraspecific helping behaviour, such as pay-to-stay models (Kokko *et al.*, 2002) and reproductive skew theory (Keller & Reeve, 1994; Johnstone, 2000; Cant, 2006). In Kokko *et al.*'s (2002) pay-to-stay model, for example, cooperation is not favoured because of any of the four main mechanisms identified by Lehmann and Keller, but because the threat of eviction is sufficient to make cooperation preferable to defection. This threat would presumably be categorized in their classification as a 'modifier' of the costs and benefits of cooperation, like other forms of punishment. But this is to impose a rather arbitrary distinction between those mechanisms they consider fundamental, and those that are simply modifiers. If this kind of negative reciprocity is classed as a modifier then the same should hold for positive reciprocity. Given the paucity of biological evidence for positive reciprocity and the widespread evidence of exit threats, we suggest that it is punishment by exit that may play the more fundamental role in the evolution of cooperation.

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