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The economic basis of cooperation: tradeoffs between selfishness and generosity

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The current study examined the economics of cooperation in controlled-payoff games by using captive blue jays, *Cyanocitta cristata.* This investigation used a special feeding apparatus to test for the stability of cooperative choice in a series of iterated games. The jays experienced experimentally determined game theoretical payoff matrices, which determined the distribution of food to themselves and their opponent, depending on their decision to cooperate or defect. The experiment tested four game matrices, called the cooperate only, defect only, prisoner's dilemma, and opponent control treatments. This study found little cooperation in the defect only and prisoner's dilemma treatments. Cooperation occurred significantly more often in the opponent control treatment. These findings suggest that the jays attend to short-term consequences; they do not cooperate in the absence of an immediate benefit (defect only), even if a long-term benefit may exist (prisoner's dilemma). The opponent control treatment suggests that cooperation can occur when an individual's benefits depend completely on the actions of others; therefore, generosity is cheap. This study, therefore, agrees with recent studies in proposing alternative models of cooperation.
Key words: blue jay, cooperation, game theory, Pavlov, prisoner's dilemma, Tit for Tat. *[Behav Ecol 15:255–261 (2004)]*

During the past 20 years, the central paradigm of nonkin cooperation in nonhuman animals has been reciprocal altruism. Trivers (1971) formulated the concept of reciprocal altruism as an investigation of altruism via turn-taking. Axelrod and Hamilton (1981) spurred the economic examination of reciprocal altruism by championing the concept of Tit for Tat—a strategy of copying your opponent's last choice—in a prisoner's dilemma game. Despite a massive theoretical effort investigating the evolutionary stability of the Tit for Tat strategy (for review, Dugatkin, 1997), there is little empirical evidence supporting Tit for Tat or reciprocal altruism as a primary explanation for cooperation or altruism, suggesting the need to examine alternative models (Connor, 1995; Dugatkin et al., 1992; Pusey and Packer, 1997; Stevens and Stephens, 2002). Critics of reciprocal altruism argue that it is unnecessarily complex. For example, the inherent time delay between cooperation and repayment in reciprocal altruism makes it difficult to implement. In addition, tracking debts owed and favors given requires complex score-keeping that may exceed the cognitive capabilities of many animal species (Stevens and Hauser, 2004). This study is part of a larger effort to understand the behavioral constraints on cooperation, and use this understanding to develop more plausible alternative models.

This study extends the study of Clements and Stephens (1995), which found that blue jays (*Cyanocitta cristata*), placed in an iterated prisoner's dilemma (IPD) situation, did not cooperate. They did, however, readily cooperate in a simpler mutualistic situation in which there was no temptation to cheat. Despite this early lack of evidence for cooperation, recent studies have been more promising. Stephens et al. (2002) did find that the jays can cooperate in an IPD. This cooperation, however, only occurred under special circumstances, in which the opponent (a trained stooge) used a Tit for Tat strategy and the jays' tendency to discount future rewards was mitigated by accumulating benefits. Therefore, strategic reciprocity and reduced discounting were necessary to maintain cooperation in blue jays.

We continue to use blue jays as a model system. In an effort to test our predictions in a different context, we designed a novel feeding apparatus. Figure 1 shows our design. At the beginning of each "play," food was distributed to six bins in view of, but inaccessible to, the players. Each player controlled three of the bins, in the sense that one option shifted the three bins to the left, and another shifted them to the right. When the bins slid to the left or right, the food within them was drawn over openings that distributed the food to one of three destinations (Figure 1a). Food in bin 1 distributed food either to "self" or to "other," food in bin 2 distributed food to "other" or to no one ("trash"), and food in bin 3 distributed food either to "self" or to no one. We could, therefore, control the nature of the game by varying the amounts of food distributed to each bin. To clarify this, let A_1, A_2, and A_3 represent the amounts in bins 1, 2, and 3, respectively. The design of the feeding apparatus means that subjects must choose between delivering amount A_1 or A_3 to itself; yet, if it chooses A_3, it also delivers amounts A_1 and A_2 to its opponent. This creates a game matrix shown in Table 1.

Consider, for example, a situation in which $A_1 = 2$, $A_2 = 1$, and $A_3 = 0$. If both players choose "C," each delivers three units to its opponent, but if both choose "D," they both deliver the two units to themselves. The amount A_2, therefore, represents a cooperative premium, that is, the additional value of a cooperative act. On the other hand, if the focal player chooses D when its opponent chooses C, it obtains five units while its opponent gets nothing. This is, of course, the traditional prisoner's dilemma game.

This design provides the opportunity to explore important conceptual issues in cooperation. The amount in bin 1 (A_1) represents the classic conflict between selfishness and generosity: should I keep A_1 for myself or give it to another? The amounts in bins 2 and 3 represent two different ways of modifying the value of generosity, by making the generous act more valuable to the recipient (increasing A_2) or more valuable to the actor (increasing A_3). By comparing situations that vary in the presence of a cooperative premium and the temptation to defect, we examine the tradeoff between

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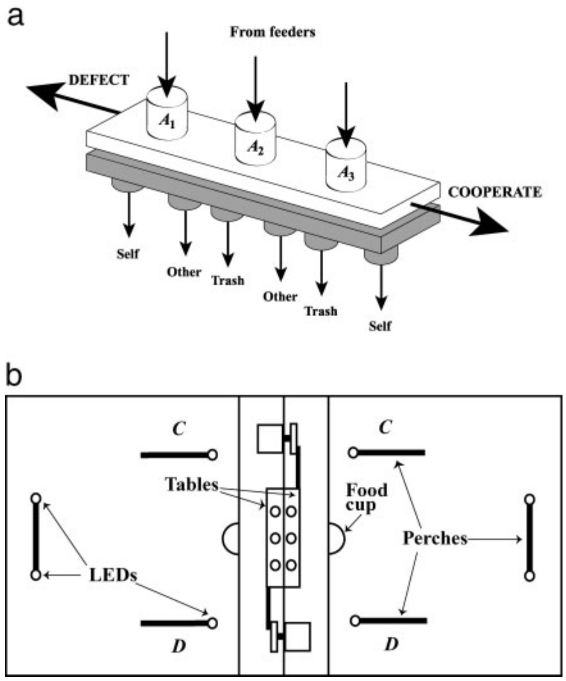

Figure 1
(a) Diagram of table apparatus. Pellets from three feeders drop into the three transparent food bins. Depending on which perch the blue jay occupied, the top piece slides to the right or left (lower, dark piece remains stationary), dropping the pellets into transparent tubes that lead to subject's own food cup (self), the opponent's food cup (other), or an inaccessible trash bin (trash). (b) Diagram of operant conditioning chamber (top view). We placed one jay on each side of the box that was separated by a transparent partition.

Table 1
Payoffs to focal player resulting from opponent's choice

		Opponent	
	Focal player	C (slide table right)	D (slide table left)
	From self	A_3	A_3
C	From other	$A_1 + A_2$	0
	Total	$A_1 + A_2 + A_3$	A_3
	From self	A_1	A_1
D	From other	$A_1 + A_2$	0
	Total	$2A_1 + A_2$	A_1

selfishness and generosity. In this experiment, we test payoff matrices that include no cooperative premium and substantial temptation for selfishness (defect only), a cooperative premium and a temptation for selfishness (prisoner's dilemma), and a cooperative premium and no temptation for selfishness (opponent control). Also, our apparatus allows us to explore the extreme situation in which cooperative action is the only way to obtain food (opponent control). Because the birds' choices determine their opponents' payoffs and not their own, this treatment permits us to study a case of generosity with minimal direct costs to the donor.

METHODS

Subjects

We used four pairs of blue jays (*Cyanocitta cristata*) of unknown sex and varied age in the experiment (birds 3 and 140, 70 and 85, 4 and 122, 130 and 208). The within-subjects design of this experiment controls for any differences in sex and age. Before the experiment, we maintained the jays on a diet of mealworms and Lafeber's cockatiel food, housing them in individual cages (measuring 38 × 38 × 61 cm) in a colony of 25. The housing room had an average temperature of 23°C with lights on from 0600–2000 h (for further housing information, see Clements and Stephens, 1995).

Apparatus

We used two operant boxes consisting of two adjoining chambers constructed of galvanized sheet metal (61 × 124 × 51 cm) (Figure 1b). We separated the chambers with transparent Plexiglas partitions. We attached the table apparatus (Figure 1a) to both sides of the central partition. Each table had a static acrylic base with six 1-cm holes to which we connected flexible transparent Tygon tubing (10 mm inner diameter, 13 mm outer diameter). Each tube led to (1) the feeding cup on the same side of the partition, (2) the feeding cup on the other side of the partition (by passing through a hole in the partition), or (3) an inaccessible but visible Plexiglas "trash bin" at the bottom of the partition (Figure 1a). We constructed the top portion of the table from a transparent acrylic "slide" with three 2-cm holes (bins) that were offset from the six holes in the base. We connected the slide to a cam attached to a motor. One revolution of the motor/cam moved the slide to the right 2.5 cm, back past the center to the left 2.5 cm, stopping back at the center of the table. Tygon tubes (13 mm inner diameter, 16 mm outer diameter) connected three Med Associates 20 mg pellet dispensers to the holes on top of the slide. Transparent Plexiglas partitions separated the jays from the table, motor, tubes, and feeders. This design allowed each bird to dispense food to itself, its partner, or the trash, depending on its choice. Varying the number of pellets dispensed to the bins allowed us to create different payoff matrices.

Each chamber contained three perches (one back and two front perches) with microswitches under the crossbars that activated when the birds occupied the perches. We attached light emitting diodes (LEDs) to the perches (two orange LEDs for the back perches and one either red or green LED for the front perches). Light color for the C perch (red or green) was counterbalanced between pairs, and side for C perch (right or left) was counterbalanced between subjects within pairs.

A C++ computer program recorded all inputs (microswitches on perches) and controlled all outputs (LEDs, pellet dispensers, slide motors) via an Alpha Products input/output computer interface system. The program controlled the timing of all aspects of the experimental trials.

General procedure

In this experiment we created a closed economy system in which all of the food the jays received resulted from successfully completing the experimental trials. Therefore, the jays remained in the operant boxes for 23 h/day, 7 days/week. They were maintained at 80% of their normal weight (measured daily) by ensuring a minimum of 7 g and a maximum of 10 g of food per day.

At 0600 h the room lights turned on, and at 0700 h the computer program initiated the day's trials. The trials repeated until 1100 h, when we removed the jays from the operant

Table 2

Payoff matrices used as treatment levels (includes number of pellets in table apparatus)

(a) Cooperate only	Cooperate	Defect	$A_1 = 0$
Cooperate	$R = 3$	$S = 3$	$A_2 = 0$
Defect	$T = 0$	$P = 0$	$A_3 = 3$
(b) Defect only	Cooperate	Defect	$A_1 = 2$
Cooperate	$R = 2$	$S = 0$	$A_2 = 0$
Defect	$T = 4$	$P = 2$	$A_3 = 0$
(c) Prisoner's dilemma	Cooperate	Defect	$A_1 = 2$
Cooperate	$R = 3$	$S = 0$	$A_2 = 1$
Defect	$T = 5$	$P = 2$	$A_3 = 0$
(d) Opponent control	Cooperate	Defect	$A_1 = 0$
Cooperate	$R = 3$	$S = 0$	$A_2 = 3$
Defect	$T = 3$	$P = 0$	$A_3 = 0$

boxes and placed them in their home cages for 1 h while we cleaned the operant boxes and replenished fresh water. At 1200 h we returned the jays to the experimental boxes, and the trials resumed until 1600 h when the program terminated the trials. Overhead lights extinguished at 2000 h.

Trials

To initiate a trial, the back perch lights (LEDs) for both subjects illuminated to signal the start of a trial. After both players occupied the back perches (facing each other), the lights extinguished and the feeders dispensed pellets into the appropriate table bins. After a 1-s delay, the lights on both subjects' front perches illuminated. When both players concurrently occupied one of their front perches, the lights extinguished and both tables simultaneously slid in the direction of the chosen perch (independently for each player). For example, if player 1 occupied the perch to its right, or "C" perch, the slide on that side of the partition slid to the subject's right, so that pellets in bins 1 and 2 went to the other player, and pellets in bin 3 went to its own food cup (Figure 1a). Because the players faced each other, the right perch represented C for one player and D for the other (Figure 1b), and the slide mechanisms were mirror images of one another. Thus, if player 2 occupied its right perch (opposite from player 1), its table slid to the right, delivering the pellets in bin 1 to itself and the pellets in bins 2 and 3 to the trash bin. Distributing the pellets completed a trial and initiated the 45-s intertrial interval.

We used forced, or no choice, trials to ensure that the jays experienced the consequences of all possible choice combinations. We randomly assigned 20% of the trials as forced trials, in which we forced both birds to make a predetermined choice between C and D. We illuminated only one of the two front lights for each of the players and required them to land only on the perch with the illuminated light, thereby forcing them to face a specific choice combination. This ensured that the birds faced all choice combinations, thus reducing the possibility of an arbitrary choice. Because no other signals indicated a change in treatment, forced trials also accelerated the process of learning a new set of payoffs.

Experimental design

This experiment follows a three-by-three repeated-measures design, using payoff-matrix treatment and time block as factors. For the payoff treatments, we subjected the jays to three test treatments and a baseline treatment before each test treatment. Each test treatment lasted for 1700 trials (about 11 days), and the baseline treatment lasted until the jays mutually cooperated on at least 75% of the trials for three consecutive days.

Payoff matrices

From this point forward, we will use the terms "cooperate" and "defect" to refer to choosing the C and D perches, respectively. By using the economic definition "joint action for mutual benefit" (Clements and Stephens, 1995; Dugatkin, 1997), cooperation maps to C in all matrices except defect only. We use cooperate and defect to compare the same behavior across treatments, while avoiding the awkwardness of the C/D terminology.

We used a cooperate only treatment as the baseline treatment. In this treatment, three pellets dropped in bin 3, allowing the jays to receive the pellets if they cooperate and dropping the pellets into the trash if they defect, creating the payoff combination in Table 2a. Because the Nash equilibrium (Nash, 1951) is mutual cooperation, we used this procedure to establish cooperative behavior before subjecting pairs to any of the test matrices. Game theoretical solutions are stability solutions, so by establishing cooperative action before a test situation begins, we tested whether cooperation persists in a given test situation, as the game theoretical models predict. In our experiment, training the jays to land on the C perch in the baseline treatment tests the importance of the temptation to cheat (D perch) in the prisoner's dilemma. This procedure also minimizes any effects that might "carry-over" from one test matrix to the next.

The test matrices (treatments) included defect only, prisoner's dilemma, and opponent control payoffs (Table 2).

First, in the defect only treatment, two pellets dropped only in bin 1 ($A_1 = 2$, $A_2 = 0$, $A_3 = 0$), so cooperation dispensed all pellets to the opponent and defection allowed the player to keep all pellets (Table 2b). All defection is both the single game and repeated game equilibrium.

Second, our prisoner's dilemma treatment was similar to the defect only scenario, except one pellet also dropped into bin 2 (i.e., $A_1 = 2$, $A_2 = 1$, $A_3 = 0$), where it was dispensed to the opponent if the player cooperated or fell into the trash bin if the player defected. The single game Nash equilibrium is mutual defection, but Tit for Tat, Pavlov, and all defection have been proposed as stable for repeated games.

Finally, in the opponent control treatment, three pellets dropped into bin 2 ($A_1 = 0$, $A_2 = 3$, $A_3 = 0$), which distributed all pellets to the opponent when cooperating and to the trash bin when defecting (Table 2d). In this treatment, a player could not dispense food to itself but was forced to rely on its partner. The single game Nash equilibrium is all pairs of pure and mixed strategies, and virtually any strategy is stable in repeated games.

We randomized the order of treatment matrices for each pair of birds. In addition, a baseline treatment preceded each test matrix, so each pair experienced a series of treatments such as cooperate only–opponent control–cooperate only–prisoner's dilemma–cooperate only–defect only.

Time block

We divided the total trials per treatment into three blocks of time. We expected a time block effect because it takes time to adjust to a new treatment matrix. Therefore, choice behavior in the later trials provided a better estimate of the jays' preferences.

Data analysis

By using the S-PLUS statistical package, we conducted repeated-measures ANOVAs using the arcsine/square-root

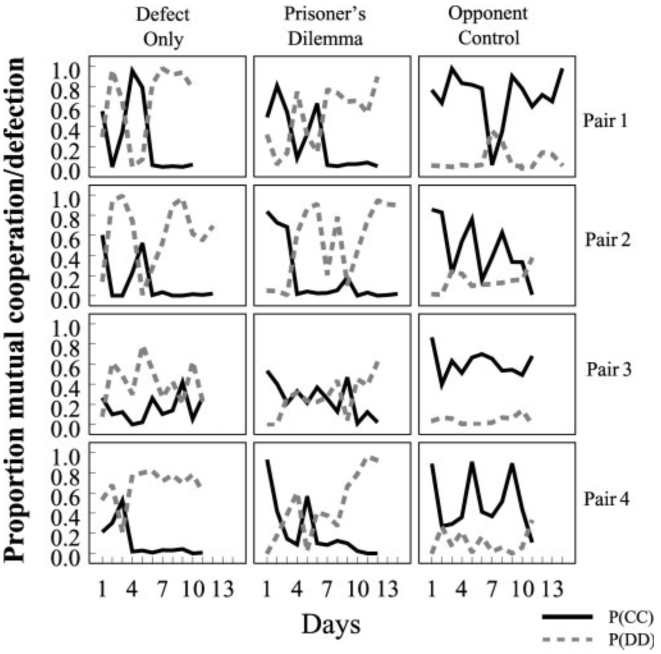

Figure 2
Graph of each pair's proportion mutual cooperation (CC) and mutual defection (DD) per day as a function of treatment matrix (solid line indicates mutual cooperation; dotted line, mutual defection). Stable mutual defection occurs in defect only and prisoner's dilemma treatments, whereas the opponent control treatment indicates higher but unstable levels of mutual cooperation.

transformation (to normalize the data) of the mean proportion of cooperation as our response variable. When examining proportion of mutual cooperation (CC), we tested effects within a pair; however, when examining individual cooperation (C), we tested effects within each subject nested in pair. We included treatment (defect only, prisoner's dilemma, and opponent control) and time block (one through three) as factors. We then conducted Tukey paired comparisons to contrast treatment differences.

RESULTS

Figure 2 gives an overview of the data, showing that defection quickly replaced cooperation in the prisoner's dilemma and defect only conditions. In contrast, mutual cooperation was maintained at a relatively high level in the opponent control treatment. Confirming these observations, a two-factor repeated-measures ANOVA (Table 3) on the proportion mutual cooperation indicates highly significant treatment effects (ANOVA: $F_{2,6} = 166.09$, $p < .01$) and block effects (ANOVA: $F_{2,6} = 11.75$, $p < .01$) but no interaction between treatment and block (ANOVA: $F_{4,12} = 1.60$, $p = .24$) (Figure 3). A Tukey paired comparison on treatments shows no difference between the proportion mutual cooperation in the prisoner's dilemma and defect only treatments, but the birds cooperated significantly more in the opponent control treatment than in the prisoner's dilemma and defect only treatments (mean ± SE; defect only: 0.16 ± 0.04; prisoner's dilemma: 0.23 ± 0.04; opponent control: 0.57 ± 0.04). A paired comparison on block suggests that significantly less cooperation occurred in the last block compared with the first block pooled over all treatments (mean ± SE; block 1: 0.45 ± 0.05; block 2: 0.31 ± 0.04; block 3: 0.22 ± 0.04). Because of the 75% mutual cooperation criteria for the cooperate only baseline treatment, the birds began all test treatments with a high level of cooperation. Therefore, the block effect suggests that the birds began each treatment cooperating but quickly defected as they learned the defect only and prisoner's dilemma payoff structure.

Table 3

ANOVA table for arcsine/square-root transformed proportion mutual cooperation as a function of payoff-matrix treatment and time block

Source of variation	df	SS	*F*	*p*
Payoff-matrix	2	1.41	166.09	<.01*
Error: pair × matrix	6	.03	—	—
Time block	2	.51	11.75	<.01*
Error: pair × block	6	.13	—	—
Matrix × block	4	.20	1.6	.24
Error: pair × matrix × block	12	.37	—	—

* Statistically significant effects.

In both defect only and prisoner's dilemma treatments, the jays cooperated less often than expected by chance (25% is the chance expectation for mutual cooperation, because if both birds choose C 50% of the time, we have $0.5 \times 0.5 = 0.25$) in the last third of the trials (mean ± SE; defect only: 0.06 ± 0.03; one-sample *t* test: $\mu = 0.25$, $t = -3.56$, $p = .04$; prisoner's dilemma: 0.05 ± 0.03; one-sample *t* test: $\mu = 0.25$, $t = -5.79$, $p = .01$). The jays cooperated above chance levels during the last third of the opponent control treatment (mean ± SE; 0.54 ± 0.06; one-sample *t* test: $\mu = 0.25$, $t = 3.23$, $p = .05$) (Figures 2 and 3).

Strategic analysis

We calculated strategy vectors to explore the finer-scale properties of the blue jay's decision rules (Stephens et al., 1997, 2002). These vectors represent the probability of cooperating following a previous payoff. For example, *t* represents the probability of cooperating in the trial after a payoff of *T* (player defects, opponent cooperates). Table 4 illustrates the theoretical strategy vector for a pair of Tit for Tat or Pavlov strategists. If two players played Tit for Tat, we would expect high *t* and *r* values and low *p* and *s* values. That is, cooperation should follow previous opponent cooperation (*T* and *R* trials). Pavlov predicts the "win-stay, lose-shift" strategy, in which players will repeat a rewarding choice and switch after a punishing choice (Kraines and Kraines, 1989; Nowak and Sigmund, 1993). Therefore, we would expect high *r* and *p* values and low *t* and *s*. The blue jays, however, diverged from both theoretical strategies. In all three treatments, the jays showed high *r* and *s* values but low *t* and *p* values (Table 4). Rather than following their opponent's previous choice or shifting choices based on reward/punishment contingencies, our results demonstrate the maintenance of cooperation after cooperation and defection after defection. The jays focused on the short-term benefits by reaping the temptation to cheat, *T.*

Contingent behavior

Do the jays make choices contingent on their opponent's behavior? It is quite possible that each jay is acting in isolation of the other jay. Given the nature of the apparatus (transparent partition separating subjects and choice perches facing each other), the jays have access to information on the current as well as previous choices made by their opponents. There are two ways to test whether they respond to the behavior of

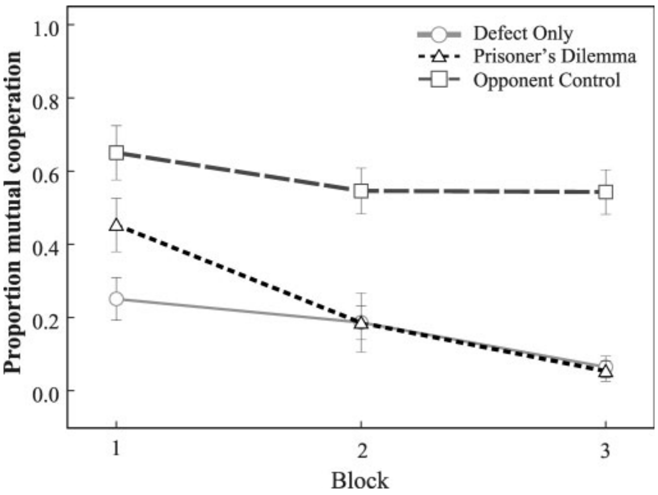

Figure 3
Graph of mean proportion mutual cooperation (CC) pooled over all pairs but separated by payoff-matrix treatment and time block (error bars represent standard error; circles indicate defect only; triangles, prisoner's dilemma; and squares, opponent control). In both defect only and prisoner's dilemma treatments, the jays mutually cooperate significantly less often than by chance in the last third of the trials. In the opponent control treatment, they cooperate more often than by chance (25%).

others. First, we can examine how previous opponent behavior influences current behavior (generalization of strategic analysis proposed above). Second, we examine how the second jay to choose modifies its behavior based on its opponent's choice.

To test how an opponent's previous decision influences a subject's current behavior, we conducted a repeated-measures ANOVA examining the effect of treatment and opponent's choice in the previous trial on individual cooperation, using the last third of the data. As expected, treatment influenced cooperation (ANOVA: $F_{2,14} = 24.06$, $p < .01$). Interestingly, the jays tended to cooperate more often after their opponent's cooperation (ANOVA: $F_{1,7} = 106.51$, $p < .01$), possibly depending on treatment (i.e., a trend for interaction; ANOVA: $F_{2,14} = 3.41$, $p = .06$). Therefore, the jays do appear to exhibit contingent behavior based on the previous trial (Figure 4a).

To examine how current opponent behavior influences choices, we examined order effects. Because the jays could see each other's choices in this experiment, the second bird to choose had the advantage of reacting to its opponent's choice. Given this knowledge of the opponent's choice, any reaction other than indifference indicates a response to the opponent's behavior. To examine this phenomenon, we calculated the probability that each choice was made by the second bird after a given choice was made by the first bird, using the last third of the data. A repeated-measures ANOVA examined the effects of treatment and the choice of the first subject to choose on proportion individual cooperation. We found a significant treatment effect (ANOVA: $F_{2,6} = 13.60$, $p < .01$), an effect of first choice (ANOVA: $F_{1,3} = 27.06$, $p = .01$), but no interaction (ANOVA: $F_{2,6} = 0.97$, $p = .43$). In all treatments, the jays appear to respond to cooperation by cooperating and to defection by defecting even before rewards are dispensed (Figure 4b).

DISCUSSION

Our experiment indicates that the blue jays do not cooperate in the prisoner's dilemma despite ample opportunity and perform no differently than when no premium for cooperating exists (defect only treatment). Nevertheless, in the absence of a temptation to cheat (opponent control treatment), they consistently cooperate. In addition, the jays do not use Tit for Tat or Pavlov strategies in any of the treatments, although their behavior is contingent on their opponent's choices.

Table 4

Transition vectors describing probability of cooperating following previous payoffs for Tit for Tat and Pavlov strategies (theoretical predictions) and defect only, prisoner's dilemma, and opponent control matrices (observed data)

	t	*r*	*p*	*s*
Tit for Tat	1	1	0	0
Pavlov	0	1	1	0
Defect only	0.20	0.86	.08	0.58
Prisoner's dilemma	0.23	0.81	.12	0.67
Opponent control	0.31	0.88	.39	0.83

Defect only treatment

The defect only treatment is important because it provides a temptation to defect without a cooperative premium (Table 2b): $T = 4$, $R = 2$, $P = 2$, $S = 0$. Mutual defection is the Nash equilibrium. Both the prisoner's dilemma and defect only treatments involve a temptation to defect; however, the prisoner's dilemma also includes a cooperative premium (Table 2c): $T = 5$, $R = 3$, $P = 2$, $S = 0$. Recall that the cooperative premium is simply the additional value of cooperation; in our case, one extra food pellet. Therefore, the single-game Nash equilibrium for the prisoner's dilemma is again defection; however, the cooperative premium has made mutual cooperation more profitable than mutual defection.

This additional unit of benefit has profound theoretical effects on choice behavior. Many theorists suggest that the presence of the cooperative premium can allow higher level strategies (Tit for Tat, Pavlov, etc.) to permit stable cooperation (Axelrod and Hamilton, 1981; Dugatkin, 1997; Nowak and Sigmund, 1993). They would predict stable defection in our defect only treatment and stable cooperation in our prisoner's dilemma treatment. Our laboratory investigation of the treatments, however, indicates that the animals do not consider these two treatments to be fundamentally different. That is, despite its theoretical significance, the cooperative premium is not functionally important in our experiments. Similar experiments on rats and pigeons also show very low levels of cooperation in these controlled-payoff games (Flood et al., 1983; Gardner et al., 1984; Green et al., 1995; Hall, 2003). In fact, the generality of this phenomenon is evident by extremely low levels of cooperation in prisoner's dilemma games played by humans, one of the most cooperative animals (Andreoni and Miller, 1993; Baker and Rachlin, 2001; Rilling et al., 2002).

One of the primary reasons that animals may ignore the cooperative premium is because they discount the future rewards of playing the game and focus on immediate benefits. Theoretical and empirical evidence reveals that animals may prefer an immediate reward despite higher long-term payoffs for a delayed reward (Benson and Stephens, 1996; McDiarmid and Rilling, 1965). This preference may be caused by discounting the value of future rewards that may not materialize (Kagel et al., 1986; McNamara and Houston, 1987; Stephens et al., 1995; Stevens, 2000), although this discounting effect can be overcome, increasing the probability of cooperation (Baker and Rachlin, 2002; Stephens et al.,

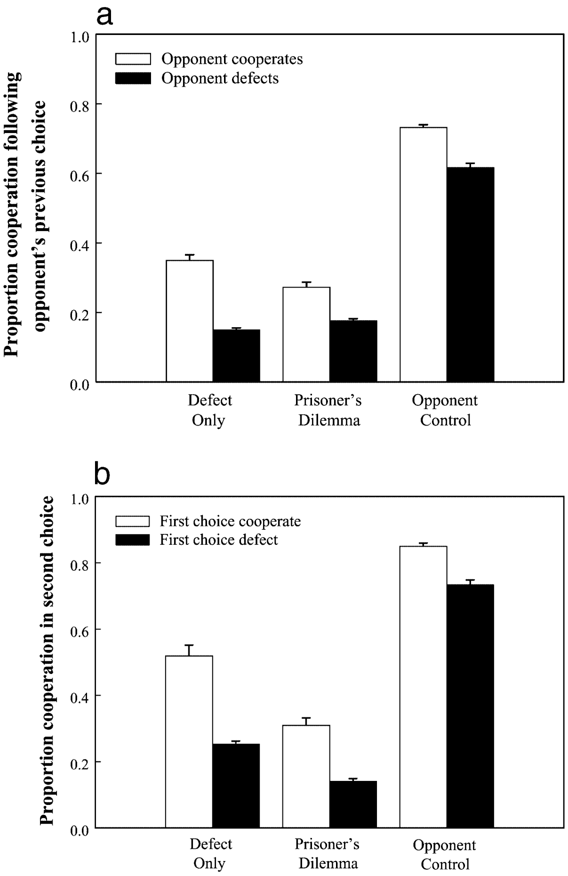

Figure 4

(a) Graph of mean proportion individual cooperation (C) after the opponent's behavior on the previous trial (error bars represent standard error). The jays cooperated more if their opponents cooperated on the previous trial. (b) Graph of mean proportion individual cooperation (C) after the choice of the subject that moves first (error bars represent standard error). In all treatments, cooperation occurs less frequently after defection by the subject that moves first.

2002). If the jays do discount steeply, they may ignore future interactions and play each trial as a one-shot game.

Opponent control treatment

The opponent control treatment offers an interesting conflict for the jays because the players control the payoffs to their partner rather than to themselves. Thus, generosity is cheap because players do not pay a cost for cooperating (there is no temptation to defect), but they can increase their opponents' fitness (cooperative premium). We find that the jays cooperate more frequently in the opponent control treatment than in the prisoner's dilemma and defect only treatments. This result could arise via a number of pathways, and further studies are required to distinguish among them.

First, the temptation to defect is an enormous barrier for cooperation. Once that barrier is lifted, generosity becomes cost-free. Tooby and Cosmides (1996) predict that cost-free generosity can evolve when organisms can recognize the contingencies of the situations. Through simple reinforcement, individuals can act in such a way to elicit beneficial behavior from others: "X could increase the frequency with which Y emits zero-cost behaviors that incidentally benefit X by providing contingent rewards" (Tooby and Cosmides, 1996). Tit for Tat is certainly a means of establishing the contingency; however, the jays did not use Tit for Tat. Nevertheless, they did demonstrate contingent behavior by cooperating after their opponent's cooperation (Figure 4). Therefore, it is possible that this mutual contingent benefit could have maintained cooperation in this treatment.

Similarly, there could be other benefits associated with cooperation. For example, if group membership is beneficial (via predator avoidance, group foraging, cooperative breeding, etc.), cooperation may help keep other individuals around, thereby increasing an individual's fitness. These types of group augmentation may play a role in the maintenance of groups of birds, lions, and meerkats, among other species (Clutton-Brock, 2002; Packer et al., 2001; Woolfenden and Fitzpatrick, 1978). Although group augmentation seems particularly powerful in these cheap generosity situations, it remains unclear whether the jays received other benefits from cooperating in our experiment. These types of hypotheses could be tested by using asymmetric matrices, that is, making cooperation differentially advantageous for the two players.

Second, psychological constraints on animal decision making may affect cooperation in this situation. Standard animal learning models propose an important psychological difference between zero and nonzero payoffs (Stephens and Clements, 1998). Animals avoid making choices resulting in no reward when the alternate choice yields any positive reward. This inherent motivation to avoid zero choices could account for the levels of cooperation in our opponent control treatment. Again, we predict that a study comparing the current opponent control treatment with one in which we substitute one pellet for the zero-pellet payoffs would show a decrease in overall cooperation in the nonzero treatment. Stephens and Clements (1998) presented jays with a similar matrix ($T = 5$, $R = 5$, $P = 1$, $S = 1$) and found lower levels of cooperation.

Finally, although mutual defection is the Nash equilibrium in the defect only and prisoner's dilemma treatments, in the opponent control treatment the equilibrium is all mixed strategies. Nash actually described a similar matrix in the original formulation of his equilibrium, describing the solution as "all pairs of mixed strategies" (Nash, 1951). This means that there is a mixed evolutionarily stable strategy (Maynard Smith, 1982) in which all ratios of cooperation to defection (including zero and one) are equilibria—no frequency dependence exists. Therefore, initial probabilities of cooperation will remain neutrally stable. For example, individuals that already cooperate with kin may maintain cooperation with nonkin because of the initial bias. Alternatively, because mutual cooperation Pareto dominates (Binmore, 1992) all other equilibria, we may see elevated levels because no player can be better off outside of mutual cooperation. This economic explanation combined with contingent benefits and avoidance of zero payoffs probably accounts for much of the cheap generosity seen in the opponent control matrix.

Pavlov

Nowak and Sigmund (1993) advocate a win-stay/lose shift strategy called Pavlov (Kraines and Kraines, 1989), in which the player repeats rewarding choices but switches choices after punishing results. Nowak and Sigmund suggest that Pavlov provides a strategy that outcompetes Tit for Tat because it responds better to mistakes and is resistant to obligate cooperators. In addition, they offer this strategy as a psychologically sound strategy founded on the law of effect (Thorndike, 1911). In the prisoner's dilemma, Nowak and Sigmund's Pavlov strategy considers T and R as "wins" and P

and *S* as "losses". Our opponent control situation represents a strong test of the Pavlov strategy, because *T* and *R* produce identical wins, whereas *P* and *S* produce unambiguous and identical losses (no food).

Consequently, if Pavlov is a viable mechanism of cooperation, it should be employed in our opponent control treatment because the players are rewarded for *T* and *R* choices and punished for *P* and *S* choices. Table 4 illustrates the theoretical strategy vector for a Pavlov strategist. Examining the strategy vector for our prisoner's dilemma and opponent control treatments indicates low probabilities of cooperating after *T* and high probabilities of cooperating after *S*. These results agree with Clements and Stephens' critique of the Pavlov strategy, in questioning its importance, even in this situation in which it is most likely to apply.

Cheap generosity

The opponent control matrix represents a situation in which generosity is cheap. Although not stable, cooperation could occur in this situation via contingent behavior or Pareto optimality (alternatives to cooperation reduce one of the player's payoffs). This cheap generosity could serve as a precursor to cooperation in more altruistic situations, providing interesting conceptual implications for the evolution of cooperation.

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