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Long-term social bonds promote cooperation in the iterated Prisoner's Dilemma

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Reciprocal altruism, one of the most probable explanations for cooperation among non-kin, has been modelled as a Prisoner's Dilemma. According to this game, cooperation could evolve when individuals, who expect to play again, use conditional strategies like tit-for-tat or Pavlov. There is evidence that humans use such strategies to achieve mutual cooperation, but most controlled experiments with non-human animals have failed to find cooperation. One reason for this could be that subjects fail to cooperate because they behave as if they were to play only once. To assess this hypothesis, we conducted an experiment with monogamous zebra finches (*Taeniopygia guttata*) that were tested in a two-choice apparatus, with either their social partner or an experimental opponent of the opposite sex. We found that zebra finches maintained high levels of cooperation in an iterated Prisoner's Dilemma game only when interacting with their social partner. Although other mechanisms may have contributed to the observed difference between the two treatments, our results support the hypothesis that animals do not systematically give in to the short-term temptation of cheating when long-term benefits exist. Thus, our findings contradict the commonly accepted idea that reciprocal altruism will be rare in non-human animals.

Keywords: Iterated Prisoner's Dilemma; cooperation; reciprocal altruism; social bond; zebra finch; tit-for-tat

1. INTRODUCTION

Over the last four decades, extensive theoretical work has been conducted on the Prisoner's Dilemma (PD), a two-player model of the evolution of non-kin cooperation that includes two choices: cooperate or defect (Trivers 1971). In this game, it is always best to defect, no matter what the opponent does. Consequently, the expected outcome is mutual defection if the opponents interact only once. However, because players get a greater payoff from mutual cooperation than from mutual defection, Axelrod & Hamilton (1981) suggested that cooperation could emerge and be maintained when the game is repeated such that the opponents, who expect to play together for an unknown number of interactions, adopt a conditional strategy like tit-for-tat (TFT). TFT players cooperate in the first round and then copy their opponent's previous move on all subsequent plays. Since the original formulation of this game, many theoretical models of reciprocity have been developed to improve its realism. Some of them, for instance, have included the possibility that players make mistakes and report that other conditional strategies like a generous TFT (Nowak & Sigmund 1992) or Pavlov (Nowak & Sigmund 1993) could then lead to stable mutual cooperation. Both strategies outperform TFT because they can correct occasional mistakes: generous TFT players cooperate with a certain probability after the opponent's defection whereas players using Pavlov—referred to as a 'win-stay, lose-shift' strategy—keep the same play when rewarded but change when punished.

Although there is evidence that humans use such reactive strategies to achieve mutual cooperation in games with a PD-like payoff structure (Wedekind & Milinski 1996; Milinski & Wedekind 1998), available data suggest that reciprocal events will be rare in animals. Indeed, a number of experimental and field studies with fishes (e.g. Millinski 1987; Ward *et al.* 2002; Bshary *et al.* 2008), birds (e.g. Godard 1993; Olendorf *et al.* 2004; Krams *et al.* 2008), vampire bats (*Desmodus rotundus*; Wilkinson 1984) and primates (e.g. Packer 1977; Hauser *et al.* 2003) have found apparent evidence for reciprocity. In most cases, however, the situation resembles a PD but the fitness costs and benefits of cooperation are not precisely measured and hence remain ambiguous. In addition, as reciprocal events frequently occur among kin in natural situations, alternative explanations cannot generally be ruled out. To counter these problems, several laboratory experiments with controlled payoff games have been conducted, but most of them failed to find cooperation (Gardner *et al.* 1984; Reboreda & Kacelnik 1993; Clements & Stephens 1995; Green *et al.* 1995; Hall 2003; Stevens & Stephens 2004; but see Stephens *et al.* 2002, 2006). One possible explanation for the fragility of cooperation in the iterated Prisoner's Dilemma (IPD) is that subjects fail to cooperate because they expect that their chances of encountering the same opponent later are so low that they behave as if they were to play only a single round of the game. Indeed, the success or failure of cooperation in the IPD is clearly dependent on the probability of future play with the same player (Axelrod & Hamilton 1981). Consequently, only individuals that have established long-lasting relationships should show stable levels of cooperation (Sachs *et al.* 2004) because

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then the conditions for reciprocal altruism are more easily met. Although this prediction has as not yet been experimentally verified, reciprocity among animals has been found only among individuals that form stable associations and therefore have many opportunities to reciprocate during their lifespan. This is the case, for instance, in female vampire bats, that have been found to preferentially share blood with familiar roost mates who are likely to have shared with them in the past (Wilkinson 1984).

Thus, in this study we investigated whether zebra finches (*Taeniopygia guttata*) could initiate and maintain mutual cooperation when interacting with either their social partner or an experimental opponent of the opposite sex. We used these two treatments to manipulate the degree of uncertainty of future play, because monogamous species with biparental care form long-term pair-bonds and have to coordinate their activities to the needs of the offspring. The members of a pair-bond, therefore, expect to interact repeatedly with each other during at least one breeding season (Black 1996), and hence they should use, unlike experimental opponents, long-term accounting strategies.

2. MATERIAL AND METHODS

(a) *Subjects*

In this study, we used 16 commercially purchased adult zebra finches—eight males and eight females that had never been in contact before. All birds were marked with a unique combination of two coloured plastic leg bands, and were kept on a 13:11 light:dark photoperiod at a constant temperature of approximately 23°C. Two days before the beginning of the training session, pairs were randomly formed, and each was kept in an individual cage (38 × 38 × 48 cm³) for the duration of the experiment. The pairs were established only two days before the training began because zebra finches live in arid and semi-arid regions of Australia where the conditions favourable for breeding are rare (Zann 1996). Individuals therefore reproduce opportunistically and form a strong pair bond very quickly (Silcox & Evans 1982). Accordingly, all individuals displayed specific behaviours associated with pair bonds (i.e. clumping and preening) towards their social partner during the two days following pair formation. Outside the training and experimental sessions, birds had ad libitum access to water and food, which consisted of a commercial preparation of finch seeds.

(b) *Apparatus and experimental procedure*

The experimental apparatus (figure 1) replicated a two-player, two-choice game in which each bird could either cooperate or defect. It was composed of two identical 31 × 39 × 43 cm adjacent chambers. Each chamber housed a single bird, always a male on one side and a female on the other side. These chambers were covered and separated by a wire mesh partition, so the birds could always hear and see each other. They were then exposed to a PD-like situation, in which they did not decide independently to cooperate or defect, but instead the bird responding last could see the move of its opponent before choosing its own. We decided to use this experimental procedure because allowing the subjects to communicate and make their decision one after another makes the situation much more natural and realistic (e.g. Frean 1994). In addition, the strategy that performs best may be quite different if the players make their decision at the same moment or

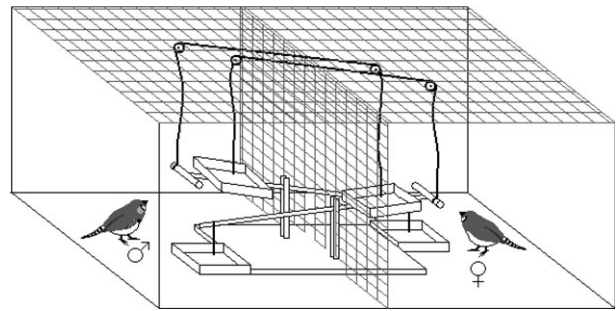


Figure 1. Side view of the experimental apparatus, with a male on one side and a female on the other. During each trial, pair members received the number of food items that corresponded to the combination of their respective decision. Both could perch in front of either the upper cup, representing the decision to cooperate, or stand in front of the lower cup, representing the decision to defect.

asynchronously. More precisely, Pavlov is expected when players make their decision simultaneously, and generous TFT does better than any other strategy in the asynchronous game (Nowak & Sigmund 1993; Frean 1994). However, the rate at which individuals cooperate should be the same in an alternating or a simultaneous game. Accordingly, Clements & Stephens (1995) compared the propensity of blue jays to cooperate when the partition between the two adjacent chambers was either clear or opaque and found no significant difference between the two treatments.

The chambers comprised two food cups. One cup, the lower cup, was placed on the ground, whereas the other, the upper cup, was fixed 14 cm above ground in a horizontal position at the end of a 30-cm-long lever. Both subjects' food cups in a chamber were covered by a transparent acetate lid that opened only when its opponent perched in front of its upper cup, which then operated the lever, thereby allowing the subject to feed from its cups. Otherwise, the cups remained closed, preventing the bird from eating. Hence, each bird could decide either to cooperate (i.e. perch in front of the upper cup) or to defect (i.e. stand in front of the lower cup). Note, however, that in the payoff matrices we used, it could happen that a bird received a payoff despite its opponent having defected. In that case, the experimenter activated an assisted opening mechanism, so that the bird could get access to the food. The beginning of a trial was signalled by the sound of a bell, and once each of the two birds had chosen to either defect or cooperate, the experimenter provided them with the corresponding number of food items via plastic tubes that were directly connected to each cup. Trials were considered to be valid only if the two birds had made a choice less than 10 s after the sound of the bell.

(c) *Training*

Before testing the birds, we trained them to operate the apparatus. The training of each bird took approximately 30 days to complete and was done with a training partner that was either their social partner for half of the birds, or an opponent of the opposite sex (the social partner of another bird) for the other birds. Each pair was placed in the apparatus for 1 h in the morning following 16 h of food deprivation, and 1 h in the afternoon after 4 h of food deprivation. At the beginning of the training, we used the apparatus in its simplest form, that is, without the acetate lids and plastic tubes, so that the birds would become

familiar with the environment and learn how to eat from all the food cups. Then, we successively added each element of the apparatus, until both members of each pair were capable of systematically making a choice following the sound of the bell. Until this step, the birds always received the same number of seeds when they had access to their lower or upper food cup. At the end of the training, however, we used two different payoff distributions to ensure that they had understood the mechanism of the apparatus and hence could modify their behaviour according to the expected immediate payoffs. So, we considered two payoff treatments, the mutualism (M) treatment with the payoff matrix

$$M = \begin{pmatrix} R = 3 & S = 1 \\ T = 1 & P = 0 \end{pmatrix},$$

and the defection (D) treatment with the payoff matrix

$$D = \begin{pmatrix} R = 1 & S = 0 \\ T = 3 & P = 5 \end{pmatrix}.$$

In both payoff matrices, R denotes the number of seeds that each bird received when they both chose to cooperate, and P corresponds to their payoff when they were both defecting. When only one bird cooperated and the other defected, the rewards were S and T for the cooperator and defector, respectively. As mentioned above, the experimenter had to open the food cups in the defection treatment when both individuals decided to defect so that they could each receive five seeds. This was also the case in the mutualism treatment when only bird cooperated and the other defected, so that the cooperator could receive one seed.

Each pair experienced these two payoff treatments for approximately 10 consecutive days. First, they were exposed to the M treatment, in which mutual cooperation is the expected outcome, and then they experienced the D treatment, in which mutual defection is the expected outcome. During a given treatment, all four food cups were of the same colour, but we used a different colour for each matrix to increase the probability that the birds rapidly learned that payoffs have changed when they experienced a new treatment. We ended exposure to M and D when the birds had experienced a given treatment during at least three days and provided they had reached a frequency of 85 per cent or more of mutual cooperation or mutual defection and maintained it for two consecutive sessions. In one day, each bird experienced 15 consecutive trials in the morning session and 10 in the afternoon session, for a total of 25 trials per day, with an interval of 3 min between two consecutive trials.

(d) Treatments

After the training was completed, each bird experienced a three-phase 'PD-M-PD' payoff sequence twice, once with its social partner and once with an experimental opponent of the opposite sex that was different from the training partner. As above, M represents the mutualism treatment, and PD represents the Prisoner's Dilemma treatment with the payoff matrix

$$PD = \begin{pmatrix} R = 3 & S = 0 \\ T = 5 & P = 1 \end{pmatrix}.$$

In this treatment, mutual cooperation provides the highest expected gain when the same opponents play together for an unknown number of interactions. On the other hand, when they play only once, mutual defection is the expected outcome.

As for the training, the food cups were painted in a different colour when the birds experienced PD or M. In addition, as in the defection treatment, the experimenter had to open the food cups in the PD treatment when both subjects decided to defect, so that they could each receive one seed.

The order of the treatments was balanced, so that four pairs were tested first with an experimental partner and then immediately after with their social partner, while the other four pairs were tested first with their social partner and then with an experimental partner. Each bird was tested with the same experimental partner during the entire 'PD-M-PD' payoff sequence and was submitted in total to 30 days of testing (five days per matrix). The birds experienced 25 trials in the morning session and 15 in the afternoon session, for a total of 40 trials per day.

(e) Analyses

During each trial we noted the birds' decision, C (cooperate) or D (defect), and then we tested whether the probability that both individuals in a pair make the same decision in a trial (i.e. CC or DD) was different when they had their social or their experimental partner as their opponent. To do that, we calculated for the 16 pairs of birds (i.e. eight social pairs and eight experimental pairs) the percentage of trials in which both subjects had made a similar choice for the entire 'PD-M-PD' payoff sequence (i.e. 600 trials), and compared the mean values with a *t*-test.

We also characterized the type of strategy that the birds used when they were exposed to the PD treatment by calculating for each of the 16 subjects the number of trials in which they had received each of the four potential payoffs T, R, P and S. As the birds stabilized at mutual cooperation in this treatment only when they had their social partner as their opponent, we compiled the data only from the ten days of testing that corresponded to these two PD payoff matrices. So, we had a total of 400 events per bird (i.e. 200 trials for each exposure to PD). For each bird, we estimated a strategy vector (t, r, p, s), where the parameters t, r, p and s represent its probability of cooperating after obtaining payoffs T, R, P and S, respectively (Stephens *et al.* 2002; Stevens & Stephens 2004). Then, to determine whether the observed strategy used by the birds agrees with TFT or Pavlov (table 1), we performed paired two-tailed *t*-tests from the eight male or female strategy vectors comparing the mean probabilities two by two. Because both TFT and Pavlov predict $s = 0$ and $r = 1$, individuals should be more likely to continue cooperating after R than after S, if they use one or the other strategy. On the other hand, TFT predicts $t = 1$ and $p = 0$ (i.e. players switch from defection to cooperation after T but not after P), whereas Pavlov predicts $t = 0$ and $p = 1$. If the birds use TFT rather than Pavlov, therefore, they should be more likely to switch to cooperation after T than P. Probabilities calculated from less than four events were excluded from the analyses. Because our data conformed to the standard assumption of homogeneity of variance and normality, we conducted parametric tests using SPSS version 16.0 for Windows.

3. RESULTS

The mean probability that both individuals in a pair make a similar decision in a trial was not significantly different when they were tested with either their social partner (0.929 ± 0.012) or their experimental partner (0.868 ± 0.035 ; *t*-test, $t_{14} = 1.649$, $p = 0.135$). On the other

Table 1. Observed and expected probability that a subject chooses to cooperate in a given trial after having received payoffs T, R, P and S, respectively, when exposed to the PD treatment with its social partner. Although a TFT player systematically defects after its opponent's defection, an individual playing a generous TFT strategy is expected to continue cooperating with a probability α after both payoffs P and S.

	<i>t</i>	<i>r</i>	<i>p</i>	<i>s</i>
male strategy (mean \pm s.e.m.)	0.499 \pm 0.124	0.979 \pm 0.071	0.044 \pm 0.008	0.390 \pm 0.154
female strategy (mean \pm s.e.m.)	0.569 \pm 0.137	0.945 \pm 0.012	0.046 \pm 0.007	0.508 \pm 0.113
TFT	1.0	1.0	0	0
Pavlov	0	1.0	1.0	0
generous TFT	1.0	1.0	α	α

hand, as shown by figure 2, the frequency of mutual cooperation was influenced by the treatments. More precisely, when the birds experienced PD for the first time with a given opponent, they did not initiate any cooperation, regardless of whether they were tested with an experimental opponent or with their social partner, and after only two days of testing, the pairs were mutually defecting at nearly 100 per cent. Then, when we changed payoffs from PD to M, the previously established mutual defection quickly declined to be replaced by stable mutual cooperation in all eight pairs, under both treatments. Finally, when we made the third payoff change from M back to PD, there was a striking difference between the social and experimental pairs: when the birds were tested with their experimental opponent, they stopped cooperating and fell back to 0 per cent cooperation (figure 2*a*), while they sustained cooperation when they had their social partner as their opponent (figure 2*b*).

Zebra finches apparently maintained high levels of cooperation in this condition by adopting a TFT-like strategy rather than a Pavlovian strategy (table 1). Indeed, we found that the birds had a higher probability of continuing to cooperate after R than after S (females, $r = 0.945$, $s = 0.508$, paired *t*-test, $t_6 = 3.576$, $p = 0.012$, figure 3*a*; males, $r = 0.979$, $s = 0.390$, paired *t*-test, $t_6 = 4.372$, $p = 0.005$, figure 3*b*), while the probability that they switch from defection to cooperation was significantly higher after T than after P (females, $t = 0.569$, $p = 0.046$, paired *t*-test, $t_6 = 4.317$, $p = 0.005$; males, $t = 0.499$, $p = 0.044$, paired *t*-test, $t_6 = 4.337$, $p = 0.005$). Furthermore, the subjects were extremely forgiving, cooperating at rates near 50 per cent after they had been deceived, as predicted by generous TFT. Nevertheless, we observed a striking difference for this component of the strategy between the two PD treatments: when the birds experienced PD for the first time, they rarely cooperated after receiving payoff S (females, $s = 0.209$; males, $s = 0.375$), but, inversely, they switched from cooperation to defection only occasionally in the second PD treatment (females, $s = 0.919$; males, $s = 0.769$).

4. DISCUSSION

We found that mutual cooperation persisted in our tests of the PD only when the birds had their social partner as their opponent, and they stabilized at mutual defection in all PD treatments when tested with their experimental opponent. Thus our results apparently support the hypothesis that non-human animals can maintain high levels of cooperation in the IPD under no special circumstances other than likely future interactions. Recent

experimental studies have shown that some species, including primates (Mulcahy & Call 2006) and corvids (Clayton *et al.* 2005; Raby *et al.* 2007) have the ability of anticipating and behaving on the basis of future consequences. There would be, therefore, no reason why animals that demonstrate this ability in other contexts should systematically give in to the short-term temptation of cheating in an IPD game when long-term benefits exist. However, even if our data are consistent with our expectation that animals should cooperate only when they expect to interact repeatedly with the same opponent, a simpler explanation could account for these findings.

Indeed, one could imagine that zebra finches continued to cooperate with their social partner after having been exposed to the mutualism treatment because they ignored the fact that the payoffs had changed. They behaved, therefore, as in the previous treatment, without being confronted with the temptation of cheating. This explanation is plausible because the gain for mutual cooperation was the same in both the M and PD treatments and the subjects consequently had to stop cooperating to learn that the payoffs had changed. However, as the levels of mutual cooperation were extremely high from the beginning of the PD treatment when individuals were tested with their social partner, they had very few opportunities to learn that defecting might provide a higher payoff. Although possible, this explanation cannot easily explain why the birds sustained cooperation in the PD treatment with their social partner, while they stopped cooperating very quickly with their experimental partner. Maybe experimental partners could learn more quickly the new payoff distribution because they preferred to stay away from each other in the test apparatus and hence tended to take more frequently different positions (i.e. one bird on the floor and the other bird on the upper perch) than did social partners. However, if it were the case, they would certainly not have stabilized at mutual defection or mutual cooperation as they did in the PD or in the M treatments, respectively, and we would have detected a significant difference in the percent of mixed trials (CD and DC) between social and experimental pairs, which was not the case. As a consequence, we do not believe that the observed difference between the two conditions is attributable to a difference in the birds' learning rates.

As predicted by the asynchronous IPD game (Nowak & Sigmund 1993; Frean 1994), we found that the birds achieved mutual cooperation with their social partner by apparently using a generous TFT strategy: they usually copied their opponent's last choice but they were

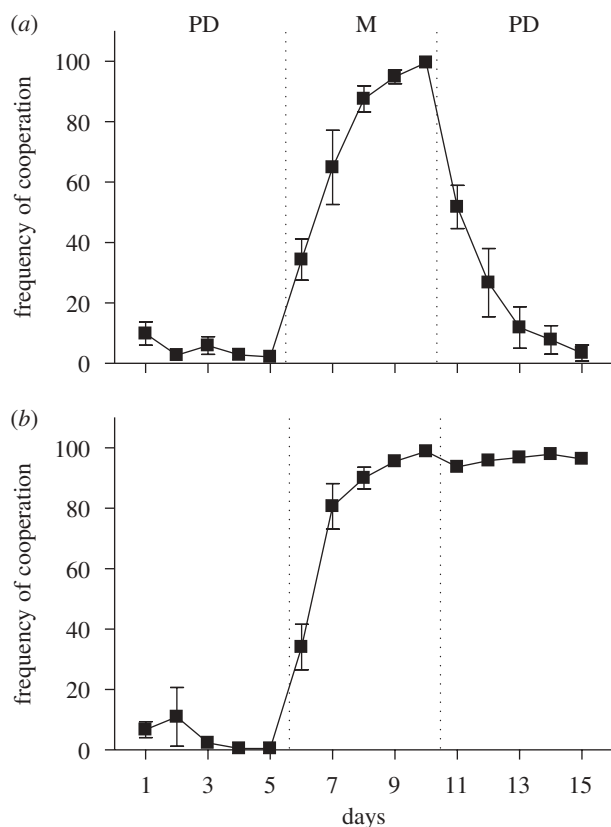


Figure 2. Average change of mutual cooperation over time. Mean frequencies (\pm s.e.m.) of trials completed per day when the birds were tested with either (a) their experimental partner or (b) their social partner. The dotted lines represent the transition to the next payoff matrix. PD denotes the Prisoner's Dilemma treatment and M the mutualism treatment.

nevertheless capable of correcting mistakes by sometimes being cooperative after their opponent's defection. However, the rate at which they forgave after they have been suckered was very low in the first PD treatment compared to the second one. This explains why the birds could only maintain mutual cooperation once it was established, but not initiate it in the first PD treatment. Indeed, as they rarely cooperated after the opponent's defection in the first PD treatment, mutual defection was the expected outcome in the subsequent round most of the time, and in the second PD treatment, mutual cooperation was achieved frequently after one opponent had defected. Consequently, despite the birds having made some errors or cheated occasionally, their propensity to forgive allowed mutual cooperation to be easily re-established in this treatment. Thus, our study demonstrates that animals can adjust their behavioural decisions not only to the identity of the partner they interact with, but also to their past experience, and suggests that reciprocal altruism might be more common among non-human animals than originally thought (Hammerstein 2002; Stevens & Hauser 2004; but see Pfeiffer *et al.* 2005; Krams *et al.* 2008). To date, however, the importance of reciprocity has probably been underestimated to the detriment of simpler mechanisms, because most controlled experiments that have failed to find cooperation imposed unrealistic constraints. For instance, in experimental situations, animals are generally forced to interact with a given partner, whereas under natural

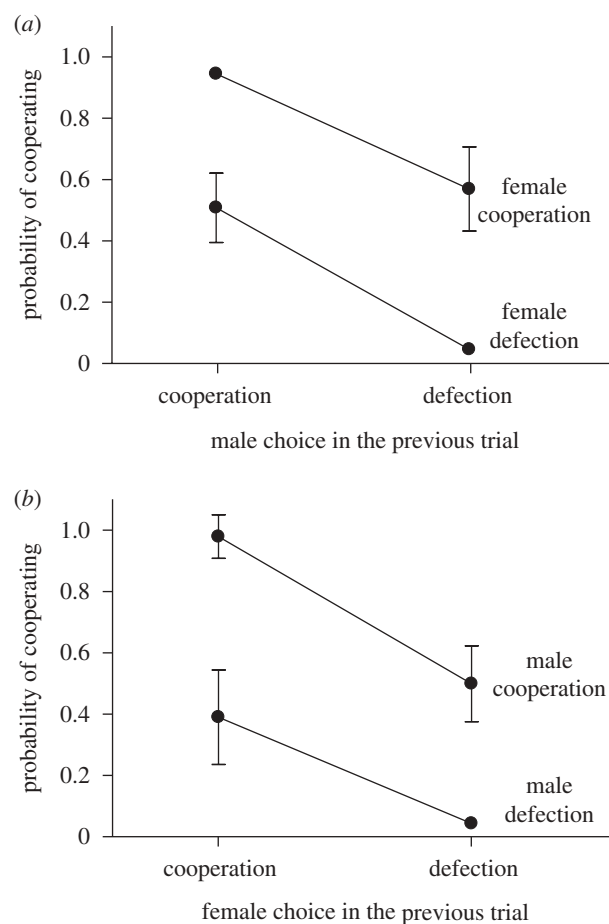


Figure 3. Mean probability of cooperating. Mean probability (\pm s.e.m.) that (a) a female or (b) a male decides to cooperate during a given trial, in relation to its own decision and that of its partner in the previous trial. The upper lines represent the bird's own cooperation in the previous trial, and the lower lines represent the bird's own defection in the previous trial.

conditions, they can choose or refuse partners, based on their level of attachment toward them or even on their reputation (e.g. Rutte & Taborsky 2007, 2008). We recommend, therefore, that future studies be conducted in more natural situations, to evaluate how widespread reciprocal altruism is among animals.

The research presented here was carried out under animal care permit 06-042 provided by Université de Montréal and conforms to guidelines of the Canadian Council for Animal Care.

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