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 Materials and Methods
 Figs. S1 and S2

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Discounting and Reciprocity in an Iterated Prisoner's Dilemma

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The Iterated Prisoner's Dilemma (IPD) is a central paradigm in the study of animal cooperation. According to the IPD framework, repeated play (repetition) and reciprocity combine to maintain a cooperative equilibrium. However, experimental studies with animals suggest that cooperative behavior in IPDs is unstable, and some have suggested that strong preferences for immediate benefits (that is, temporal discounting) might explain the fragility of cooperative equilibria. We studied the effects of discounting and strategic reciprocity on cooperation in captive blue jays. Our results demonstrate an interaction between discounting and reciprocity. Blue jays show high stable levels of cooperation in treatments with reduced discounting when their opponent reciprocates, but their levels of cooperation decline in all other treatment combinations. This suggests that stable cooperation requires both reduced discounting and reciprocity, and it offers an explanation of earlier failures to find cooperation in controlled payoff games.

The Prisoner's Dilemma illustrates the economic barriers to cooperative action. In this game, the defecting (noncooperative) option is always the best choice for a single play of the game, even though both players could do better if they cooperated. Axelrod and Hamilton (1) argued that cooperation could be a game theoretical equilibrium if (i) the game was played repeatedly and (ii) the players adopted a reciprocating strategy. In their argument, repetition and reciprocity combine to make mutual cooperation a viable strategy, because although a defector will receive an immediate reward, reciprocity means that it will suffer for this choice in the long run.

Although theoreticians have exploited this paradigm with great success, it has been markedly less successful empirically (2–5). Nonhuman animals show a strong tendency to defect in experimentally created Prisoner's Dilemmas (6–9). These studies raise important questions, because we cannot usually confirm that the payoffs in naturalistic studies conform to the Prisoner's Dilemma. This uncertainty has led to controversy in some cases (10–12), and in others, it has led to questions about whether simpler explanations of observed behavior might not be more appropriate (5, 13, 14). More than 20 years after Axelrod declared the Prisoner's

Dilemma to be “the *E. coli* of social psychology” (15), there is still no single unambiguous case of stable nonhuman cooperation in a verifiable Prisoner's Dilemma.

One possible explanation for the fragility of cooperation in the Iterated Prisoner's Dilemma (IPD) is strong temporal discounting. In theory, animals should cooperate in an IPD because cooperation leads to higher payoffs in the long run, but animals may not value these long-term benefits because they strongly discount the future. Psychological studies support this idea. In these studies (16–18), experimentalists offer animals a choice between small immediate and large delayed food rewards. These experiments show very strong preferences for immediacy. Fitted discounting functions suggest that the first second of delay reduces the value of food reward by as much as 50% (19). These data, therefore, suggest that animal discounting may be much stronger than rates typically assumed by economists and other students of human behavior [e.g., 4% per year (20)].

An alternative explanation of the fragility of cooperative equilibria might hold that animals fail to cooperate, not because they discount strongly, but because they do not implement the appropriate strategy. In the IPD framework, the opponent's reciprocation means that cooperation now enhances long-

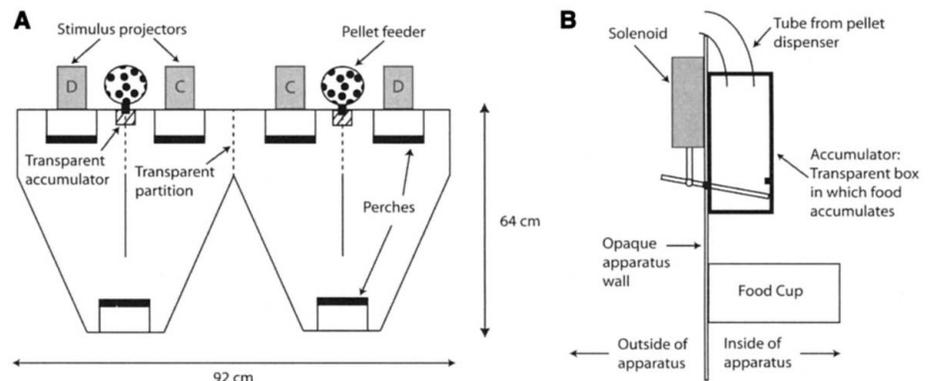


Fig. 1. (A) Top view of apparatus. The apparatus consists of side-by-side compartments, each in the shape of a V. Each compartment is equipped with three perches. Each perch has a microswitch that reports its status to a controlling computer. Each compartment houses a single bird, one of which is designated the subject and the other is designated the stooge. The subject chooses freely, but the stooge follows an experimentally imposed strategy. At the beginning of a play, the birds wait on their respective rear perches (at the apex of the V). At a programmed time, the controlling computer switches on stimulus lights on the front panel signaling that a trial has begun. The subject may hop forward to one of the two front perches to indicate its choice. A hop on the inside perch indicates a cooperate (or “C”) choice, whereas a hop on the outside perch indicates a defect (or “D”) choice. The stooge only sees one stimulus light and must hop on the associated perch. The apparatus is designed with transparent partitions across the front and opaque partitions elsewhere so that the birds can see each other after they have made a choice (hopped to the front), but not before. When both birds occupy one of the front perches, the pellet dispensers deliver food into the accumulators. **(B)** Accumulator. A transparent plastic box, front and center in each compartment, received food from the pellet dispenser. The bottom of the box was a flap that could be opened by the controlling computer. Thus, during accumulated treatments, subjects could see their food gains but not consume them until the flap was opened.

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term gains by increasing the likelihood of future cooperation; without such a strategy, there is no reason to cooperate, even if animals do not discount strongly.

We conducted a factorial experiment, manipulating discounting and strategy, to assess the contributions of discounting and strategic reciprocity to the fragility of the cooperative equilibrium. The subjects were 16 blue jays (*Cyanocitta cristata*) of unknown sex and mixed experimental histories. We assigned these 16 individuals to eight pairs of unrelated individuals. We designed an experimental chamber composed of side-by-side V-shaped compartments so that each member of the pair had its own compartment (Fig. 1A).

To manipulate discounting, we used payoff-accumulation treatments in which subjects had to complete a sequence of plays before obtaining the accumulated benefits from that sequence (21). Intuitively, this should emphasize the combined benefits of a sequence of interactions. To implement payoff accumulation, our apparatus dispensed food into a transparent box (Fig. 1B) so that

subjects could see their winnings but not consume them until a flap at the bottom of the box opened. In accumulated (low discounting) trials, we held food in the accumulator for four plays of the experimental game, dispensing the subject's accumulated gains at the end of the fourth play in a sequence. In unaccumulated treatments, the flap dispensed food after every play. A preliminary experiment confirmed that accumulation reduced discounting as predicted (22).

To manipulate strategies, we randomly designated one individual in a pair to be the subject and the other to be the "stooge." During data collecting trials, the subject chose freely between cooperating (C) and defecting (D) in a Prisoner's Dilemma (23). The stooge, however, played one of two experimental strategies: unilateral defection (All-D) or tit-for-tat (TFT) (cooperate initially but copy your opponent's previous move on all subsequent plays). The stooge, therefore, was forced to choose either C or D, according to its preprogrammed strategy. In broad outline, therefore, our experiment was

a conventional two-by-two factorial experiment with two levels of accumulation (accumulated and unaccumulated) and two levels of opponent strategy (All-D and TFT).

Game theoretical equilibria are stability concepts, so our design tested the effects of these four treatments on the stability of cooperation in a Prisoner's Dilemma. To achieve this, we presented each subject with a baseline matrix, which quickly led to high levels of the C response. After establishing high levels of C, we switched to a Prisoner's Dilemma payoff matrix and measured changes in the frequency of C over 1000 free-choice trials. The experiment followed a within-subjects design so that each pair experienced all four treatments in a randomly determined order (22).

Results from the four treatments are shown in Fig. 2 (22). When the opponent always defected, the frequency of cooperation declined toward zero, regardless of whether food accumulated. When the opponent reciprocated, however, we observed elevated levels of cooperation, but there was a striking difference between accumulated and unaccumulated treatments. In accumulated treatments, where in theory we reduced the effects of discounting, levels of cooperation are high and stable. In unaccumulated treatments, levels of cooperation are elevated but declining, parallel to the pattern shown in the All-D treatments. A repeated measures analysis of variance shows a significant accumulation by strategy by time interaction ($F_{2,14} = 4.31$, $P = 0.03$), supporting the idea that reduced discounting and strategic reciprocity combine to influence the stability of cooperation.

Fig. 2. Stability of cooperation in each of our four treatments. The y axis shows the relative frequency of the C response. The x axis divides trials into thirds, roughly the first 333 trials, the second 333 trials, and the third 333 trials. (A) Data for the accumulated (reduced discounting) treatments. (B) Unaccumulated (normal discounting) treatments. The dashed line shows treatments in which the opponent plays the reciprocating strategy TFT, and the solid line shows treatments in which the opponent plays All-D. Error bars indicate 95% confidence levels.

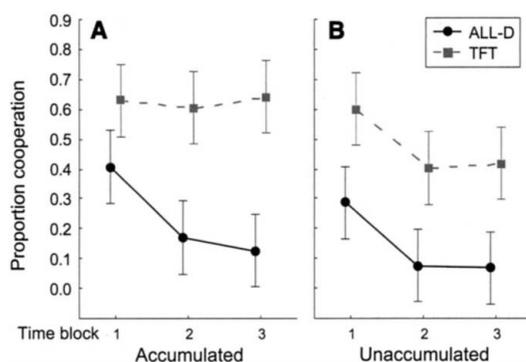
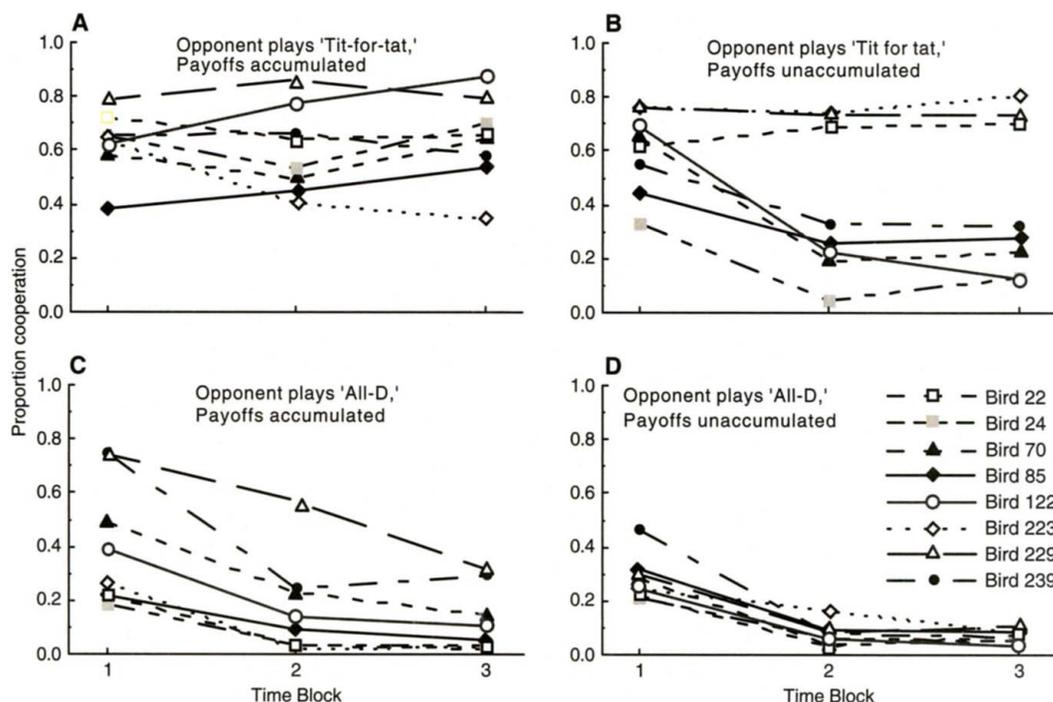


Fig. 3. Stability of cooperation showing individual variation. This is similar to Fig. 2, except that individual subjects are distinguished as shown in the legend. (A and C) Accumulated (reduced discounting) treatments. (B and D) Unaccumulated (normal discounting) treatments. In (A and B), treatments are shown in which the opponent plays the reciprocating strategy TFT, and in (C and D), treatments are shown in which the opponent plays All-D.



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Table 1. Observed and theoretical strategies. The probability of the subject cooperating in the trial following the T , R , P , and S payoffs was calculated for accumulated and unaccumulated trials in the TFT treatment. A bootstrap sampling technique was used to establish confidence limits. This technique generated 1000 strategy vectors from the data. The values for TFT and Pavlov represent predicted strategy vectors for subjects implementing those strategies. Numbers in parentheses are 95% confidence limits.

| Source | t | r | p | s |
|-----------------------|----------------------|----------------------|----------------------|----------------------|
| Data: | 0.644 (0.600, 0.683) | 0.755 (0.731, 0.780) | 0.394 (0.349, 0.437) | 0.587 (0.545, 0.628) |
| Accumulated Data: | 0.381 (0.338, 0.425) | 0.686 (0.652, 0.720) | 0.225 (0.202, 0.248) | 0.496 (0.450, 0.542) |
| Unaccumulated Theory: | 1.0 | 1.0 | 0.0 | 0.0 |
| Tit-for-tat Theory: | 0.0 | 1.0 | 1.0 | 0.0 |
| Pavlov | | | | |

Data in Fig. 3 are similar to those in Fig. 2, except that Fig. 3 shows separate results for each subject. Individuals were most consistent in the All-D/unaccumulated condition, where all eight subjects approached zero cooperation by the end of the treatment. In the TFT/accumulated treatment, there is more variation, but all individuals were cooperating at elevated levels at the end of the treatment. In the TFT/unaccumulated condition, we observed some intriguing bimodality, with three of eight birds showing stable levels of cooperation (as in the TFT/accumulated treatment) and the other five birds showing an erosion of cooperation that parallels the data in the All-D treatments. The elevated levels of cooperation observed in the TFT/unaccumulated treatment (Fig. 2B) are largely due to these three individuals.

Our data allow some characterizations of the subjects' strategies in response to the experimentally created reciprocity of the stooge. One can represent a variety of first-order strategies with the vector representation (t, r, p, s) , where t is the probability of cooperating after obtaining payoff T [subject defected, stooge cooperated (23)], r is the probability of cooperating after obtaining payoff R (both subject and stooge cooperated), and so on (21). Using this notation, we represent TFT as $(1, 1, 0, 0)$, All-D as $(0, 0, 0, 0)$, and Nowak and Sigmund's (24) Pavlov as $(0, 1, 1, 0)$. Table 1 shows calculated strategy vectors for the two treatments in which the opponent played TFT (25).

We saw three patterns. First, all four components of the strategy vector were higher in the accumulated treatment than in the unaccumulated treatment. We observed especially striking differences between the accumulated and unaccumulated treatments for the t and p components of the strategy. This means that subjects were more likely to switch from defection to cooperation when payoffs accumulated, regardless of whether their most recent defection resulted in a large (T) or mediocre (P) payoff. In contrast, the r and s components of the strategy varied relatively little, suggesting that the main effect of accu-

mulation is an increased willingness to switch from defection to cooperation. Second, the overall pattern of the observed strategy was $r > t \approx s > p$; that is, subjects were most likely to cooperate after mutual cooperation and least likely to cooperate after mutual defection, but they cooperated at roughly equivalent intermediate levels in the two "mixed" situations (t , subject defected and stooge cooperated; s , subject cooperated and stooge defected). Third, as Table 1 shows, the observed strategy disagrees strikingly with both Pavlov and TFT. For example, both Pavlov and TFT predict that $s = 0$ (do not cooperate with a player who has just "suckered" you), but our subjects were extremely forgiving, cooperating at rates near 50% after they had been suckered.

Our results show that discounting and strategy both affect the stability of cooperation; we observed high stable levels of cooperation when payoff accumulation reduced discounting and the opponent played the strongly reciprocating strategy TFT. We observed declining levels of cooperation in all other treatments. Several recent critiques of the Prisoner's Dilemma have focused on discounting (7, 9, 26, 27). Our result is in general agreement with these critiques, but it also emphasizes the complementary relation between discounting and strategy. It is, after all, the strategy that creates a pattern of future gains.

Our work suggests that the timing of benefits can be the difference between stable cooperation and cooperation that erodes to mutual defection. These results agree in some respects with Axelrod and Hamilton's influential framework (1), because they show that reciprocity combines with future value to stabilize cooperative action. Yet, our results also agree with the work of those who have challenged the general applicability of the IPD framework to real animal cooperation, because the experimental machinations required to stabilize cooperation in our study are special. Specifically, our results disagree with the field's traditional focus on simple undiscouraged repetition. In contrast, they provide

solid evidence for the role of discounting and impulsivity in animal cooperation and therefore raise questions about what factors can reduce discounting enough to promote cooperation. Information about when benefits are realized in cases of natural cooperation may provide important insights into the organization of animal social behavior.

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