Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma

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Abstract. Since 1981, the iterated Prisoner's Dilemma has dominated studies of non-kin cooperation. Alternative models have received relatively little attention. The simplest alternative is mutualism, in which mutual cooperation always pays best. The behaviour of three pairs of blue jays, *Cyanocitta cristata*, was tested in precisely controlled iterated mutualism and Prisoner's Dilemma games. Although the jays readily cooperated in the mutualism game, cooperation neither developed nor persisted in a Prisoner's Dilemma. No empirical justification was found for the status of the iterated Prisoner's Dilemma as the basic paradigm of non-kin cooperation.

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In 1950, Merrill Flood and Melvin Dresher of the RAND corporation challenged John Nash's concept of strategic equilibrium by presenting a simple 'non-cooperative' game. This game became known as the Prisoner's Dilemma based on a scenario presented by Albert Tucker (Poundstone 1992). In 1981, Axelrod & Hamilton argued that the Prisoner's Dilemma was a generally useful paradigm for the study of cooperation between unrelated animals. The Prisoner's Dilemma has since dominated both theoretical and empirical studies of non-kin cooperation (Lombardo 1985; Boyd & Lorberbaum 1987; Milinski 1987; Dugatkin 1988; Boyd 1989; Nowak 1990; Nowak & Sigmund 1992, 1993). Recently, however, some have argued that the Prisoner's Dilemma is only one of several alternatives to consider (Noë 1990; Dugatkin et al. 1992; Mesterton-Gibbons & Dugatkin 1992).

The Prisoner's Dilemma has motivated some clever studies of animal strategic behaviour (Gardner et al. 1984; Lombardo 1985; Milinski 1987; Dugatkin 1988), although all empirical studies that claim to provide evidence of non-kin cooperation in a Prisoner's Dilemma suffer two deficiencies. First, no study has verified, through measurement or experimental control, that the payoffs governing the reported behaviour conform to a Prisoner's Dilemma. Second, no study has explicitly considered alternative models of non-kin cooperation. Our study addresses both of these deficiencies.

The Alternatives

Mesterton-Gibbons & Dugatkin (1992) framed a basic model of animal cooperation in terms of a two-player game whose general characteristics are given by the matrix

$$\begin{array}{cc} & C \ \ D \\ \begin{array}{c} C \\ D \end{array} & \begin{bmatrix} R & S \\ T & P \end{bmatrix} \end{array}$$

During any play of the game, each player may cooperate (C) or defect (D), to receive a payoff that is based on both its own choice (the rows of the matrix) and its opponent's choice (the columns). Thus, if both players cooperate, both receive R units of payoff. If one player cooperates and the other defects, the cooperator receives S and the defector T. If both defect, both receive P. Following Mesterton-Gibbons & Dugatkin (1992), we define cooperation in terms of its economic consequences, not in terms of social interaction: mutual cooperation is a joint action for mutual benefit. This definition has two mathematical components. First, $R > P$ so that if both players deviate from mutual C, both do worse. Second, $R > \min(S, T)$ so that if one player deviates from mutual C, at least one player does worse.

This approach can describe four distinct cooperative situations, each defined by the two inequalities above, plus two unique inequalities. If $R > T$ and $S > P$, as in the matrix

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$$\mathbf{M} = \begin{pmatrix} R = 4 & S = 1 \\ T = 1 & P = 0 \end{pmatrix} \quad (1)$$

then we have Mutualism (West-Eberhard 1975), in which cooperation is a 'dominating choice' (the best choice regardless of your opponent's decision). In this game, mutual C is a unique, strong Nash equilibrium. (A Nash equilibrium is a pair of actions such that neither player can gain more by deviating. If deviating leads to a loss, as opposed to no change in payoff, the Nash equilibrium is called 'strong'. A strong Nash equilibrium is an evolutionarily stable state (ESS), sensu Maynard Smith 1982.) Mutualism is the simplest model of non-kin cooperation and is clearly consistent with well-known principles of behavioural change (e.g. the law of effect).

If $R > T$ and $P > S$, as in the matrix

$$\mathbf{S} = \begin{pmatrix} R = 4 & S = 2 \\ T = 1 & P = 3 \end{pmatrix} \quad (2)$$

then we have Synergism, or 'synergistic mutualism' (Maynard Smith 1983), in which both mutual D and mutual C are Nash equilibria. Stable mutual cooperation and stable mutual defection are both game-theoretical 'solutions', and predicted behaviour will depend on initial conditions.

If $T > R$ and $S > P$, as in the matrix

$$\mathbf{C} = \begin{pmatrix} R = 4 & S = 2 \\ T = 5 & P = 1 \end{pmatrix} \quad (3)$$

then we have the Cruel Bind (Trivers 1972), in which neither mutual C nor mutual D is a Nash equilibrium. In this game, it is better to cooperate when your opponent defects, but it is better to defect when your opponent cooperates.

Finally, if $T > R$ and $P > S$, as in the matrix

$$\mathbf{P} = \begin{pmatrix} R = 3 & S = 0 \\ T = 5 & P = 1 \end{pmatrix} \quad (4)$$

then we have the celebrated Prisoner's Dilemma. During any single play of the Prisoner's Dilemma, each player can do better by defecting, regardless of what its opponent does. The dilemma is that if both players defect, each does worse than if both had cooperated.

In a repeated or Iterated Prisoner's Dilemma, mutual cooperation pays best in the long run (in an Iterated Prisoner's Dilemma, it is conventional to require that $R > (S + T)/2$, so mutual C pays better than alternating between C and D; this guarantees the second component of our defi-

nition of cooperation). Axelrod & Hamilton (1981) suggested that cooperation could be maintained in an Iterated Prisoner's Dilemma if individuals used a strategy called Tit for Tat (cooperate on the first play then do what your opponent did on the previous play). Although many have questioned the Tit-for-Tat strategy (Boyd & Lorberbaum 1987; Farrell & Ware 1989; Nowak & Sigmund 1992), the Iterated Prisoner's Dilemma has become the basic paradigm for non-kin cooperation (Nowak & Sigmund 1993).

METHODS

Subjects

We used six blue jays, *Cyanocitta cristata*, of unknown sex. We maintained all of the jays on a diet of Lafeber's aviera parrot food. We housed the jays in individual cages (measuring $38 \times 38 \times 61$ cm) in a colony of 24. The housing room had an average temperature of approximately 25°C, and a 14:10 h light:dark cycle, with lights on at 0700 hours.

Apparatus

We used two adjoining operant chambers. The chamber walls were primarily galvanized sheet metal, and the tops were wire mesh. A centre 'partition', which could be opaque or clear, formed a common wall between the two chambers. The front panel in each chamber contained one perch, two keys, and one food cup mounted between and slightly below the keys. Stimulus projectors outside the chambers illuminated the keys with various colours. Pellet dispensers delivered 20-mg food pellets to the food cups. A bowl in each chamber provided water for drinking and bathing. A computer controlled the projectors and dispensers, and detected pecks at the keys.

General Procedure

We randomly assigned the six jays to three pairs. We completed all data collection for a given pair before moving to the next. Before a pair started, we randomly assigned one member to the left chamber. The two jays lived in their assigned chambers and worked for all of their daily food,

until data collection for the pair was complete. We chose a closed economy approach for two reasons: (1) it more closely approximates natural feeding and (2) it avoids potential health risks associated with food deprivation (Moran 1975). Because we did not limit their food intake, the jays usually maintained their weights well above standard deprivation levels. As a precaution, however, we monitored the jays' weights, food intake and health, supplementing their diets as needed (supplemental feeding was rarely required; two or three times per pair).

The jays spent each night in their chambers. A timer switched on the room light each morning at 0700 hours. Another timer switched on the computer and a white-noise generator (to mask outside noise) at 0715 hours. We began data collection at 0730 hours. The jays worked at their own pace over a series of discrete trials until 1330 hours, when we placed them in their home cages (without food), and then cleaned the chambers and bowls. We returned the jays to their chambers and resumed trials at 1430 hours. Data collection ended at 2030 hours. Timers switched off the noise and computer at 2045 hours, and the room light at 2100 hours.

Trial-by-trial Procedure

During each trial, both jays chose to cooperate or defect by pecking one of the two keys in their chambers. A different key colour represented each choice (e.g. a jay might peck a red key to cooperate or a green key to defect). We assigned each pair of jays a unique pair of colours and reversed the meaning of the colours between members of the pair. Both colours were shown during each trial, one on the left key and one on the right. Which key showed which colour was randomized with the exception that each colour appeared equally often on both keys.

One jay started a trial and the other ended it. Both jays were equally likely to start a trial. Trials were divided into two stages: the choice stage, during which both jays chose to cooperate or defect, and the payoff stage, during which both jays received payoffs according to their choices. We denote the four behavioural combinations possible during a trial with CC, CD, DC and DD, where C represents cooperation and D defection. The left letter represents the choice of the jay in the left chamber.

Experimental Manipulations

The number of food pellets each jay received during each trial depended on the combination of both jays' choices in a 2×2 payoff matrix. We used two matrices: the Prisoner's Dilemma matrix, **P** (see equation 4), and the mutualism matrix, **M** (see equation 1). Using a standard 'A-B-A' experimental design, we exposed pairs first to **P**, then to **M**, and then again to **P**.

We ended both the first exposure to **P** and the subsequent exposure to **M** when one of three behavioural categories, CC, DD, or CD and DC combined, accounted for more than 90% of the daily completed trials over 4 consecutive days. For the second exposure to **P**, we additionally required that the exposure last for at least 7 days (because we viewed this treatment as a test of the stability of cooperation; see below).

Each pair experienced this three-phase, '**P-M-P**' payoff sequence twice: once with the opaque partition and once with the clear (pairs 1 and 3 experienced the opaque partition first, pair 2 the clear). We assigned each pair two new key colours when we switched partitions. We introduced the clear partition to increase 'communication' between the jays, making the situation slightly more natural while knowingly sacrificing independent choice.

RESULTS

General Behaviour

The jays completed an average ($\pm$ SE) of 200.43 ± 8.82 trials per day. A two-way repeated-measures ANOVA showed that neither the payoff phase nor the partition type affected the number of days the pairs took to complete each phase (phase: $F_{2,4}=3.13$, $P=0.15$; partition: $F_{1,2}=0.53$, $P=0.54$; interaction: $F_{2,4}=1.02$, $P=0.44$). Pair 3 often took longer to complete a phase than the other pairs, but the overall behavioural trends were similar between pairs (Fig. 1).

Responses to Payoff Manipulations

When the jays first experienced the Prisoner's Dilemma, in each partition treatment, they initially chose to cooperate or defect roughly equally (Fig. 1). Within 8 days at most, however, each pair was mutually defecting (DD), at nearly
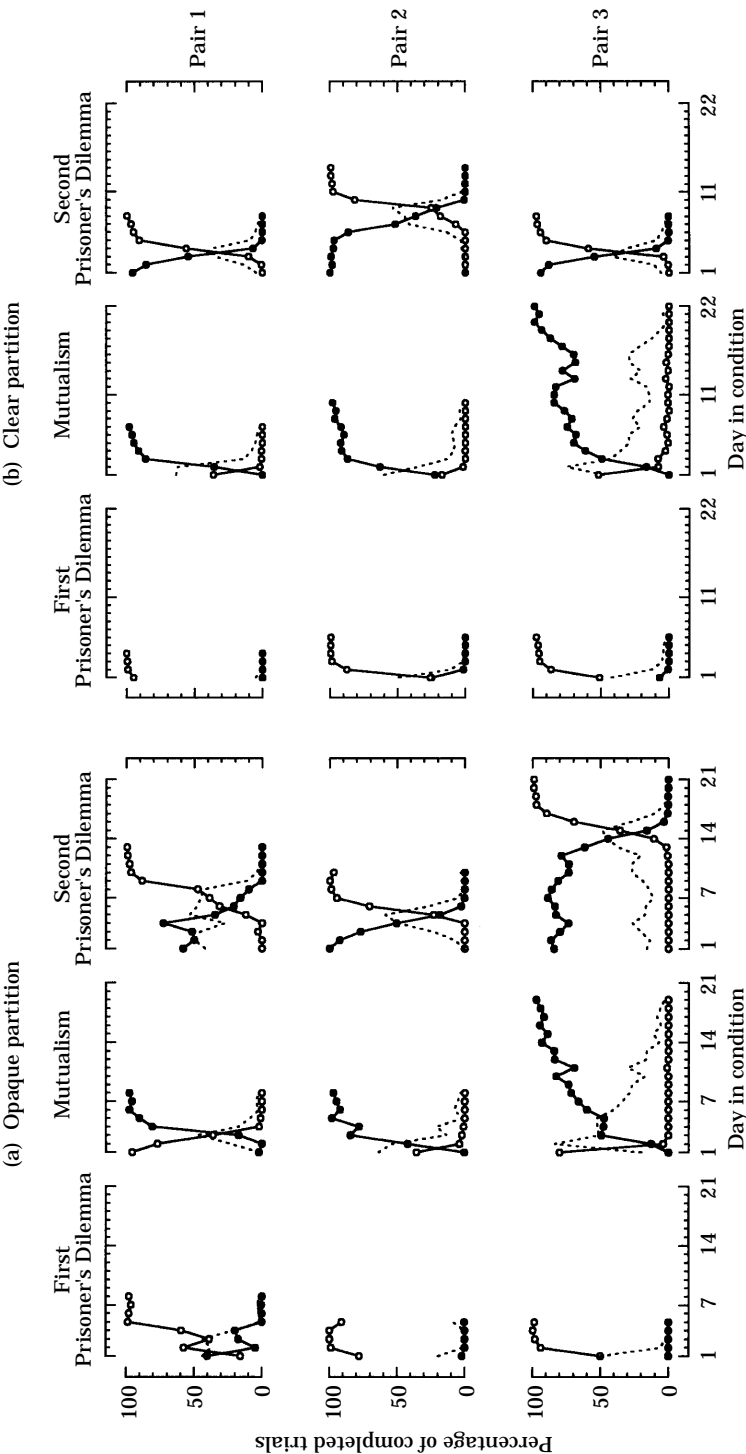
Figure 1. Changes in behaviour over time, expressed as percentages of trials completed per day: mutual cooperation (CC trials: ●), mutual defection (DD trials: ○), and mixed trials (CD and DC trials: dotted line). Each panel shows all three pairs' performance over one **P-M-P** payoff sequence. (a) Performance in the opaque-partition treatment; (b) performance in the clear-partition treatment.

100% in both partition treatments. This pattern replicates results from studies of rats (Flood et al. 1983; Gardner et al. 1984), and is generally consistent with studies using human subjects (Scodel et al. 1959; Rapoport & Chammah 1965). When we changed payoffs from the Prisoner's Dilemma to the mutualism matrix, the previously established mutual defection quickly declined, to be replaced by stable, mutual cooperation (CC) in all three pairs, under both partition treatments (Fig. 1).

When we made the third payoff change, from mutualism back to the Prisoner's Dilemma, mutual defection again developed in all three pairs, under both partition treatments (Fig. 1). Unlike their first exposure to the Prisoner's Dilemma, pairs began their second exposure by mutually cooperating. Our experiment, therefore, represents the first direct test of the stability of mutual cooperation in a known Prisoner's Dilemma (for animal or human subjects). Stability tests are important because all game-theoretical equilibrium concepts, whether evolutionary or economic, are strategic stability concepts. A model that predicts the evolutionary stability of mutual cooperation also implies behavioural stability.

DISCUSSION

No Cooperation in the Iterated Prisoner's Dilemma

Current, widely accepted models predict cooperation in an Iterated Prisoner's Dilemma. Contrary to this expectation, mutual cooperation neither developed nor persisted in our tests of the Iterated Prisoner's Dilemma. Instead, our jays repeatedly stabilized at mutual defection in all of our Iterated Prisoner's Dilemma conditions. We explore some of the possible reasons for this outcome in the following section.

Repetition of the game

Cooperation in an Iterated Prisoner's Dilemma requires that players expect to play each other repeatedly, without knowing when the game will end (Axelrod & Hamilton 1981; Mesterton-Gibbons 1992). It might be argued that the jays did not play each other often enough to

cooperate. This possibility seems unlikely: our jays lived in adjacent compartments 23 h per day, for an average of 60 days, and averaged 200 plays per day. At the time the stability test began, the pairs had played an average of 3435 times, three orders of magnitude more repetition than required by Axelrod & Hamilton's (1981) model for matrix **P**.

An unnatural situation

Although our methods offer precise experimental control, pecking a key seems an unlikely act of cooperation. We do not suppose that natural selection has favoured cooperative key-pecking in Skinner boxes. Indeed, we offer no argument that blue jays ever faced Prisoner's Dilemmas in their evolutionary history. Rather, our experiment addresses the general significance of the Prisoner's Dilemma as a model of non-kin cooperation. Supporters of the Prisoner's Dilemma have made sweeping claims about its generality (Axelrod & Hamilton 1981), and have asserted its status as 'the leading metaphor for the evolution of cooperation among selfish agents' (Nowak & Sigmund 1993, page 56). Given these claims, it is reasonable to suppose that natural selection has equipped animals with the ability to recognize and implement cooperative strategies, in novel situations, when economic circumstances favour cooperation. This view is supported by the fact that mutual cooperation developed readily with our seemingly arbitrary procedures, but only in our mutualism treatment: mutual cooperation neither developed nor persisted in our Iterated Prisoner's Dilemma treatments. Thus, of the two models of cooperation we tested, mutualism was the more generally applicable. In addition, we note that ESSs (Maynard Smith 1982) are always Nash equilibria (Mesterton-Gibbons 1992), and as such there is no requirement of special evolutionary origin: Nash equilibria require only that organisms recognize, and act in, their own self-interest (and, as we explain below, cooperation and selfishness are not mutually exclusive).

Discounting delayed rewards

The implicit assumption in the Iterated Prisoner's Dilemma family of models that animals cooperate to gain long-term benefits may, in fact, be unrealistic when compared to what we

know about how animals value benefits over time. Foraging animals discount the future, showing strong, well-documented preferences for immediate food rewards (Logue 1988). This has important implications for Iterated-Prisoner's-Dilemma-based models of cooperation because, despite May's (1981) admonition about the possible role of time discounting in the Iterated Prisoner's Dilemma, current theory relies almost exclusively on repetition and undiscounted future rewards to make cooperation worthwhile in the Prisoner's Dilemma. Evidence suggests that assuming undiscounted rewards is unrealistic, and our results suggest that repetition is not enough. Cooperation in an Iterated Prisoner's Dilemma may also require unusual economic circumstances (Kagel et al. 1986; Stephens & Krebs 1986; Logue 1988) that discourage the myopic behaviour that characterizes animal feeding preferences (Kagel et al. 1986).

Recognition and recall

Cooperation in an Iterated Prisoner's Dilemma, through Tit for Tat or any other strategy, requires that the players possess certain cognitive abilities. A player must be able to recognize other individuals and recall the outcomes of past interactions with them (Axelrod & Hamilton 1981; Dugatkin & Wilson 1992). It is possible that blue jays lack these abilities. If so, the jays would treat each trial as a single-play Prisoner's Dilemma, in which mutual defection is the only strong equilibrium. This possibility seems unlikely, given the large body of evidence for recognition in vertebrates (Myrberg & Riggio 1985; Cheney & Seyfarth 1990), including the related pinyon jay, *Gymnorhinus cyanocephalus* (Marzluff 1987; Marzluff & Balda 1992), but it is easily tested.

Variants of Tit for Tat

An enormous amount of attention has focused on the relative merits of different strategies, mostly variants of Tit for Tat, in the Iterated Prisoner's Dilemma (Boyd & Lorberbaum 1987; Boyd 1989; Nowak 1990; Nowak & Sigmund 1992, 1993). The preoccupation with new and improved strategies has sometimes distracted from the main point: explaining animal cooperation. Nowhere is this distraction more clearly seen than in Tit for Tat itself, a strategy which, despite its

celebrity, does not actually predict stable mutual cooperation under realistic circumstances (Molander 1985; Nowak 1990). Strategies that do lead to stable mutual cooperation (e.g. generous Tit for Tat, Pavlov) in theoretical treatments of the Iterated Prisoner's Dilemma are clearly inconsistent with our results.

Pavlov

Our results are especially relevant to the 'Pavlov' strategy proposed by Nowak & Sigmund (1993). A Pavlov strategist repeats its previous choice after experiencing one of the two higher payoffs in an Iterated Prisoner's Dilemma (R or T), but swtiches to the other choice after experiencing one of the two lower payoffs (S or P). Nowak & Sigmund argue that Pavlov is a manifestation of the 'widespread' psychological mechanism, 'win–stay/lose–shift'. Nowak & Sigmund's variant of win–stay/lose–shift assumes that animals in an Iterated Prisoner's Dilemma categorize both R and T as 'wins' and both S and P as 'losses'. In contrast, standard psychological tests of the win–stay/lose–shift strategy define a win as a response that leads to reward, and a loss as a response that leads to no reward. Interestingly, blue jays are known to implement win–stay/lose–shift in such standard tests (Kamil et al. 1977), but they did not cooperate in our tests of the Iterated Prisoner's Dilemma.

Our results agree with a large body of literature, such as Vaughn & Herrnstein's (1984) idea of melioration, suggesting that animals will categorize wins and losses in terms of immediate or 'momentary' rates of reward (see also Hinson & Staddon 1983; Staddon 1983). For example, when a jay in an Iterated Prisoner's Dilemma increases its payoff from S to P by defecting, it is likely to perceive the payoff as a win rather than a loss. Our results stand in stark contrast to Nowak & Sigmund's claims of psychological realism.

Cooperation, Altruism and Reciprocity

Our use of mutualism as an alternative model of cooperation has been challenged by some who feel that mutualism is not a 'legitimate' form of cooperation, because animals cooperating mutualistically are acting in their immediate self-interest. This criticism confuses altruism (donation of benefit to a recipient at a loss to the donor) with cooperation (joint action for mutual benefit).

Cooperation may or may not be altruistic. Cooperation in an Iterated Prisoner's Dilemma is altruistic in the short term, because cooperators forego the temptation to defect (Boyd 1988), but cooperation in mutualism is not altruistic in any sense. If we represented cooperation and altruism as a Venn diagram, they would be overlapping, but not identical circles (see also Mesterton-Gibbons & Dugatkin 1992; Krebs & Davies 1993).

A similar, but more complex, confusion arises in the relationship between cooperation and reciprocity. There is no necessary link between cooperation and reciprocity. Animals may cooperate without reciprocating, as in mutualism (West-Eberhard 1975; Packer 1988), or they may reciprocate without cooperating, as with two Tit for Tat strategists once mutual defection is established. Reciprocity can be related to cooperation in two distinct ways: (1) reciprocity can be the 'force' that stabilizes long-term altruistic cooperation, as Axelrod & Hamilton (1981) originally argued, or (2) reciprocity may be a form of mutual cooperation, as in 'I feed you when your stomach is empty, and you feed me when mine is empty' (as suggested of vampire bats; Wilkinson 1984). Cooperative reciprocity can usually be explained by mutualism when benefits are measured on the time scale of a complete cycle of reciprocation. It should be clear, therefore, that evidence of animal reciprocity (Wilkinson 1984; Reboreda & Kacelnik 1993) is weak evidence, at best, for the Iterated Prisoner's Dilemma family of models.

Understanding the ambiguities surrounding cooperation and evidence of reciprocity helps to clarify the distinctions between our study and a procedurally similar study by Reboreda & Kacelnik (1993). Reboreda & Kacelnik tested starlings, *Sturnus vulgaris*, in a game 'inspired by the prisoner's dilemma' (page 67). They reported that 'some level of cooperation persisted' (page 67). This result seems at odds with ours, but the apparent contradiction is eliminated when one realizes that Reboreda & Kacelnik confused cooperative reciprocity maintained by mutualism, with mutual cooperation maintained by reciprocity. The starlings played the following game (the matrix shows the payoffs to the 'row' player):

	Peck	Withhold peck
Peck	NA	0
Withhold peck	Food	0

A starling received food only on trials when it did not peck but its opponent did. The first animal to peck terminated the trial, delivering food to its opponent, so mutual pecking was not available in the game (NA in the Peck–Peck cell). Such a game strongly favours a reciprocating strategy, because the players must adopt some form of alternation for both to obtain some food.

Reboreda & Kacelnik repeatedly called the peck response 'cooperative', but it is unclear how this could be so: joint pecking was not possible and, therefore, could not pay better than joint withholding (recall the inequalities above that define cooperation). What was mutually beneficial was alternation of pecking and withholding, so that mutual cooperation could occur only over two-trial 'plays' of the game. At this time scale, their game bears little resemblance to a Prisoner's Dilemma, but instead is a mutualism-like game in which joint alternation is the only strong equilibrium.

Conclusion

The Prisoner's Dilemma presents a compelling mathematical puzzle with a rich intellectual history. Moreover, the Iterated Prisoner's Dilemma has stimulated 14 years of ingenious biological theorizing. Yet despite this display of theoretical competence, there is no empirical evidence of non-kin cooperation in a situation, natural or contrived, where the payoffs are known to conform to a Prisoner's Dilemma. In addition to not controlling or measuring the payoff matrix, studies purporting to test the Prisoner's Dilemma usually fail to test it against alternatives. Biological interest in the Prisoner's Dilemma cannot be justified only by the conceptual appeal of the problem: there is no meaningful sicentific rigour without empirical rigour. The time for studies that confirm Tit-for-Tat-like behaviour in presumptive Prisoner's Dilemma-like circumstances has, in our view, passed. We need critical tests of alternatives in games with demonstrable economic consequences.

Some will say that the Prisoner's Dilemma was never intended to fit precisely any particular natural situation, that it is simply a caricature of some biological systems. We point out that mutualism is also an over-simplified caricature of natural situations. Yet cooperation is readily demonstrated in the mutualism caricature but not in the Prisoner's

Dilemma caricature. Despite our enthusiasm for mutualism as the most parsimonious alternative to the Prisoner's Dilemma, we feel that neither model captures all the biological possibilities. Mutualism and the Prisoner's Dilemma represent end points of a range of conceivable cooperative situations. Perhaps it is time to explore the rich set of possibilities between mutualism and the Prisoner's Dilemma.

ACKNOWLEDGMENTS

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