

Calculated reciprocity? A comparative test with six primate species

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Abstract Little evidence of calculated reciprocity has been found in non-human primates so far. In this study, we used a simple experimental set-up to test whether partners pulled a sliding table to altruistically provide food to each other in short-term interactions. We tested 46 dyads of chimpanzees, bonobos, gorillas, orangutans, brown capuchin monkeys and spider monkeys to examine whether a subject's tendency to provide food to a partner was directly affected by the partner's previous behaviour, by the species, by the condition (i.e., whether the partner could access the food provided by the subject) and by the social tolerance levels within each dyad. Chimpanzees and orangutans were the only species pulling significantly more when the partner could retrieve the food altruistically provided. However, no species reciprocated food exchanges, as subjects' probability to pull was not affected by the previous number of the partner's pulls, with the possible exception of one orangutan dyad. Although subjects clearly

knew how the apparatus worked and easily obtained food for themselves, individuals did not usually take the opportunity to provide food to their partners, suggesting that calculated reciprocity is not a common behaviour and that food exchanges are usually not reciprocated in the short-term within dyads.

Keywords Calculated reciprocity · Great apes · Capuchin monkeys · Spider monkeys · Altruism

Introduction

Reciprocity can be defined as the reciprocal exchange of resources or services between partners (Trivers 1971). During reciprocal exchanges, actors and recipients repeatedly interact and exchange their roles, and actors are able to discriminate against non-reciprocating recipients (Trivers 1971; Stevens and Hauser 2004). Reciprocity might have played an important role in the evolution of cooperative behaviour between unrelated individuals, since this exchange of resources or services implies that individuals

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suffer temporary costs to subsequently obtain larger benefits (Trivers 1971; Clutton-Brock 2009).

The mechanisms for reciprocity can be of three main kinds (Brosnan and de Waal 2002). Symmetry-based reciprocity is the least cognitively demanding mechanism and implies altruism being directed to group mates on the basis of symmetrical aspects of their relationships (de Waal and Luttrell 1988). In emotionally based reciprocity, which also requires a limited cognitive load, altruism received in the past by a certain partner engenders positive emotions promoting altruism toward that partner (Schino and Aureli 2009, 2010a). Calculated reciprocity is the most cognitively demanding kind of reciprocity and is proximately motivated by the expectation of a future reward based on past experience (de Waal and Luttrell 1988). In calculated reciprocity, the exchange is intentional, transferred resources or services have a known value, partners keep track of exchanges over time, they understand present costs and future benefits of each altruistic interaction and expect the same or other resources or services to be returned (de Waal and Luttrell 1988; Dufour et al. 2009; Schino and Aureli 2010a). Therefore, calculated reciprocity requires memory, the ability to make calculations and a limited temporal discounting, so that only species possessing these cognitive skills could show this form of reciprocity (Stevens and Hauser 2004; Dufour et al. 2009). Because of the necessity to keep track of exchanges over time, it is conceivable that calculated reciprocity happens, if ever, in short-term interactions. In this study we therefore focus on short-term calculated reciprocity and monitor whether subjects adapt their behaviour to what the partner does during the short-time frame of the experimental test, although it is impossible to rule out that emotions also play a role.

It has been argued that most reciprocal exchanges in non-human animals are probably based on symmetry- or emotionally based rather than calculated reciprocity (Brosnan and de Waal 2002). Correlational evidence of a temporal relation between giving and receiving has been reported, for example, in grooming exchanges in mandrills (*Mandrillus sphinx*, Schino and Pellegrini 2009) and between grooming and agonistic support in long-tailed macaques (*Macaca fascicularis*; Hemelrijk 1994), baboons (*Papio hamadryas ursinus*; Cheney et al. 2010) and chimpanzees (*Pan troglodytes*; Koyama et al. 2006; Gomes et al. 2009). In these studies emotionally based reciprocity was likely the mechanism underlying the exchanges. In an experimental context, brown capuchin monkeys (*Sapajus apella*) reciprocated food transfers with their partner during short-term exchanges (Hattori et al. 2005; Sabbatini et al. 2012). Importantly, however, when provided with the opportunity to choose the partner to interact with, capuchin monkeys made their choice based on the quality of their

long-term social relationship rather than on the food obtained in previous exchanges (Sabbatini et al. 2012). Even more importantly, individuals only actively gave food in 0.37 % of all the trials, the great majority of food exchanges consisting of tolerated thefts. Furthermore, cotton-top tamarins (*Saguinus oedipus*) provide more food to conspecifics that were altruistic in previous interactions (Hauser et al. 2003; but see Stevens 2010), although the results of this study have never been replicated. Language-trained chimpanzees actively transferred tools to a partner, shared the food obtained and alternated roles, but only did so after extensive training (Savage-Rumbaugh et al. 1978). Indeed, reciprocal transfers did not take place when pairs of chimpanzees could alternatively provide food to each other (Brosnan et al. 2009; Yamamoto and Tanaka 2009), with the possible exception of one chimpanzee dyad (Brosnan et al. 2009). Finally, when testing gorillas (*Gorilla gorilla*), orangutans (*Pongo abelii*), bonobos (*Pan paniscus*) and chimpanzees, Pelé et al. (2009) found that only one dyad of orangutans exhibited spontaneous reciprocal transfers of tokens of different values. Importantly, although transfers were initially biased in one direction, they became more balanced towards the end of a follow-up study of the same dyad, with reciprocity being evidenced both between and within trials (Dufour et al. 2009).

In this study, we used a simple experimental set-up to test short-term calculated reciprocity in six primate species. The set-up allowed dyads of individuals to altruistically give food to each other, switching their roles several times in each session. The short-term nature of the interactions made the set-up ideal to test calculated reciprocity in a non-human animal, by allowing us to monitor whether subjects' behaviour during exchanges was directly affected by the partner's previous behaviour. Subjects tested included dyads of chimpanzees, bonobos, gorillas, orangutans, brown capuchin monkeys and Geoffroy's spider monkeys (*Ateles geoffroyi*). All these species possess the cognitive prerequisites needed for calculated reciprocity, including memory (Amici et al. 2010), limited temporal discounting (Amici et al. 2008; Addessi et al. 2011) and the ability to make simple calculations (Call 2000; Beran 2001; Addessi et al. 2008).

Since *Ateles*, *Pan* and *Pongo* display better inhibitory skills than other primates (Amici et al. 2008), and inhibitory skills may be linked to an enhanced ability to delay gratification, these species may also show enhanced reciprocity. Levels of allomaternal care might also favour reciprocity. In this regard, brown capuchin monkeys, which show higher levels of allomaternal care than other species, might show enhanced reciprocity (Burkart et al. 2009; Burkart and van Schaik 2010). However, evidence for calculated reciprocity in these six species is still lacking or controversial. We therefore used this set-up to examine

whether individuals' propensity to reciprocally give food to each other was affected by the partner's previous behaviour, by the species, by the condition (i.e., whether the partner could access the food provided by the subject or not) and by the social tolerance levels within each dyad.

Methods

Subjects

We tested 10 dyads of chimpanzees (comprising 9 individuals), 4 dyads of bonobos (5 individuals), 6 dyads of gorillas (4 individuals) and 6 dyads of orangutans (4 individuals), all housed at the Wolfgang Koehler Primate Research Center in the Leipzig Zoo, Germany. Moreover, we tested 8 dyads of brown capuchin monkeys (comprising 7 individuals) housed at the ISTC-CNR Primate Center in Rome, Italy and 12 dyads of Geoffroy's spider monkeys (comprising 7 individuals) at the Animaya Zoo in Merida, Mexico. Individuals were tested with more than one partner, without following a specific order. For each species, we included individuals of both sexes, two age classes (subadults and adults) and three dominance rank categories (high, middle or low, in relation to the whole group). Dominance rank categories were estimated by the experimenter and keepers working at the different facilities following the approach used in previous studies (e.g., Freeman et al. 2010; Herrelko et al. 2012). This approach provided us with information on dominance rank categories of numerous individuals at several facilities, but we are aware that this approach has limitations over dominance tests. For each species we also included dyads with different levels of social tolerance (see below). Table S1 (in Supplemental Material) includes a complete list of the individuals participating in the study. All individuals were born and reared in captivity, except for the spider monkeys and one gorilla, who were born in the wild. The spider monkeys were raised as pets before being rescued and had extensive experience in the zoo environment, but no further details on their lives were available. All subjects were housed in groups with conspecifics, in enclosures with outdoor and indoor areas. They were used to being temporarily isolated in testing areas (apart from mothers who were tested with their infants) and were tested by familiar experimenters only after they were comfortable with the set-up and the testing area. All the individuals had previously participated in experimental tasks, but none of them had been previously tested on the present task. Before or during the experiment, individuals were never deprived of food or water and took part in the procedure on a voluntary basis.

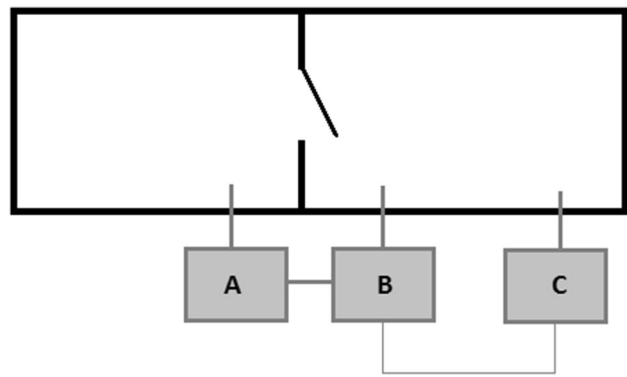


Fig. 1 Diagram of the apparatus. Three platforms (labelled A, B, C) located in front of two adjacent testing rooms (connected by a door) could be pulled towards the front mesh of the rooms by the handles attached to them (depicted as a *single perpendicular line* to the front of the rooms). The precise combination of platforms and handles present in each trial varied as a function of the condition (see text for further details)

Materials and procedure

The apparatus consisted of three sliding platforms (labelled A, B and C from the left to the right) located in front of two adjacent testing rooms (Fig. 1). The platforms could be pulled towards the front mesh of the testing rooms by pulling a handle. Depending on the condition, subjects could enter one or two testing rooms and access the food located on one or more platforms once those had reached the front mesh (Figures S1–S3 in Supplementary Material). Handles were added to or removed from each of the three platforms, depending on the trial and condition (Fig. 2; see below). Food placed on one platform could only be reached after the platform had been pulled against the testing room's front mesh. Platforms A and B were connected so that pulling one closer to the mesh also moved the other towards the mesh. In contrast, platforms B and C could never be brought simultaneously to the mesh (i.e., one slid backwards and out of reach if the other one was pulled forwards).

The task consisted of three different conditions: training, experimental and control. In the training condition, we tested subjects' understanding of the set-up (Fig. 2a, Figure S1 in Supplementary Material). Only platforms B and C had handles that could be pulled. Subjects were tested alone while alternating sessions with the door connecting the two testing rooms closed and sessions with that door open. When the door was closed, the subject only had access to platforms B and C, whereas when the door was open she had access to all three platforms. Each session was composed of 6 trials, in which only one of the 3 platforms was baited with a visible piece of food (with the order in which platforms were baited being randomized

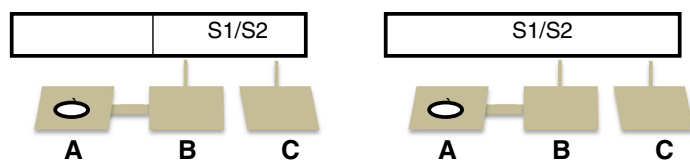
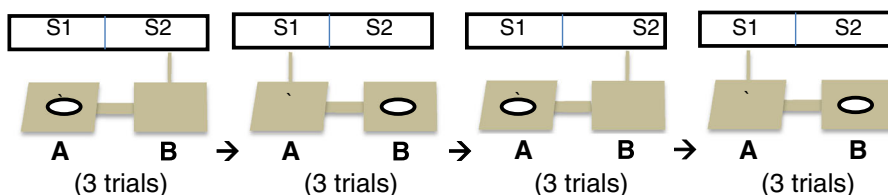
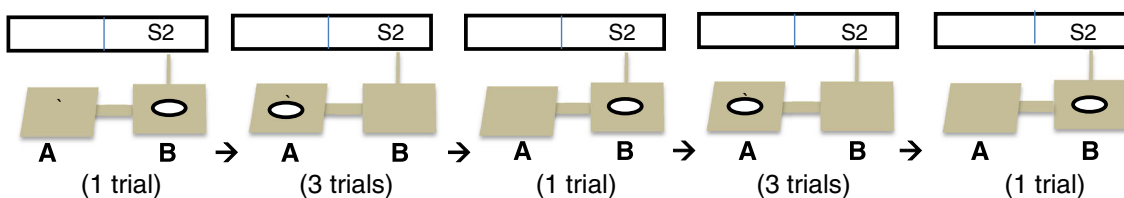
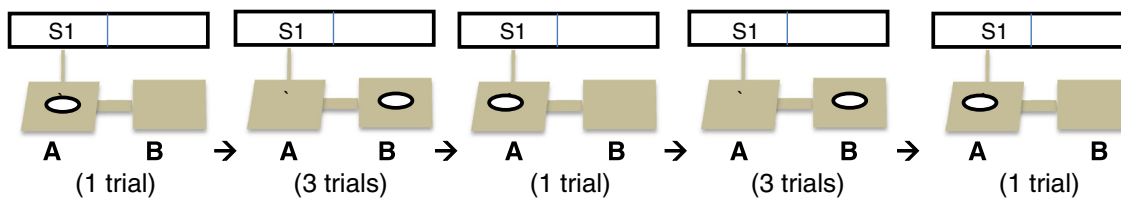
a TRAINING CONDITION: S1/S2 has access to B & C, or access to A, B & C**b EXPERIMENTAL CONDITION: 6 trials by S1 and 6 trials by S2****c CONTROL CONDITION: 6 trials and 3 motivational trials by S2****d CONTROL CONDITION: 6 trials and 3 motivational trials by S1**

Fig. 2 Illustration of the set-up during **a** training, **b** experimental and **c**, **d** control conditions. The presence of food is indicated by a *circle* on the platform. The door connecting the two rooms was closed in all conditions except the training condition in which the subject could potentially access all platforms. In the training condition the subject could either potentially access only platforms *B* and *C* or all

platforms. In the experimental condition each subject could only pull the handle that gave food to her partner. In the control condition the subject (in different trials) could pull the handle to either get food for herself (motivational trials), or displace the baited platform towards an empty room (no partner present)

and each platform being baited twice in each session). Subjects had to make their choice within 30 s after the baiting. We considered that subjects understood the set-up (i.e., met the training criterion) if in two consecutive sessions (1) they always pulled platform *B* when this platform was baited and pulled platform *C* when platform *C* was baited and the door closed (i.e., only platforms *B* and *C* were accessible), and (2) they always pulled platform *C* when this platform was baited and pulled platform *B* when platform *A* or *B* was baited and the door was open (i.e., all platforms were accessible).

Upon meeting the training criterion, subjects received the experimental and control conditions. Conditions were

administered in a random order, never administering more than three sessions of the same condition in succession. In the experimental condition, platform *C* was removed and two subjects participated. One subject entered the testing room with platform *A* and the other subject entered the adjacent testing room with platform *B* (Fig. 2b, Figure S2 in Supplementary Material). In the first block of 3 trials, only platform *B* had a handle. The experimenter baited platform *A* with a visible piece of food and waited for 30 s. If the subject with access to platform *B* pulled the handle attached to this platform, platform *A* was drawn within reach of the partner who could retrieve the food. In this case, the experimenter let the partner get the food before

pulling back the platforms to their initial position to begin the next trial. If the subject with access to platform B did not pull the handle within 30 s, the experimenter removed the food from platform A and dropped it in a bucket, before repositioning the platforms to their starting position. In the very few cases in which the subject was distracted by external noises, the experimenter stopped the countdown of the 30 s until it was quiet again. After the first block of 3 trials in which platform A was baited, the experimenter removed the handle from platform B and placed it on platform A. Then, the experimenter administered a second block of 3 trials in which the roles of the two subjects were reversed, so that platform B was now baited and the subject with access to platform A had the choice to provide food to the partner by pulling platform A within 30 s. The entire 6-trial procedure was repeated again so that each session consisted of 12 trials. For each trial, the experimenter recorded whether the subjects pulled the accessible platform, thus providing food to their partner. Pulling the platform was considered an altruistic action, as the actor incurred in some costs (i.e., pulling) in order to provide food to the partner. Crucially, subjects had to actively provide food to the partners (i.e., tolerated thefts were not possible), and food was provided in small quantities to maintain its high value throughout the test.

In the control condition, the subject was tested alone in the same room where she was tested in the experimental condition (e.g., in the room with access to platform B: Fig. 2c; or in the room with access to platform A: Fig. 2d; Figure S3 in Supplemental Material). During the whole session, only the accessible platform had a handle. The experimenter administered two blocks of 3 trials in which only the inaccessible platform was baited (e.g., platform A was baited when the subject had access to platform B) and the subject had 30 s to pull it. In order to motivate the subject, the experimenter also administered motivational trials consisting of baiting the platform with the handle attached (e.g., baiting platform B when the subject had access to this platform). These motivational trials were only administered in the control condition because otherwise the subject would have had no opportunity to receive any food reward throughout the session, in contrast to what happened in the experimental condition, in which individuals always had the opportunity to obtain food from the partner. Subjects received 3 motivational trials per session (one at the beginning and at the end of each session, and one between the two blocks of control trials). Thus, taken together, subjects received 9 trials per session (6 control and 3 motivational trials). For each trial, the experimenter recorded whether the subject pulled the accessible platform.

In order to assess individuals' social tolerance levels toward the partner, each dyad was tested in two adjacent

testing rooms. Each individual was in one of the two rooms with a drinking bottle filled with juice attached to each room in close proximity (separated by a mesh partition) (Amici et al. 2012). The session ended when one of the two drinking bottles was empty or after 120 s had elapsed. For each individual, we calculated the proportion of time spent drinking simultaneously with the partner by dividing the time spent drinking simultaneously with the partner by the time spent drinking (i.e., the sum of the time spent drinking simultaneously with the partner and the time spent drinking alone). As the measure of social tolerance for each dyad, we used the mean of the proportions of the two individuals in each dyad. All dyads received 10 sessions of the experimental condition and both individuals in each dyad received 10 sessions of the control condition. Capuchin monkeys were tested for 3 sessions instead of 10 because of time constraints at the facility. Each dyad also received 3 sessions of the social tolerance task on 3 different days. For logistic reasons, bonobos could not be tested in the social tolerance task.

Scoring and data analyses

We scored the behaviour live during each session. We also videotaped all the 13,624 trials (except for 115, due to technical problems) and later checked the live-scored behaviour against the videotapes for accuracy. A second observer coded 18.5 % of the videotaped trials to assess the inter-observer reliability for pulling the platform by the subjects, which was excellent (Cohen's $k = 0.98$).

To test which factors affected the probability of pulling the platform we ran a generalized linear mixed model (GLMM, Baayen 2008). The response variable was the number of trials (0, 1, 2 or 3 out of 3) in which individuals pulled the platform in each 3-trials block, and therefore the model was fitted with a binomial error structure and logit link function (McCullagh and Nelder 2008). Consequently, we essentially modelled the proportion of trials in which the subjects pulled the platform. In the model we included three test predictors as fixed effects: species, condition (control or experimental) and number of partner's pulls in the previous 3-trials block (to examine whether individuals reciprocated, i.e., whether they pulled according to their partners' previous behaviour), as well as all the interactions among the three predictors up to the third order. As control variables, we included further fixed effects, namely session number (numeric variable with values 1–10), block of trials (second, third or fourth 3-trial block within a session) and rank difference (i.e., the difference between the rank categories of the two individuals in each dyad) to control for their potential effects. Since directly including the subject and partner's age and sex as fixed effects would have made the model too complex, we included each of them individually. Given that

none of them significantly altered the effects of the other factors, we excluded them from our final model. As random effects we included the identity of the two individuals in each dyad, as well as the dyad. Finally, we included random slopes within dyads for the number of previous pulls, the condition and their interaction in order to control for the possibility that the effects of those variables vary between dyads and keep type I error rate at the nominal level of 5 % (Schielzeth and Forstmeier 2009). The reason why we did not include random slopes within subject and partner was that otherwise the model would have been too complex. In an initial model we also included dyadic social tolerance as a fixed effect into the model, as high social tolerance levels might be an indicator of good relationship quality, which might in turn affect the tendency to show contingent reciprocation (see Silk 2003; Silk et al. 2013). However, dyadic social tolerance did not have a significant effect on the probability of pulling (estimate \pm SE = 2.35 ± 1.87 , $z = 1.26$, $P = 0.209$). As dyadic social tolerance was not available for the bonobos, we removed it from the subsequent model to make use of all data. If a significant effect of the three-way interaction was found, we also tested for the effect of the number of pulls by the partner in the previous 3-trial block separately for each combination of species and condition (post hoc tests within species and condition). Moreover, if a significant effect of the interaction between species and condition was found, we also split the data by species and then, for each species, we ran models as described above, including the same fixed and random effects as above, with the exception of all terms involving species. These analyses allowed us to understand whether individuals of each species pulled the platform significantly more often in the experimental than in the control condition.

As an initial test of the overall effect of the three test predictors and all their interactions we ran a likelihood ratio test (Dobson 2002) comparing the full model described above with a null model lacking the test predictors and all their interactions. Hence, the null model comprised the fixed effects control predictors session number, block of trials and rank difference, the random effects for the two individuals in each dyad and the dyad itself, and the random slopes components present in the full model. Such a full-null model comparison gives an overall test of the test predictors considered and reduces the risk of erroneous significances that would otherwise arise in our model, which included three test predictors, as well as three two-way and one three-way interaction between them (Forstmeier and Schielzeth 2011). To verify the models' validity we inspected variance inflation factors (VIF; Quinn and Keough 2002; Field 2005) which revealed that collinearity was not a problem (maximum VIF = 2.5). We tested for model stability excluding subjects, partners and dyads one by one, ran the models again and inspected P values and

estimated coefficients for outliers. This procedure revealed no issues for the P values in the model including social tolerance (and therefore excluding bonobos), as even the largest P values for the full-null model comparison as well as the three-way interaction revealed significance ($P < 0.05$). In the model excluding social tolerance (and thus including all species) the significance of the full-null model comparison was robust (all $P < 0.05$). However, the test of the three-way interaction revealed two P values (out of 117; one model did not converge, i.e., the function used was not able to reliably identify one combination of estimates to be the best fitting) being larger than 0.05 (0.093 and 0.101). Similarly, with regard to the estimated coefficients, the model including social tolerance was relatively stable (i.e., particularly in the case of the estimates derived for the three-way interaction and social tolerance) and only estimates with values close to zero were unstable with regard to their sign. For the model not including social tolerance, stability of the estimates was fairly low (i.e., those of the three-way interaction were even unstable with regard to their sign). Presumably this was in part due to complete separation (Field 2005) which happened because pulling was overall very rare or did not happen at all in certain combinations of species and condition. The models were implemented in R (version 3.0.1; R Core Team 2013) using the function `lmer` of the R package `lme4` (Bates et al. 2013). VIF values were derived using the function `vif` of the R package `car` (Fox and Weisberg 2011). The total sample size, including all species, was 2,382 3-trial blocks for 46 dyads involving 36 individuals.

We also analysed whether individuals' pulling behaviour was influenced by the partner's pulling behaviour in the longer term (i.e., across all the 10 sessions of the experimental condition). For each species, we ran a Spearman correlation to examine whether there was an association between the two individuals' overall frequency of pulling. We did not find any significant correlation ($P > 0.5$ in all cases). However, these results should be treated with caution, as the same individuals were involved in multiple dyads. We had originally planned to use GLMMs (controlling for identity of the two individuals), but the respective models were highly unstable, presumably due to the models being relatively complex, in combination with pulling being relatively rare overall.

Results

Effects of species, condition and partner's previous behaviour

Pulling the platform was rare as individuals pulled the platform in only 18.6 % of all the experimental and control

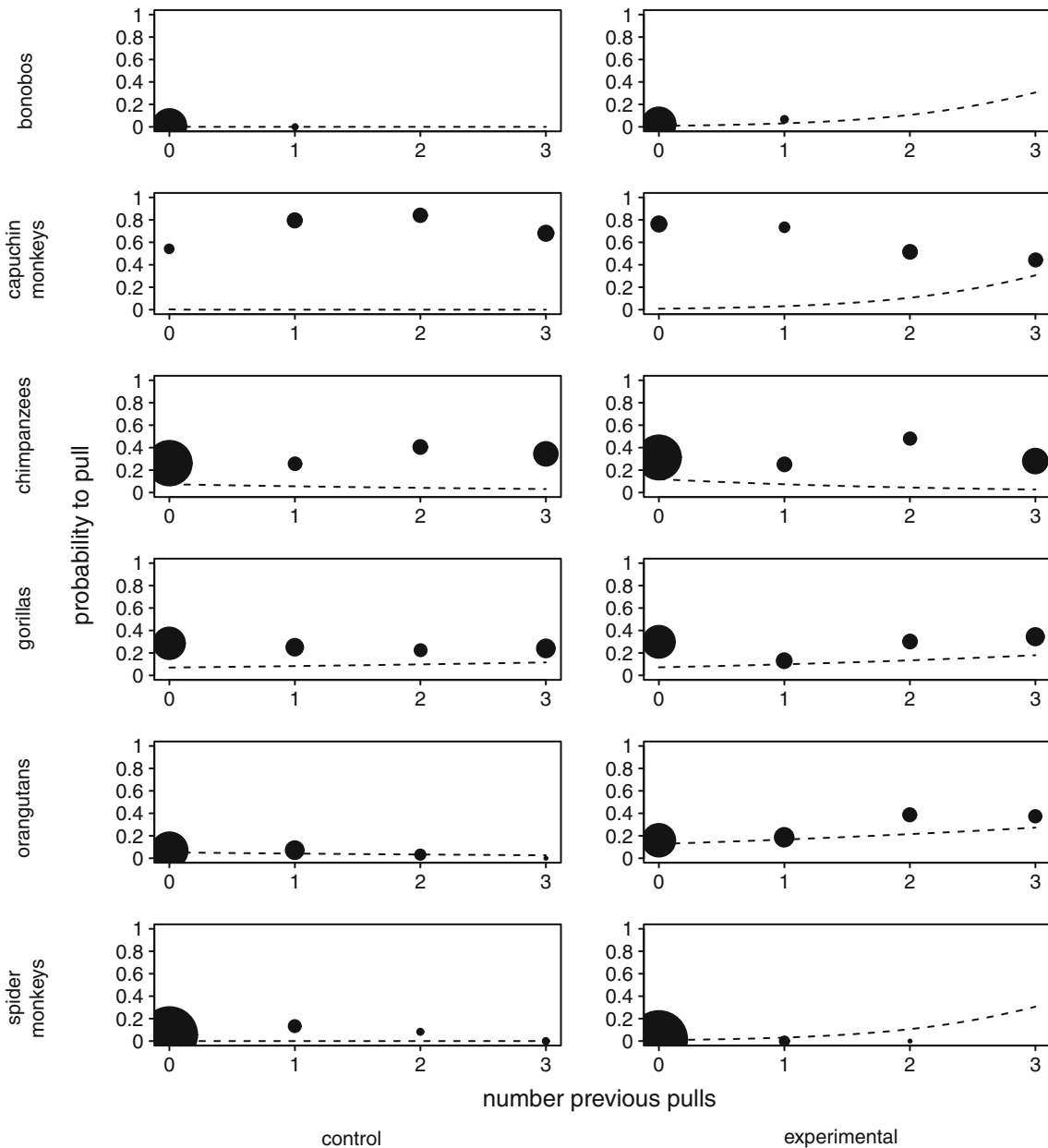


Fig. 3 Mean probability (based on the fitted logistic GLMM model: see text for more details) of pulling the platform as a function of the partner's number of pulls (0, 1, 2 or 3) in the previous 3 trials, for each combination of species and condition. In the experimental condition (*right panel*), subjects and partners switched roles every 3 trials, and the probability that subjects pulled the platform (*y axis*) is plotted as a function of the number of partner's pulls (*x axis*) within

the same session. In the control condition (*left panel*), as subjects were tested alone, the probability that subjects pulled the platform is plotted as a function of the partner's number of pulls when tested (alone) in the same control condition. The size (area) of the *black circles* indicates the number of trials in which subjects pulled the platform for the respective *x* values (a higher number of trials in which subjects pulled is represented by *larger circles*)

trials. However, individuals pulled the platform in 99.2 % of the motivational trials. Overall, the full model was significant as compared to the null model (likelihood ratio test: $\chi^2 = 122.37$, $df = 23$, $P < 0.001$). More specifically, there was a significant effect of the three-way interaction among condition, species and number of partner's pulls in the previous 3-trial block ($\chi^2 = 16.49$, $df = 5$, $P = 0.006$).

However, when we tested for the effect of the number of partner's pulls in the previous 3-trial block separately for each combination of species and condition (Fig. 2), the only significant effect was for capuchin monkeys in the experimental condition, who pulled *less* if the partner had pulled more in the previous block of trials (estimate \pm SE = -1.10 ± 0.41 , $P = 0.023$; P value based on

likelihood ratio test, random slopes of number of pulls in previous trials included; all other $P > 0.12$).

When splitting the data by species to examine in detail the interaction between species and condition, orangutans and chimpanzees pulled more in the experimental than in the control condition ($\chi^2 = 31.46$, $df = 1$, $P < 0.001$; $\chi^2 = 4.36$, $df = 1$, $P = 0.037$, respectively; Fig. 3a). In contrast, spider monkeys pulled more in the control than in the experimental condition ($\chi^2 = 26.31$, $df = 1$, $P < 0.001$). When examining the interaction between species and number of pulls by the partner in the previous 3-trial block, however, orangutans and chimpanzees only showed a tendency to pull more in the experimental than in the control condition ($\chi^2 = 3.22$, $df = 1$, $P = 0.073$; $\chi^2 = 3.07$, $df = 1$, $P = 0.080$, respectively). In contrast, capuchin monkeys pulled significantly more in the control than in the experimental condition ($\chi^2 = 7.09$, $df = 1$, $P = 0.008$; Fig. 3b).

Effects of control variables

There was a significant decrease of the probability to pull over the course of sessions (-0.06 ± 0.02 , $z = -3.45$, $P = 0.001$), an increase in the probability to pull in later blocks of trials (0.13 ± 0.06 , $z = 2.28$, $P = 0.023$), but no effect of rank difference (-0.08 ± 0.13 , $z = -0.68$, $P = 0.496$). There was an effect of the random slopes based on the comparison of the model with all random slopes terms with the model not comprising any of them ($\chi^2 = 16.67$, $df = 3$, $P = 0.001$). However, there was no suggestion that the effect of the interaction between species and treatment varied between dyads ($\chi^2 < 0.01$, $df = 1$, $P = 0.999$). After the removal of this term we also found no difference between dyads with regard to how their pulling rate differed between control and experimental trials ($\chi^2 = 1.16$, $df = 1$, $P = 0.281$) but an effect of random variation between dyads with regard to how they responded to variation in the number of pulls in the previous block ($\chi^2 = 15.27$, $df = 1$, $P < 0.001$; Fig. 4). In particular, the orangutan dyad Bimbo–Dokana showed the strongest relation between the number of pulls by the partner in the previous 3-trial block and the subject's number of pulls in the current 3-trial block (largest positive estimate for the random slopes component; Figure S4 in Supplementary Material).

Discussion

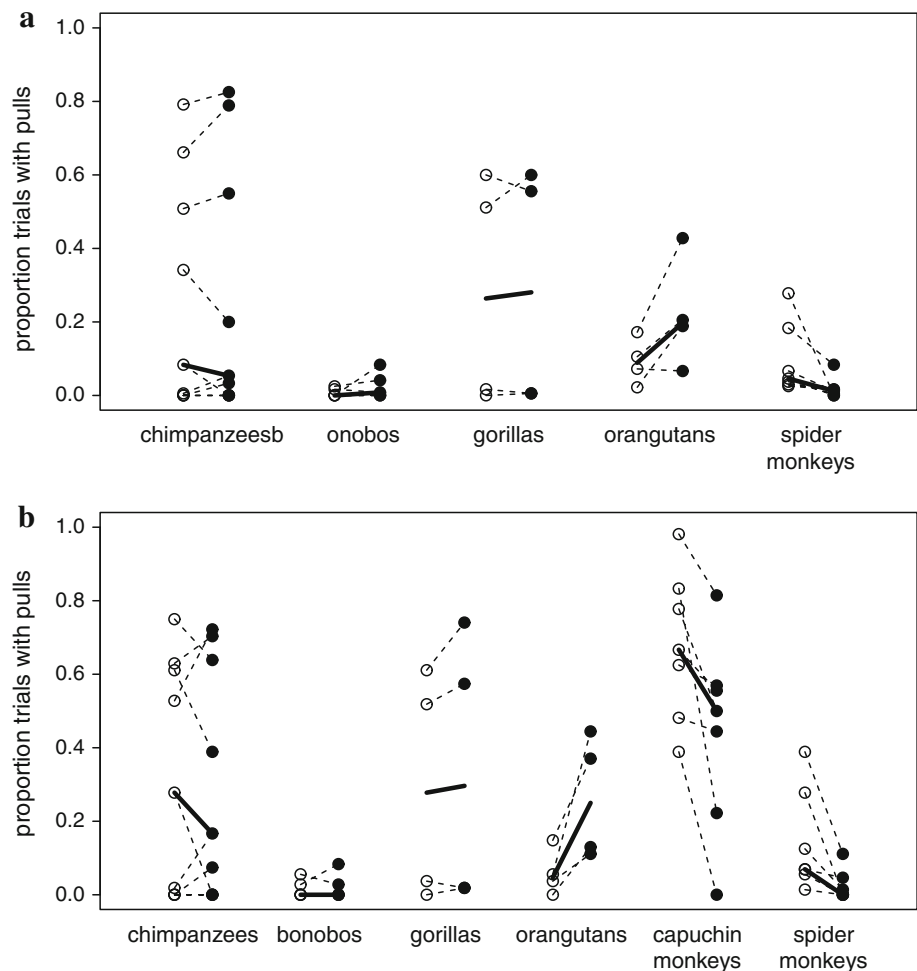
Chimpanzees and orangutans were the only species pulling significantly more in the experimental than in the control condition, i.e., when a partner could retrieve the food altruistically provided. However, we cannot conclude that

individuals were reciprocating food exchanges, because subjects' probability of pulling was not affected by the number of pulls by the partner in the previous 3-trial block, for any species. It might be argued that chimpanzees and orangutans, although they did not reciprocate food exchanges, were the only species in which subjects gave food to their partners with an altruistic motivation. This is of course possible, and would be in line with findings that have evidenced altruistic or prosocial behaviour in some primate species with a similar set-up (e.g., *Sapajus apella*: Hattori et al. 2005; Lakshminarayanan and Santos 2008; *Callithrix jacchus*: Burkart et al. 2007). So far, however, similar set-ups have not elicited altruistic motivation in great apes (e.g., Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008; Yamamoto and Tanaka 2010). Moreover, when we tested the same dyads with a similar set-up aimed to measure altruistic pulls across dyads, out of a reciprocity-context, both species showed no evidence of altruistic behaviour (Amici, Call, Visalberghi, unpublished data). One possible explanation is that some chimpanzees and orangutans provided food to their partners not out of an altruistic motivation, but rather in order to “start reciprocation” and get something back — an attempt that basically failed. This would imply that at least some individuals fully appreciate the potential of the set-up and, given the appropriate context, might start strategically providing food to the partners in order to initiate reciprocation. Although this behaviour could be described as altruistic (i.e., they incur in some costs to provide benefits to a partner), the motivation could not (e.g., Schino and Aureli 2010b).

Apart from chimpanzees and orangutans, species showed no evidence of pulling more when a partner could retrieve the food. Moreover, spider monkeys pulled even less when a partner could retrieve food than when the partner could not, and capuchin monkeys pulled even less when the partner had pulled in the previous 3-trial experimental block than when the partner had not pulled. Higher levels of inhibitory control (chimpanzees, bonobos, orangutans and spider monkeys), a higher degree of allomaternal care (capuchin monkeys) or phylogenetic relatedness (great apes) did not predict reciprocity in this study. One reason why only chimpanzees and orangutans provided food to their partners (without reciprocation) might be that the set-up used in this task is too cognitively demanding by, for example, requiring individuals to understand and represent the partner's role in the task for future exchanges. Therefore, only a few species and individuals might have fully mastered all the task intricacies (including the temporal dimension) needed to elicit calculated reciprocity in this set-up. Perhaps a larger sample size would have revealed other dyads also capable of solving the task by engaging in reciprocal exchanges.

The orangutan dyad Bimbo–Dokana showed the strongest relation between the number of pulls by the partner in the

Fig. 4 Proportion of trials in which each subject pulled the platform in the control (*white dot*) and in the experimental condition (*black dot*) in **a** all 10 sessions (capuchin monkeys are excluded) and **b** in the first 3 sessions for each individual (*dotted line*). For each species, a *continuous line* connects the species median in the control and in the experimental condition (see Table S2 in Supplementary Material for the individual values)



previous 3-trial block and the subject's number of pulls in current 3-trial block, suggesting that some level of reciprocity took place. These results are in agreement with previous studies, in which a token-exchange paradigm was used to test calculated reciprocity in great apes and the authors found no evidence for it, with the exception of the dyad Bimbo–Dokana (Dufour et al. 2009; Pelé et al. 2009). The fact that different experimental set-ups led to similar results provides stronger evidence to the fact that the dyad Bimbo–Dokana might be especially prone to reciprocate. The reason why this might be the case, however, is to date unclear. The dyadic mean social tolerance level, for example, was high (93.14 %), but not the highest. Furthermore, Dokana and Bimbo are not kin, in contrast to some kin dyads tested in this study, which failed to reciprocate. Moreover, Bimbo and Dokana have usually performed at average level when tested individually on a variety of cognitive tasks (e.g., Amici et al. 2008, 2010). Future studies focusing specifically on this issue might discover the extent and reason of Bimbo and Dokana's high tendency to reciprocate.

Dyadic social tolerance levels had no significant effect on the probability of pulling the platform. Moreover, pulling decreased over the course of sessions, suggesting that evidence for reciprocity or at least altruistic behaviour would have probably not been detected by simply administering more sessions. In this respect, the fact that capuchin monkeys were only administered 3 sessions probably did not affect our results in an important way. However, subjects' pulling increased in the later 3-trial blocks, suggesting that receiving food from the partner had an effect, if any, only in the short-term (i.e., during the few minutes of a session, across blocks of trials), but not in the longer term (i.e., across sessions administered on different days).

Overall, pulling the platform was rare, with individuals pulling the platform in only 18.6 % of the trials (Fig. 2). The rarity of the response variable created some problems when fitting the model, and therefore our conclusions need to be tentative. In addition, our set-up had limitations in terms of focusing on food exchanges between given partners, whereas other studies found reciprocity between

currencies other than food (e.g., Koyama et al. 2006) and when individuals had the opportunity to choose the partner (Melis et al. 2006, 2008; Schino and Aureli 2010a; Sabbatini et al. 2012). Our study focused on a short temporal frame for the exchanges because it is probably the most suitable context for investigating calculated reciprocity. However, evidence for reciprocity is more often found when analysing longer-term exchanges (e.g., Schino and Aureli 2008; Gomes et al. 2009; Jaeggi and Gurven 2013). Primate dyads with well-established relationships interact daily in a variety of contexts and might therefore reciprocate over a longer timescale, without keeping track of individual exchanges (de Waal 1997; Silk 2003; Melis et al. 2008; Gomes et al. 2009; Tan and Hare 2013). Still, it is interesting that our set-up was generally not used by the subjects to provide and obtain valuable food. Individuals knew how the apparatus worked, having successfully mastered the training condition, they easily obtained food for themselves in the motivational trials of the control condition, food was visible and the effort required to provide it to partners was low. However, individuals did not usually take the opportunity to provide food to their partners: a similar result to those found in other studies (e.g., Brosnan et al. 2009; Yamamoto and Tanaka 2009). In this respect, it seems that calculated reciprocity is not a common behaviour and that food exchanges are usually not reciprocated in the short-term within dyads, with few possible exceptions. It is conceivable that the majority of reciprocal exchanges probably rely on more basic emotionally based mechanisms (Schino and Aureli 2009).

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References

- Addressi E, Crescimbeni L, Visalberghi E (2008) Food and token quantity discrimination in capuchin monkeys (*Cebus apella*). *Anim Cogn* 11:275–282
- Addressi E, Paglieri F, Focaroli V (2011) The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition* 119:142–147
- Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. *Curr Biol* 18:1415–1419
- Amici F, Aureli F, Call J (2010) Monkeys and apes: are their cognitive skills really so different? *Am J Phys Anthropol* 143:188–197
- Amici F, Call J, Aureli F (2012) Aversion to violation of expectations of food distribution: the role of social tolerance and relative dominance in seven primate species. *Behaviour* 149:345–368
- Baayen RH (2008) Analyzing linguistic data. Cambridge University Press, Cambridge
- Bates D, Maechler M, Bolker B (2013) lme4: linear mixed-effects models using Eigen and R syntax. R package version 0.999999-2
- Beran MJ (2001) Summation and numerosness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). *J Comp Psychol* 115:181–191
- Brosnan SF, de Waal FBM (2002) A proximate perspective on reciprocal altruism. *Hum Nat* 13:129–152
- Brosnan SF, Silk JB, Henrich J, Mareno MC, Lambeth SP, Schapiro SJ (2009) Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Anim Cogn* 12:587–597
- Burkart JM, van Schaik CP (2010) Cognitive consequences of cooperative breeding in primates? *Anim Cogn* 13:1–19
- Burkart JM, Fehr E, Efferson C, van Schaik CP (2007) Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proc Natl Acad Sci USA* 104:19762–19766
- Burkart JM, Hrdy SB, van Schaik CP (2009) Cooperative breeding and human cognitive evolution. *Evol Anthropol* 18:175–186
- Call J (2000) Estimating and operating on discrete quantities in orangutans (*Pongo pygmaeus*). *J Comp Psychol* 114:136–147
- Cheney DL, Moscovice LR, Heesen M, Mundry R, Seyfarth RM (2010) Contingent cooperation between wild female baboons. *Proc Natl Acad Sci USA* 107:9562–9566
- Clutton-Brock TH (2009) Cooperation between non-kin in animal societies. *Nature* 462:51–57
- de Waal FBM (1997) The chimpanzee's service economy: food for grooming. *Evol Hum Behav* 18:375–386
- de Waal FBM, Luttrell LM (1988) Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethol Sociobiol* 9:101–118
- Dobson AJ (2002) An introduction to generalized linear models. Chapman & Hall/CRC, Boca Raton
- Dufour V, Pelé M, Neumann M, Thierry B, Call J (2009) Calculated reciprocity after all: computation behind token transfers in orangutans. *Biol Lett* 5:172–175
- Field A (2005) Discovering statistics using SPSS. Sage Publications, London
- Forstmeier W, Schielzeth H (2011) Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behav Ecol Sociobiol* 65:47–55
- Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks
- Freeman EW, Schulte BA, Brown JL (2010) Using behavioral observations and keeper questionnaires to assess social relationships among captive female African elephants. *Zoo Biol* 29:140–153
- Gomes CM, Mundry R, Boesch C (2009) Long-term reciprocation of grooming in wild West-African chimpanzees. *Proc R Soc B* 276:699–706
- Hattori Y, Kuroshima H, Fujita K (2005) Cooperative problem solving by tufted capuchin monkeys (*Cebus apella*): spontaneous division of labor, communication and reciprocal altruism. *J Comp Psychol* 119:335–342
- Hauser MD, Chen MK, Chen F, Chuang E (2003) Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proc R Soc B* 270:2363–2370

- Hemelrijk CK (1994) Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Anim Behav* 48:479–481
- Herrelko ES, Vick SJ, Buchanan-Smith HM (2012) Cognitive research in zoo-housed chimpanzees: influence of personality and impact on welfare. *Am J Primatol* 74:828–840
- Jaeggi AV, Gurven M (2013) Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proc R Soc B* 280:20131615
- Jensen K, Hare B, Call J, Tomasello M (2006) What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc R Soc B* 273:1013–1021
- Koyama NF, Caws C, Aureli F (2006) Interchange of grooming and agonistic support in chimpanzees. *Int J Primatol* 27:1293–1309
- Lakshminarayanan VR, Santos LR (2008) Capuchin monkeys are sensitive to others' welfare. *Curr Biol* 18:R999–R1000
- McCullagh P, Nelder JA (2008) Generalized linear models. Chapman and Hall, London
- Melis AP, Hare B, Tomasello M (2006) Chimpanzees recruit the best collaborators. *Science* 311:1297–1300
- Melis AP, Hare B, Tomasello M (2008) Do chimpanzees reciprocate received favours? *Anim Behav* 76:951–962
- Pelé M, Dufour V, Thierry B, Call J (2009) Token transfers among great apes: species differences, gestural requests and reciprocal exchange. *J Comp Psychol* 123:375–384
- Quinn GP, Keough MJ (2002) Experimental designs and data analysis for biologists. Cambridge University Press, Cambridge
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Sabbatini G, de Bortoli Vizioli A, Visalberghi E, Schino G (2012) Food transfers in capuchin monkeys: an experiment on partner choice. *Biol Lett* 8:757–759
- Savage-Rumbaugh ES, Rumbaugh D, Boysen S (1978) Linguistically mediated tool use and exchange by chimpanzees (*Pan troglodytes*). *Behav Brain Sci* 4:539–554
- Schielezth H, Forstmeier W (2009) Conclusions beyond support: overconfident estimates in mixed models. *Behav Ecol* 20:416–420
- Schino G, Aureli F (2008) Grooming reciprocation among female primates: a meta-analysis. *Biol Lett* 4:9–11
- Schino G, Aureli F (2009) Reciprocal altruism in primates: partner choice, cognition and emotions. *Adv Stud Behav* 39:45–69
- Schino G, Aureli F (2010a) Primate reciprocity and its cognitive requirements. *Evol Anthropol* 19:130–135
- Schino G, Aureli F (2010b) The relative roles of kinship and reciprocity in explaining primate altruism. *Ecol Lett* 13:45–50
- Schino G, Pellegrini B (2009) Grooming in mandrills and the time frame of reciprocal partner choice. *Am J Primatol* 71:884–888
- Silk JB (2003) Cooperation without counting: the puzzle of friendship. In: Hammerstein P (ed) Genetic and cultural evolution of cooperation. MIT Press, Cambridge, pp 37–54
- Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaró J, Shapiro SJ (2005) Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 27:1357–1359
- Silk JB, Brosnan SF, Henrich J, Lambeth SP, Shapiro SJ (2013) Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Anim Behav* 85:941–947
- Stevens JR (2010) Donor payoffs and other-regarding preferences in cotton-top tamarins (*Saguinus oedipus*). *Anim Cogn* 13:663–670
- Stevens JR, Hauser MD (2004) Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn Sci* 8:60–65
- Tan J, Hare B (2013) Bonobos share with strangers. *PLoS ONE* 8(1):e51922. doi:10.1371/journal.pone.0051922
- Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57
- Vonk J, Brosnan SF, Silk JB, Henrich J, Richardson AS, Lambeth SP, Schapiro SJ, Povinelli DJ (2008) Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Anim Behav* 75:1757–1770
- Yamamoto S, Tanaka M (2009) Do chimpanzees (*Pan troglodytes*) spontaneously take turns in a reciprocal cooperation task? *J Comp Psychol* 123:242–249
- Yamamoto S, Tanaka M (2010) The influence of kin relationship and reciprocal context on chimpanzees' other-regarding preferences. *Anim Behav* 79:595–602