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Proc. R. Soc. B 2010 **277**, 3845-3851 first published online 14 July 2010
doi: 10.1098/rspb.2010.0879

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Prosocial behaviour emerges independent of reciprocity in cottontop tamarins

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The cooperative breeding hypothesis posits that cooperatively breeding species are motivated to act prosocially, that is, to behave in ways that provide benefits to others, and that cooperative breeding has played a central role in the evolution of human prosociality. However, investigations of prosocial behaviour in cooperative breeders have produced varying results and the mechanisms contributing to this variation are unknown. We investigated whether reciprocity would facilitate prosocial behaviour among cottontop tamarins, a cooperatively breeding primate species likely to engage in reciprocal altruism, by comparing the number of food rewards transferred to partners who had either immediately previously provided or denied rewards to the subject. Subjects were also tested in a non-social control condition. Overall, results indicated that reciprocity increased food transfers. However, temporal analyses revealed that when the tamarins' behaviour was evaluated in relation to the non-social control, results were best explained by (i) an initial depression in the transfer of rewards to partners who recently denied rewards, and (ii) a prosocial effect that emerged late in sessions independent of reciprocity. These results support the cooperative breeding hypothesis, but suggest a minimal role for positive reciprocity, and emphasize the importance of investigating proximate temporal mechanisms underlying prosocial behaviour.

Keywords: reciprocal altruism; prosocial behaviour; negative reciprocity; punishment; cooperative breeding

1. INTRODUCTION

Breeding systems are classified along a continuum based on who bears responsibility for offspring care. At one end of the continuum are independent breeders with care provided nearly exclusively by the mother, as is typical of most primate species, including chimpanzees (Goodall 1986; Fernandez-Duque *et al.* 2009). At the other end of the continuum are cooperative breeders in which many group members, including the mother, father, older siblings, aunts, uncles and sometimes unrelated individuals, are actively involved in infant care and contribute substantially to the survival of the offspring (Snowdon & Ziegler 2007). Humans have been classified as cooperative breeders (Hrdy 2005) and among all primate species, the Callithrichidae (marmosets and tamarins) show the strongest reliance on cooperative breeding (Hrdy 2009).

The extreme social tolerance, attention to social cues and behavioural coordination characteristic of the cooperative breeding system of Callithrichids facilitates enhanced performance on socio-cognitive tasks, such as social learning and cooperative problem solving (reviewed in Snowdon 2001; Snowdon & Cronin 2007; Burkart & Van Schaik 2010). In fact, the 'cooperative breeding hypothesis' posits that cooperative breeding has played a central role in the evolution of human sociality (Hrdy 2005) and that cooperative breeders are motivated and psychologically predisposed to act prosocially, that is, to

behave in ways that provide benefits to others (Burkart *et al.* 2007, 2009).

However, experiments testing predictions that cooperative breeding species demonstrate prosocial preferences have produced conflicting results. Burkart *et al.* (2007) studied common marmosets (*Callithrix jacchus*) on a prosocial choice task that allowed subjects to pull in one of two trays: the prosocial tray provided a small food reward for another marmoset, and the other tray did not provide anyone with food. Marmosets chose the prosocial tray more often when there was another marmoset present to receive the food compared with control conditions in which the food would be delivered to an empty cage. However, in a nearly identical study testing a closely related Callithrichid species, cottontop tamarins (*Saguinus oedipus*) did not choose the prosocial tray more often when there was another tamarin present to receive the food compared with control conditions (Cronin *et al.* 2009; see also Stevens 2010). The tamarins' performance was more similar to that of chimpanzees on similar tasks (Silk *et al.* 2005; Jensen *et al.* 2006) and failed to support the cooperative breeding hypothesis.

However, the lack of evidence for prosocial preferences in tamarins should not be taken as evidence for its absence. Studies demonstrating prosocial behaviour on similar tasks have done so with very small effect sizes (e.g. Burkart *et al.* 2007; Lakshminarayanan & Santos 2008), and slight differences in contextual features of the task influence the frequency of prosocial responding. For example, whether or not food is in sight of the actor (Warneken *et al.* 2007), moderate differences in

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the amount of effort required of the actor (Barnes *et al.* 2008) and the past relationship between the actor and the recipient (de Waal *et al.* 2008) may affect the frequency of prosocial responding.

Here, we test whether direct reciprocity facilitates prosocial responding in cottontop tamarins. Cottontop tamarins have been shown to cooperate to solve tasks when rewards are reciprocally distributed (Cronin & Snowdon 2008), to reciprocate grooming for infant care (Ginther & Snowdon 2009) and to preferentially provide food rewards to a conspecific who gave food back over one who refrained from giving food (Hauser *et al.* 2003). Given that tamarins have demonstrated behaviour consistent with reciprocity in some contexts, and reciprocity has been identified as a proximate mechanism that may elicit prosocial behaviour (Burkart *et al.* 2009), we predicted that tamarins would transfer rewards to a partner if they were given the option to do so on behalf of a recipient who had recently provided them with rewards.

Investigating whether reciprocity facilitates prosocial behaviour in tamarins is of additional interest in light of the current debate over the importance of reciprocity in animal social interactions (Clutton-Brock 2009; Schino & Aureli 2010). Although reciprocity has been of great theoretical import since its formalization by Trivers (1971), empirical evidence for reciprocity in non-human animals is rare and its influence has been argued to be over-emphasized (Hammerstein 2003; Stevens & Hauser 2004; Clutton-Brock 2009). Cottontop tamarins are an ideal species in which to investigate reciprocity because they satisfy the conditions proposed by Trivers (1971) to be likely to favour the selection of reciprocity, including a long lifespan, a low dispersal rate leading to many repeated interactions, mutual dependence among group members, parental care, a nonlinear dominance hierarchy and aid in combat (Campbell & Snowdon 2007; Snowdon & Ziegler 2007).

In the present experiment, we tested subjects with a single partner who immediately previously either had provided them with benefits (reciprocity possible) or had provided them with no benefits (no reciprocity possible). This design minimized the cognitive demands that may impede reciprocity (Stevens & Hauser 2004) by eliminating the need for temporal discounting, numerical discrimination and long-term memory of previous interactions to engage in successful reciprocity. We quantified the difference in rewards transferred to the recipient following these two treatments (reciprocity and no reciprocity), and in a non-social control condition. The results indicated evidence for prosocial preferences among cottontop tamarins and thus provide support for the cooperative breeding hypothesis. Although we found some evidence for reciprocity, changes in the tamarins' behaviour over time indicated that reciprocity was not a sufficient explanation for the prosocial effect. Rather, tamarins exhibited an initial depression in food transfers to partners who recently denied rewards, and maintained food transfers to some degree in both social conditions but not the non-social control.

2. MATERIAL AND METHODS

(a) *Subjects and housing*

Seven male–female pairs living together for a minimum of 4.5 years were trained for inclusion in this study. Husbandry details have been published previously (Ginther *et al.* 2001).

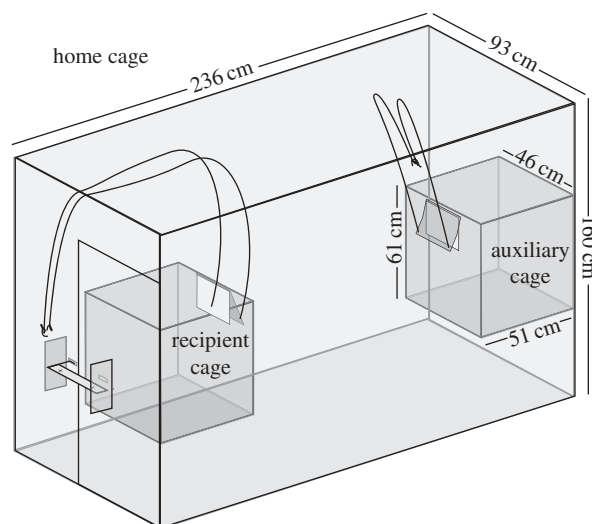


Figure 1. Three-dimensional view of the experimental set-up, to scale.

Animals were tested in their home cage inside which two smaller mesh cages were positioned at the front (recipient cage) and back (auxiliary cage). The donation apparatus spanned the front of the home cage such that when it was baited with two rewards, one reward was available to the animal in front of the handle, and the other was provided to the recipient cage (figure 1).

(b) *Training*

All but two subjects had completed similar training stages prior to their inclusion in a previous donation experiment (Cronin *et al.* 2009). Previously trained subjects were required to demonstrate that they remained calm in the recipient cage for 5 min and pulled the tray to bring themselves rewards on 10 out of 10 trials (maximum trial length 30 s) one day prior to the onset of pair testing. Subjects that had not previously been trained on the donation apparatus, and those that did not meet the above criteria, experienced the following training stages.

- *Stage 1.* Using positive reinforcement, tamarins were habituated to the recipient cage for incrementally longer durations until they were comfortable in the cage alone for 8 min. Tamarins proceeded to stage 2 once both individuals in the pair had completed stage 1.
- *Stage 2.* A single reward was placed on the tray location near the handle. The recipient cage was not present in the home cage. When the tamarin placed a hand on the handle, the experimenter slid the tray towards the tamarin. Additionally, small rewards were sometimes placed on the handle or near the apparatus to increase interest and likelihood of reaching for the handle. A pair of tamarins completed this training stage when each subject pulled the tray towards them and retrieved the reward without any experimenter involvement on 90 per cent of trials ($n = 10$, maximum trial length 30 s) in two consecutive sessions. Tamarins proceeded to stage 3 once both individuals in the pair had completed stage 2.
- *Stage 3.* Before proceeding to testing, the tamarins were required to demonstrate an understanding of the apparatus by meeting the following criteria. Each tamarin was tested alone in the home cage with the donation apparatus and the recipient cage present. A single reward was

randomly placed on either the donor side (in front of handle) or the recipient side (in front of the recipient cage) of the tray. The tamarins were required to pull the baited tray and retrieve the reward from the correct location (on half the trials, this requires the tamarin to enter the recipient cage) within 30 s on 17 out of 20 trials in two consecutive sessions, with no single session performance lower than 8 out of 10.

(c) Testing

We used a controlled food exchange context in which the transfer of benefits could be easily quantified. Mates were positioned side-by-side separated by mesh, and had vocal, auditory, olfactory and limited physical contact with one another (figure 1). Prior to testing, tamarins' food preferences were determined and a food that was highly desired by both individuals in the pair was used throughout testing for that pair (small pieces of cottage cheese, raisin, cookie or hard-boiled egg). All tamarins were tested in all conditions; each condition consisted of a 5 min treatment phase and a 5 min test phase. The experimenter immediately reset and re-baited the tray once rewards were retrieved and subjects were able to pull the tray as many times as they chose within 5 min. Focal subjects were tested in three conditions: reciprocity, no reciprocity, and non-social control (figure 2, and described below).

Random assignment within pairs determined whether the male or female would be tested first. This resulted in the male as the first focal animal in three of the seven pairs. Of the first animals to serve as focal subjects in the pair, half were assigned to the reciprocity condition first and the other half were assigned to the no reciprocity condition first, with near-equal assignment across sexes. On the second consecutive test day, the first focal animal was tested in the remaining condition (reciprocity or no reciprocity). Beginning 6 days later, the second animal in the pair was tested as the focal animal and exposed to the reciprocity and no reciprocity conditions in the opposite order of their mate, again on two consecutive days. Six days elapsed between testing of partners as focal subjects to minimize carry-over effects. However, order of testing within a pair is included in our statistical model to account for potential influences. One week after reciprocity and no reciprocity conditions were completed for the pair, subjects were tested in the non-social control. Control tests occurred on two consecutive days, testing one subject per day following the original order of testing within each pair. Testing occurred between 10.00 and 12.00, and all sessions were videotaped.

During the treatment phase of the reciprocity condition, the mate of the focal subject had access to the handle of an out-of-reach tray that, when pulled, provided a small food reward to both the mate and the focal subject. The mate was motivated to pull the tray to obtain rewards for itself, and by doing so, also delivered rewards repeatedly to the focal individual throughout the 5 min treatment (focal individuals received rewards at an average rate of 2.4 rewards per minute, s.e.m. = 0.05).

During the treatment phase of the no reciprocity condition, the tray was baited as in the reciprocity treatment, but a concealed pin prohibited the mate from being able to pull the tray, preventing both individuals from receiving rewards.

Following each treatment phase, the positions of the tamarins were immediately switched (typically within 30 s) and the test phase began. In the no reciprocity condition,

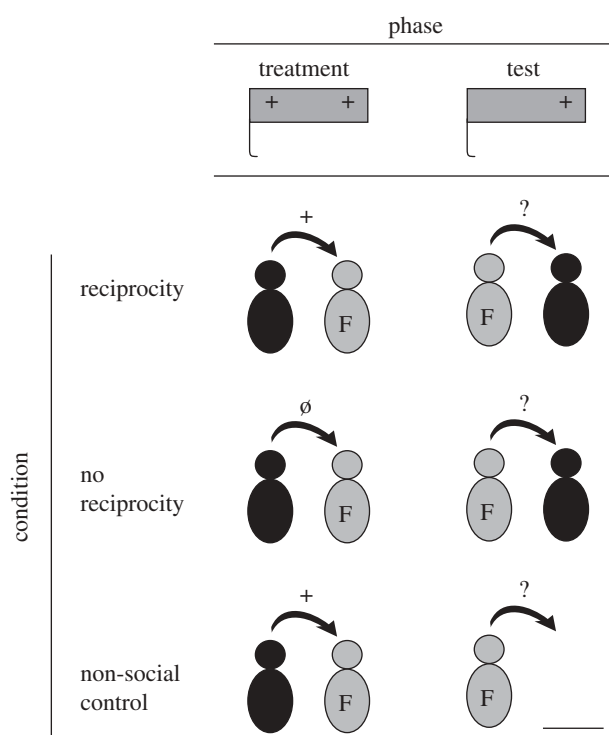


Figure 2. Experimental conditions. Each condition (represented by rows) consisted of a 5 min treatment and test phase (represented by columns). The tamarin icon with an 'F' indicates the focal subject in each pair, whereas the dark icon represents the focal subjects' partner. The trays at the top of the figure indicate which animal had access to the handle. The distribution of food rewards on the trays was consistent across conditions (food rewards represented by 'plus symbol').

the pin was removed while animals switched places, allowing the tray to move freely when pulled by the focal animal during testing. During the test phase, the focal subject had access to the handle and the tray was baited with a reward for the mate in the recipient cage only. The focal individual did not receive rewards for pulling the tray.

In the non-social control condition treatment phase, the focal subject received rewards for 5 min as a result of the partner's pulling just as in the reciprocity treatment. The partners provided an average of 2.62 rewards per minute (s.e.m. = 0.04), very similar to the rate in the reciprocity treatment. The consistency of the partners' behaviour in the reciprocity and non-social control treatments is also reflected in a significant positive correlation between the number of rewards received by subjects in both treatments (Pearson $r_{11} = 0.616$, $p = 0.025$). During the non-social control test phase, the focal individual again had access to a handle that would provide rewards to the recipient cage, but the recipient cage was empty and the partner was housed in the auxiliary cage. This control accounts for an increase in pull rate that might emerge simply from having received rewards and allows quantification of the baseline rate of pulling that occurred when no recipient was present to receive the reward (hereafter referred to as the 'sampling rate'). Primates regularly pull at some non-zero rate when presented with similar apparatuses even after having demonstrated an understanding that rewards will not be obtained (e.g. Silk *et al.* 2005; Burkart *et al.* 2007; Cronin *et al.* 2009). This may be owing to the low costs associated with

pulling and/or previous positive associations with the apparatus. When the focal subject pulled the tray, the experimenter removed the reward, and immediately reset and re-baited the tray as in the other conditions.

(d) Statistical analyses

The dependent variable was the number of pulls that occurred during the test phase of each condition. Pulls were scored from video (20% scored by a second observer, Cohen's $\kappa = 1.0$). Test sessions were divided into three 100 s blocks for analysis in order to capture behaviour early, mid- and late session, as the likelihood of transferring benefits may change over time (Hauser *et al.* 2003; Stevens & Hauser 2004; de Waal *et al.* 2008). Half of the subjects had experience providing treatment conditions for their mates during the previous week. Two aspects of this experience could potentially affect their behaviour as focal subjects: (i) they had interacted with the apparatus while the tray was locked during the no reciprocity treatment, and (ii) they had more experience receiving rewards in the recipient cage. For these reasons, order was included in the model. Data were normally distributed (Shapiro–Wilks $W = 0.949$, $p = 0.59$) and were analysed in a hierarchical linear mixed model using restricted maximum-likelihood estimation. Subjects were nested within pairs; within-subject factors included condition (reciprocity, no reciprocity, non-social control) and time (first, second or third 100 s block); between-subject factors included sex (male, female) and order (first or second focal subject within the pair). Results are reported as means \pm s.e.m. Results were considered significant at $p \leq 0.05$. Significant effects were followed with paired t -tests and all tests were two-tailed and include measures of effect size (d).

3. RESULTS

Fourteen subjects satisfied the training criteria. One subject was excluded after training for failure to retrieve rewards during reciprocity treatment. However, this subject was included as a recipient enabling testing of his mate ($n = 13$).

Results indicated significant main effects of sex ($F_{1,24} = 12.12$, $p < 0.01$), time ($F_{2,46} = 6.10$, $p < 0.01$) and condition ($F_{2,36} = 6.20$, $p < 0.01$). Order was not significant ($p = 0.18$). There was a significant interaction between condition and time ($F_{4,30} = 3.03$, $p = 0.05$). The significant effect of sex revealed that females pulled more often than males throughout the test regardless of condition (females = 14.71 ± 1.82 ; males = 4.67 ± 1.45), consistent with findings that female Callitrichids are more motivated for food than males (e.g. Box 1997).

Within-subject contrasts revealed a linear effect of time, with pulls decreasing across the 100 s blocks (initial 100 s = 5.08 ± 1.12 ; middle 100 s = 2.85 ± 0.71 ; final 100 s = 2.23 ± 0.29 ; $F_{1,9} = 8.61$, $p = 0.02$). The significant main effect of condition was followed by paired t -tests between reciprocity and no reciprocity ($t_{12} = 3.95$, $p < 0.01$, $d = 1.10$), reciprocity and non-social control ($t_{12} = 2.69$, $p = 0.02$, $d = 0.75$), and no reciprocity and non-social control ($t_{12} = 1.26$, $p = 0.23$, $d = 0.35$; figure 3a).

To investigate the interaction between condition and time, we analysed the number of pulls in a hierarchical mixed model (subjects nested in pairs, condition as the within-subject factor and sex and order as

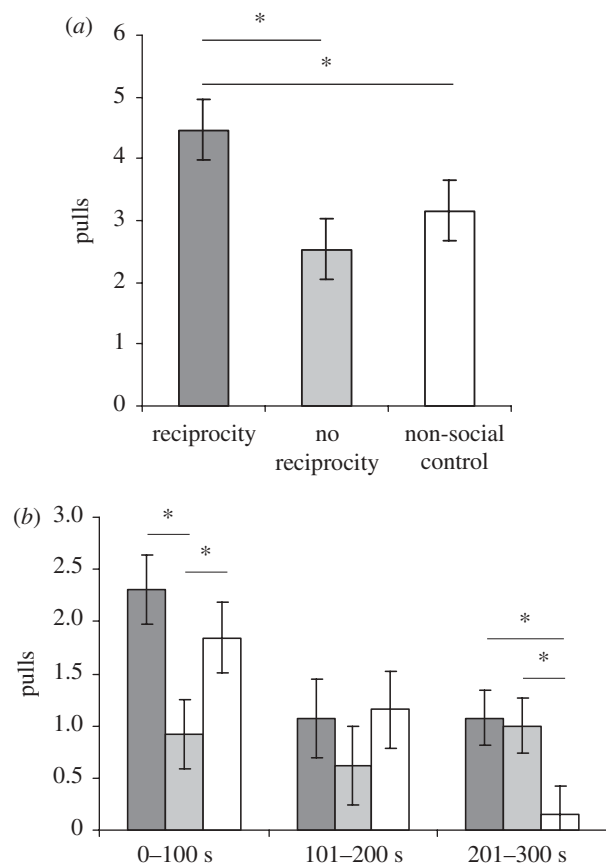


Figure 3. (a) Pulls per condition: all 300 s. (b) Pulls per condition: 100 s blocks. (a,b) Protected two-tailed paired t -tests were conducted following significant main effects. Data shown are means \pm s.e.m. Asterisk denotes significant differences between conditions. Black bars, reciprocity; grey bars, no reciprocity; white bars, non-social control.

between-subject factors) for each 100 s block. There was a significant effect of condition during each block (first 100 s: $F_{2,10} = 7.35$, $p = 0.01$; second 100 s: $F_{2,11} = 5.64$, $p = 0.02$; third 100 s: $F_{2,14} = 9.95$, $p < 0.01$; figure 3b).

Follow-up investigations indicated that tamarins pulled significantly less often during the first 100 s of the no reciprocity test than both the reciprocity test ($t_{12} = 4.15$, $p < 0.01$, $d = 1.15$) and the non-social control test ($t_{12} = 2.76$, $p = 0.02$, $d = 0.77$). There was no significant difference between the first 100 s of reciprocity and non-social control test ($p = 0.20$, $d = 0.383$). No pairwise comparisons between conditions resulted in significance during the second 100 s block (all $p > 0.18$, all $d < 0.40$). Investigations of the significant effect of condition during the final 100 s block indicated that tamarins pulled significantly less often during the last 100 s of the non-social control than either the reciprocity test ($t_{12} = 3.48$, $p < 0.01$, $d = 0.96$) or the no reciprocity test ($t_{12} = 3.19$, $p < 0.01$, $d = 0.88$). There was no significant difference between the last 100 s of reciprocity and no reciprocity tests ($p = 0.78$, $d = 0.08$).

To test whether the decrease in pulls during the first 100 s of the no reciprocity test could be explained by focal subjects avoiding the apparatus or disengaging from the experiment following the only treatment condition during which they did not receive rewards, we tested whether the latency to approach the apparatus differed between conditions. Latencies to approach were not

normally distributed, so the non-parametric two-tailed Wilcoxon test was used. The latency to approach the apparatus did not differ significantly between the no reciprocity test (17.78 ± 7.18 s) and either the reciprocity test (24.74 ± 22.98 , $Z = 1.48$, $p > 0.14$) or the non-social control test (12.89 ± 8.24 , $Z = 0.51$, $p > 0.60$).

4. DISCUSSION AND CONCLUSION

The results of this experiment support the cooperative breeding hypothesis by demonstrating prosocial preferences in a cooperative breeding primate. Although the greatest amount of food transfers occurred following the reciprocity treatment, the prosocial behaviour observed cannot be accounted for by reciprocal altruism alone. The significant interaction between condition and time indicates that the tamarins' responses to treatment conditions changed dynamically over the course of testing, and a prosocial effect (measured relative to a non-social control) emerged only late in test sessions. To fully understand the proximate mechanisms that elicited the prosocial response, we must consider how the tamarins' behaviour changed over time.

If the tamarins were responding reciprocally to their mates, we would have predicted the strongest effect of reciprocity to occur during the first 100 s of the test phase, when the shortest delay had elapsed since receiving rewards from the partner. However, during the first 100 s of testing, the number of pulls executed during the reciprocity test was not significantly greater than the non-social control test. Therefore, having recently received rewards from the partner did not cause tamarins to increase their pull rates to reciprocally provide rewards to that partner. The lack of significant increase above the non-social control was not owing to a ceiling effect, as tamarins demonstrated as many as six pulls per 100 s and the mean expressed in the first 100 s of the reciprocity test was below three.

However, the tamarins did exhibit an unexpected and significant reduction in the number of pulls executed following the no reciprocity treatment, compared with the reciprocity and non-social control conditions. This does not appear to reflect frustration or disengagement from the task, as the latency to approach the apparatus did not differ. If the non-social control reflects the sampling rate of the apparatus, this finding suggests that tamarins may have been inhibiting their tendency to pull following treatments during which their partner did not provide them with rewards. One interpretation of this effect is that the tamarins were exhibiting negative reciprocity (the matching of benefits withheld; Axelrod & Hamilton 1981) or punishment (Clutton-Brock & Parker 1995) and inhibiting their normal tendency to manipulate the apparatus to avoid providing rewards to their mate who had immediately previously denied them rewards. It has been argued elsewhere that punishment may be more likely among cooperative societies consisting of individuals with a high likelihood of repeated interactions (Clutton-Brock & Parker 1995; Hammerstein 2003). Subsequent investigations that predict this effect and rule out other interpretations would be of interest. One simpler explanation that cannot be ruled out from the present design is that the tamarins pulled more often following the reciprocity and non-social control conditions

owing to response facilitation, or the increase in the likelihood of performing an action after watching another individual do so (Byrne 1994).

During the second 100 s of testing, there were no significant differences between conditions, and the pull rates across conditions converged. By the final 100 s of testing, however, significant differences between conditions were present, with a greater number of pulls executed when a partner was present to receive the reward (the no reciprocity and reciprocity conditions) compared with the non-social control. The number of pulls executed in both social conditions was nearly identical, indicating that any effect resulting from whether the partner had previously provided or denied rewards had diminished, and the salient difference was whether a recipient was present or absent. A prosocial effect emerged only during these last 100 s of testing, with tamarins providing more rewards to a partner than to an empty cage. This is a prosocial effect as it has been defined in previous studies (e.g. Silk *et al.* 2005; Jensen *et al.* 2006; Burkart *et al.* 2007).

Considering the changes in the tamarins' behaviour over time, we suggest a simple learning explanation for the late prosocial effect. We find it likely that the tamarins initially sampled the apparatus at the start of the reciprocity and non-social control tests because the act of doing so was not costly and the apparatus has regularly been associated with desirable food rewards, as has been seen in other studies with similar designs (e.g. Silk *et al.* 2005; Jensen *et al.* 2006; Burkart *et al.* 2007; Cronin *et al.* 2009). This initial sampling was reduced following the treatment condition during which the partner apparently withheld rewards from its mate, and whether this was owing to punishment or a lack of response facilitation is undetermined. By the final 100 s of testing, tamarins had nearly ceased pulling in the non-social test condition, but pulling did not extinguish in either the no reciprocity or the reciprocity test conditions. By the end of the session, tamarins appeared to find it more rewarding to pull in the two conditions that resulted in rewards for their partner than in the condition in which the recipient cage was empty.

Other research supports the interpretation that under some conditions it is rewarding to provide benefits to social partners. A recent study of capuchin monkeys (*Cebus apella*; de Waal *et al.* 2008) reported that rates of prosocial responding increased over sessions as capuchins presumably found it rewarding to procure rewards for their partners. Although immediate benefits to the donor are not clear, providing goods or services to others may provide intrinsic benefits to the giver as well. One documented example comes from field observations of Barbary macaques (*Macaca sylvanus*), indicating that the physiological indicators of stress (faecal glucocorticoids) were reduced in response to grooming more so than being groomed (Shutt *et al.* 2007).

The learning mechanism might explain why a prosocial effect was not observed in our previous experiments with cottontop tamarins (Cronin *et al.* 2009). In the present study, there was a single contingency to learn: when the focal subject pulled the only available handle, a reward was delivered directly to the recipient cage. The outcome of pulling was consistent and did not require subjects to discriminate between multiple tray options. Subjects simply pulled or refrained from pulling to make their choice (similar to the design used successfully

with cottontop tamarins in Hauser *et al.* 2003). By contrast, in our previous experiments (Cronin *et al.* 2009), subjects were required to discriminate between two tray options, one which provided rewards to the recipient and one that did not, and the tray that would provide rewards was randomized. Although we predict this discrimination to be within the capability of cottontop tamarins (Stevens *et al.* 2007), there may not have been a sufficient number of trials to experience the reward of providing food to the mate *and* allow the sampling rate to decrease to a level that would reveal differentiation between partner present and absent conditions.

The time windows selected for the present experiment undoubtedly informed our interpretations. Three blocks were chosen in order to capture time windows with a sufficient number of events to enable comparisons across conditions while creating enough time points to analyse changes over time beyond linear decreases or increases. A different number of blocks may have influenced our interpretation. However, accounting for the changing rate at which tamarins sampled the apparatus was central to understanding the behaviour of tamarins on the present task, and should be considered in the design and interpretation of similar experiments.

Although an overall effect of reciprocity was found, positive reciprocity played a minor role, if any, in facilitating prosocial behaviour between cottontop tamarins in this experiment. The significant interaction between condition and time requires us to interpret the tamarins' behaviour throughout time, and reciprocity did not provide the best explanation of the pattern of food transfers during any single time window. The lack of strong evidence for positive reciprocity is striking, given that tamarins exemplify the characteristics originally designated by Trivers (1971) as likely to promote reciprocal altruism and the cognitive demands of reciprocity were minimized in this design (Stevens & Hauser 2004). Reciprocity could have emerged in a generalized form where the receipt of previous help increases the likelihood of providing help (Pfeiffer *et al.* 2005; Rutte & Taborsky 2007), but did not. It is unknown whether free or more frequent role reversals would have increased the likelihood of reciprocal behaviour. Additional work is needed to determine under what conditions tamarins, and other species that are posited to engage in reciprocity, do in fact respond reciprocally to partners.

In summary, these findings support the cooperative breeding hypothesis while leaving open the question of whether reciprocity is a strong governing force in animal social interactions. These findings call attention to the possibility of interpreting behaviour as reciprocal when upon closer inspection other interpretations emerge. Finally, the proposal that tamarins find it rewarding to provide benefits to conspecifics and thus increase their rate of prosocial responding over time is not a challenge to the cooperative breeding hypothesis. Rather, it offers a simple mechanism for the prosocial effect and contributes to understanding the psychological processes associated with prosocial behaviour.

The research was approved by the University of Wisconsin-Madison Institutional Animal Care and Use Committee (IACUC).

We thank Matthew J. Fuxjager, Joan B. Silk, Frans B.M. de Waal and three anonymous reviewers for thoughtful

comments on earlier versions, Robert Becker for production of figures and Andrew Mulder for construction of the apparatus. This project was supported by the University of Wisconsin Graduate Research Committee, a Hilldale Professorship to C.T.S. and a National Science Foundation Graduate Research Fellowship to K.A.C.

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