

Benefiting friends or dominants: prosocial choices mainly depend on rank position in long-tailed macaques (*Macaca fascicularis*)

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Abstract Long-term observational studies in a number of animal species suggest that exchange patterns of social acts depend on long-term emotional bonds. Therefore, it is expected that the frequency of prosocial behavior will depend on the strength of such a bond. In this study we tested whether variation in relationship quality among unrelated individuals, i.e., “friends” and “nonfriends,” is predictive of the prosocial behavior of long-tailed macaques in two experiments. First, we related relationship quality to prosociality in a dyadic prosociality test, and second, we gave subjects the choice to give to either a friend or a nonfriend in a triadic choice test. We show that prosocial behavior of long-tailed macaques in the dyadic test is not related to relationship quality. When given the choice to give to either a friend or a nonfriend in the triadic test, there is a minor indication that long-tailed macaques show a preference to give to their friends, yet this indication is neither significant nor consistent. In contrast, subordinate long-tailed macaques make a more “competitive” choice and avoid giving to the individual closest in rank. Therefore, in the short-term situation of experimental tests, prosocial behavior of long-tailed macaques seems unaffected by the relationship quality of the dyad/triad tested, and the relative dominance position of these dyads/triads seems to have a much stronger effect on their prosocial behavior.

Keywords Prosociality · Friendship · Relationship quality · Long-tailed macaques · Rank relations

Introduction

Research on reciprocal exchange patterns has changed its focus from mainly ultimate explanations to the proximate mechanism underlying exchange patterns (Brosnan and de Waal 2002). In particular, the timeframe of reciprocation has been a major focus of research (Schino et al. 2007). Many of these studies show that reciprocity is not contingent on the short term and, therefore, does not rely on a strict tit-for-tat rule (Axelrod and Hamilton 1981). Instead, these exchanges seem tolerant against short-term imbalances (exchange of grooming: capuchin monkeys, *Cebus apella*: Schino et al. 2009; chimpanzees, *Pan troglodytes*: Gomes et al. 2009; rhesus and long-tailed macaques, *Macaca mulatta* and *M. fascicularis*: Massen 2010; interchange of grooming for support: Japanese macaques, *M. fuscata*: Schino et al. 2007; ring-tailed coatis, *Nasua nasua*: Romero and Aureli 2008; rhesus and long-tailed macaques: Massen 2010; interchange of grooming for sexual access: rhesus macaques: Massen 2010). The consistency of exchange patterns, irrespective of short-term imbalances, implies that services are regularly not reciprocated immediately or within a short timeframe, and seemingly animals are not deterred by this lack of reciprocity. Such other-regarding preferences without reciprocation have been referred to as prosociality (Burkart et al. 2007).

Genuine altruism, or a costly act to benefit another, has been considered uniquely human (Fehr and Fishbacher 2003). However, prosocial behavior, which benefits the other but need not be costly to the actor, has also been

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reported for several primate and corvid species (ravens, *Corvus corax*: Heinrich 1988; jackdaws, *Corvus monedula*: de Kort et al. 2006; chimpanzees: Warneken et al. 2007; common marmosets, *Callithrix jacchus*: Burkart et al. 2007; capuchin monkeys: de Waal et al. 2008; Lakshminarayanan and Santos 2009; rooks, *Corvus frugilegus*: Scheid et al. 2008; bonobos, *Pan paniscus*: Hare and Kwetuenda 2010; long-tailed macaques: Massen et al. 2010a). Clearly, prosocial behavior is not limited to humans.

Because exchange patterns of services in several animal species seem robust against short-term imbalances yet are reciprocal in the long run, these exchange patterns can be considered a consequence of long-term emotional bonds built on mutual behavior benefiting the other (Massen et al. 2010b). Consequently, the observed exchange patterns predict that individuals with close bonds will be especially likely to act prosocially to one another or, at least, act more frequently prosocially to one another than individuals with less close bonds. Indeed, several studies report an effect of relationship characteristics on prosocial behavior; for example, only dominant long-tailed macaques seem to be prosocial (Massen et al. 2010a), and capuchin monkeys are more prosocial towards subordinates than towards dominants (Takimoto et al. 2010). Moreover, it has been shown that related individuals, which generally have a better relationship quality (i.e., affiliative relationship characteristics) than non-kin individuals, are more prosocial towards each other than non-kin individuals (common marmosets: Burkart et al. 2007; capuchin monkeys: de Waal et al. 2008; long-tailed macaques: Massen et al. 2010a; but see also Yamamoto and Tanaka 2010). However, to date there are almost no studies reporting how within-species variation in relationship quality affects the frequency of prosocial behavior towards non-kin conspecifics. One study on capuchin monkeys (de Waal et al. 2008) reports that these monkeys are only prosocial towards familiar partners and not towards strangers. A study on jackdaws (von Bayern et al. 2007) reports on the reverse connection, i.e., that prosocial behavior leads to pair bonding, yet this pattern does not show how an existing within-species variation in relationship quality relates to prosocial behavior. From a human perspective it may seem obvious that friends are more prosocial towards each other than nonfriends. However, in animals this hypothesis remains to be tested.

In this study, we tested whether variation in relationship quality (measured by affiliative behavior, i.e., contact sitting and grooming) is predictive of prosocial behavior in long-tailed macaques in two experiments. First, we used data on prosociality in long-tailed macaques from a previous experiment (Massen et al. 2010a), in which we tested whether long-tailed macaques are prosocial, and if their prosocial tendency depends on kin relations and dominance

relations. This experiment had a dyadic setup, and therefore, in the remainder of this paper we will refer to it as the dyadic prosociality experiment. In this previous study, we showed that long-tailed macaques can be prosocial, are generally prosocial towards their kin, and are more prosocial towards kin than towards non-kin. Moreover, we showed that the prosocial behavior of long-tailed macaques depends on their dominance rank and that dominant individuals are prosocial while subordinate individuals are asocial (Massen et al. 2010a). In the current study, we analyzed the prosociality data of that experiment to test whether relationship quality was related to it, while controlling for the above-mentioned rank effects. In addition, we designed a second experiment: the triadic choice experiment. In this experiment we tested in a triadic setup whether long-tailed macaques preferentially give to their friends when given the choice between a friend and a nonfriend. However, the prosocial behavior of animals depends not only on the identity of the receiving partner but also on the identity of the subject; for example, Massen et al. (2010a) report in a study on long-tailed macaques that only dominant animals provide their partner, while subordinates withhold, access to food. Therefore, in the triadic choice experiment we also analyzed the data of dominant and subordinate individuals separately. Finally, it can be argued that prosocial choices or the choice to give to a friend in our experiments are merely a byproduct of proximity (Jaeggi et al. 2010), since social animals may prefer to sit in close proximity to their conspecifics and therefore choose to pull in a slide on the corresponding side. Therefore, also the effect of proximity of the subject to its partner(s) in the test setting on the subject's choices was determined in both experiments.

Methods

Ethics statement

We conducted the experiments according to the directives of the Dutch Experiments on Animals Act. The experiments were approved by the Ethics Committee of Utrecht University (DEC 2007.I.08.103) and thus comply with Dutch Law. To avoid any stress, the animals were never forced to participate. Consequently, the animals that were tested participated voluntarily. The animals were never food or water deprived. We conducted the experiments between 21 April 2009 and 26 June 2009.

Subjects and housing

The tested animals were members of a social group housed at the Ethologie-station of Utrecht University,

The Netherlands, which consisted of 36 individuals with males and females from all life stages. The group was formed after splitting a larger group along matriline in 1994 and has since been stable. Most animals were born in this group. The group was housed in an indoor enclosure (surface 117.5 m², height 2 m) attached to an outdoor compound (surface 228.5 m², height 3.5 m), with plenty of climbing and sitting facilities. Water and commercially available monkey chow were available ad libitum. Alternately fruit, vegetables or bread were provided to the group 0.5 h after the day's testing was completed. This feeding schedule was followed regardless of whether the animals participated in a test that day.

We analyzed the dominance hierarchy in the group and the friendship status among group members prior to the experiments. We determined the dominance hierarchy by analyzing unidirectional submissive behaviors (“bare teeth” and “make room” without prior aggressive behavior) that were observed ad libitum. We arranged the results in a matrix with actors in rows and recipients in columns. We determined the dominance order most consistent with a linear hierarchy by using MatMan 1.1 (linearity index $h' = 0.7204$, $P < 0.001$), indicating a significantly linear dominance hierarchy (de Vries 1995, 1998). We ranked animals 1 (highest-ranking) to 36 (lowest-ranking). The dominance hierarchy determined in this way remained stable over the period of testing.

To measure relationship quality, we conducted time-sample scan observations (Martin and Bateson 1993) of all independent group members (i.e., excluding infants) during the 10 months prior to testing, to assess who was sitting with whom (contact sitting) and who was grooming whom. We conducted 2–4 scans a day throughout the day, always with at least 1 h in between each scan to ensure that the scans were independent of each other. If the monkeys were grooming each other, obviously they were also sitting in contact. However, to create two measures that are independent of each other, we scored this as grooming only. In total we collected 279 time-sample scan observations. We ordered social partners from 1 (most contact sitting) to 35 (least contact sitting). If a subject sat with two group-mates the same proportion of time, we used an average rank number; e.g., if they were 4 and 5, they were both numbered 4.5. If there were more individuals with whom the subject sat the least (i.e., never) in contact, we numbered them all 35. We did the same with the grooming data. For each partner, we added both numbers and then divided it by two, which led to a “relationship quality” measure ranging between 1 (i.e., best friend) and 35 (i.e., the least affiliative bonds).

Subjects and their test partners were all adult or subadult monkeys (ranging in age between 3 and 21 years) that were trained to and could easily pull in a tray of the test

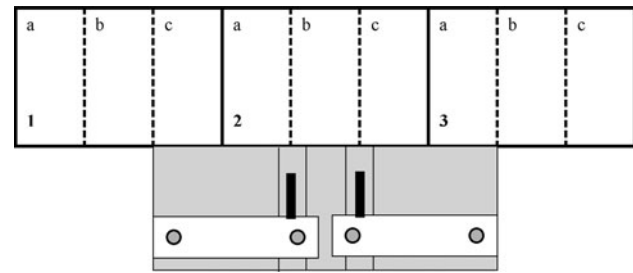


Fig. 1 Schematic representation of the test setting. *Top* the three different compartments (1–3) and their spatial subdivision (a–c) are represented. *Below* (in grey) is the test apparatus, with two different trays (white) that are connected to rails (thin black lines) and can be pulled in by the monkey in the middle compartment by pulling the bars (thick black lines). The grey circles represent slices of banana that were simultaneously dropped onto both trays in the test

apparatus (Fig. 1). In the prosociality experiment, we tested ten male and ten female long-tailed macaques (Table 1). In the choice experiment, we tested the same animals with the exception of one subject, the alpha male, which was excluded because of a lack of male friends (Table 2).

For the dyadic prosociality experiment, we chose pairs of a subject and their test partner according to their relationship quality and the subject's dominance rank, creating a sample with as much variation in both relationship quality and dominance rank as possible [relationship quality ranged from 1 to 35, with mean of 12.2 and standard deviation of 9.5; the subject's dominance rank ranged from 1 (i.e., the alpha male) to 27, with mean of 14 and standard deviation of 8] (see Table 1). To avoid reciprocation, dyads were always novel (i.e., every dyad was a unique combination of individuals). Furthermore, to avoid bargaining for sexual services (Gumert 2007), partners were always of the same sex. Consequently, all subjects were tested with a non-kin same-sex member of their group. In addition, we also tested ten (nine females and one male) out of the twenty subjects with a same-sex kin partner (Table 1). We counterbalanced whether these ten individuals were first tested with a kin or a non-kin partner.

In the triadic choice experiment, the two partners of the subject were never related to the subject, yet we chose them according to their relationship quality with the subject: one dyad with a relationship quality number as low as possible (friends ranged in relationship quality from 2.5 to 19.5, with mean of 7.3 and standard deviation of 4.5), and one partner with a relationship quality number as high as possible (nonfriends ranged in relationship quality from 12.75 to 32.75, with mean of 22.4 and standard deviation of 4.1). To avoid reciprocity, combinations of subject and partner were always novel and were not tested together in the dyadic prosociality experiment (Table 2).

Table 1 Subjects and their partner in the dyadic prosociality experiment: name, sex, and dominance rank of subjects and their same-sex non-kin and kin test partners, and the relationship quality (RQ) of the subjects with their test partners

| Subject | Sex | Rank | Non-kin partner | Rank | RQ | Kin partner | Rank | RQ |
|--------------|-----|------|-----------------|------|-------|-------------|------|-------|
| Regilio | ♂ | 1 | Tabasco | 12 | 35 | | | |
| Tonko | ♂ | 14 | Burkina-faso | 10 | 14.75 | | | |
| Tabasco | ♂ | 12 | Tonko | 14 | 6.5 | | | |
| Burkina-faso | ♂ | 10 | Santiago | 22 | 23 | | | |
| Kufo | ♂ | 27 | Inlimbo | 25 | 2.75 | | | |
| Ontarajo | ♂ | 23 | Kufo | 27 | 4.75 | | | |
| Santiago | ♂ | 22 | Ontarajo | 23 | 18.75 | | | |
| Bonobo | ♂ | 26 | Just-so | 8 | 21.75 | | | |
| Just-so | ♂ | 8 | Regilio | 1 | 32 | | | |
| Inlimbo | ♂ | 25 | Ontarajo | 23 | 4.5 | Bonobo | 26 | 5.25 |
| Latifa | ♀ | 19 | Kraa | 7 | 5.75 | Tres-bella | 20 | 1 |
| Wodka | ♀ | 2 | Latifa | 19 | 25.5 | Alfa | 5 | 26.25 |
| Alfa | ♀ | 5 | Tres-bella | 20 | 4.25 | Tamanduwa | 3 | 13 |
| Tamanduwa | ♀ | 3 | Cordoba | 16 | 4 | Kraa | 7 | 3.5 |
| Tres-bella | ♀ | 20 | Annika | 6 | 5.25 | Freya | 15 | 4.75 |
| Kraa | ♀ | 7 | Rastafa | 21 | 8 | Salsaa | 9 | 10.5 |
| Rastafa | ♀ | 21 | Wodka | 2 | 10.75 | Tres-bella | 20 | 5.75 |
| Annika | ♀ | 6 | Freya | 15 | 13.75 | Alfa | 5 | 13.75 |
| Freya | ♀ | 15 | Cordoba | 16 | 12.25 | Rastafa | 21 | 3.5 |
| Cordoba | ♀ | 16 | Latifa | 19 | 16 | | | |

Table 2 Subjects and partners in the triadic choice experiment: name, sex, and dominance rank of subjects and their same-sex friend and nonfriend partners, and the relationship quality (RQ) of the subject with the test partners

| Subject | Sex | Rank | Friend partner | Rank | RQ | Nonfriend partner | Rank | RQ |
|--------------|-----|------|----------------|------|------|-------------------|------|-------|
| Latifa | ♀ | 19 | Alfa | 5 | 6 | Tamanduwa | 3 | 24.5 |
| Wodka | ♀ | 2 | Tres-bella | 20 | 5.75 | Freya | 15 | 23.5 |
| Alfa | ♀ | 5 | Freya | 15 | 4.25 | Rastafa | 21 | 20.75 |
| Tamanduwa | ♀ | 3 | Tres-bella | 20 | 3 | Rastafa | 21 | 26 |
| Tres-bella | ♀ | 20 | Cordoba | 16 | 8 | Salsaa | 9 | 24.5 |
| Kraa | ♀ | 7 | Tres-bella | 20 | 10 | Cordoba | 16 | 23.5 |
| Rastafa | ♀ | 21 | Annika | 6 | 7.5 | Cordoba | 16 | 25.75 |
| Annika | ♀ | 6 | Cordoba | 16 | 6.25 | Latifa | 19 | 16.25 |
| Freya | ♀ | 15 | Kraa | 7 | 5.25 | Tamanduwa | 3 | 24.5 |
| Cordoba | ♀ | 16 | Salsaa | 9 | 5.25 | Alfa | 5 | 25 |
| Tonko | ♂ | 14 | Santiago | 22 | 7.75 | Just-so | 8 | 20 |
| Tabasco | ♂ | 12 | Ontarajo | 23 | 2.5 | Bonobo | 26 | 21 |
| Burkina-faso | ♂ | 10 | Just-so | 8 | 19.5 | Bonobo | 26 | 32.75 |
| Kufo | ♂ | 27 | Tonko | 14 | 3.75 | Tabasco | 12 | 22 |
| Ontarajo | ♂ | 23 | Bonobo | 26 | 6.75 | Tonko | 14 | 20.25 |
| Santiago | ♂ | 22 | Inlimbo | 25 | 18 | Kufo | 27 | 23 |
| Bonobo | ♂ | 26 | Santiago | 22 | 8 | Kufo | 27 | 19.5 |
| Just-so | ♂ | 8 | Tabasco | 12 | 8 | Kufo | 27 | 12.75 |
| Inlimbo | ♂ | 25 | Tonko | 14 | 3.25 | Just-so | 8 | 21 |

Test setting

During training and testing, the complete group entered from their home cage to the connected test cage of 32 m³ (4 m × 4 m × 2 m). From this test cage the subject and its partner(s) entered the test compartment (110 cm × 55 cm × 80 cm) (Fig. 1). The test compartment was divided into three parts by two transparent Lexan screens, to allow visual contact between the monkeys while keeping them physically separated. The subject was always in the middle compartment (compartment 2 in Fig. 1), and the partner(s) were sitting in the adjacent compartment(s) (compartment 1 and 3 in Fig. 1). The test apparatus that was placed in front of the middle test compartment consisted of two sliding trays, one on the left and one on the right. All subjects had been trained extensively to pull in a baited tray to obtain the reward and were familiar with the test apparatus and its properties.

At the beginning of each trial, four equally sized slices of banana simultaneously dropped onto the trays, two on each. If the monkey pulled in a tray, the other tray was blocked. After the monkey pulled in the tray, it could take the reward that was in the center while the reward at the other side of the tray was out of reach for the subject, though could be taken by its partner on that side, if present. After the monkey(s) had taken their reward, the remaining banana slices were removed and a new trial was started immediately. During the tests, we always allowed dependent offspring into the test compartment with their mothers. We tested neither subject nor test partner more than once on 1 day.

We recorded all test sessions using four closed-circuit television (CCTV) system black and white (B/W) cameras covering both the up-front and from-above views of the test compartments. I.J.A.F.L. coded the data. Coding could not be blind, since subjects, their behavior, and conditions were visible.

Conditions

The dyadic prosociality experiment

We tested subjects in an experimental and a control condition. Subjects were always in the middle compartment of the test setting. We first tested the subjects in a control condition, in which we determined the left/right preference of each subject without a partner. In the test condition we tested all individuals in the same way, but now with a same-sex partner sitting on the opposite side of their preferred side, as determined in the control condition. We intentionally placed the partner on the opposite side to the preferred side measured in the control condition, and consequently subjects had to deviate from their initial side preference to be prosocial. Both the control and the test

condition consisted of twenty trials that we, in order to retain the monkeys' motivation, divided over two consecutive days, with ten trials on each day. We consider the trials independent of each other, since the monkeys did not consistently pull on one side. Moreover, the subjects did not differ significantly in their side preference between the first ten trials and the second ten trials of the test condition (Wilcoxon signed-rank test $T^+ = 110$, $N = 20$, $P_{\text{exact}} = 0.559$), nor in their side preference between the first ten trials and the second ten trials of the control condition (Wilcoxon signed-rank test $T^+ = 95$, $N = 20$, $P_{\text{exact}} = 0.707$). Consequently, an initial side preference on a day did not influence the remaining trials of that day. Finally, all animals completed all trials and were generally very motivated, since they almost always took the food (18–20 times).

The triadic choice experiment

In the triadic choice experiment, we tested subjects in one condition only. Subjects were in the middle compartment, with two partners, one in each adjacent compartment (i.e., one to the left and one to the right). We intentionally placed the partner with whom the subject had the best relationship quality (low relationship quality number) on the opposite side to the preferred side measured in the control condition of the dyadic prosociality experiment, and consequently subjects had to deviate from their initial side preference to give to their friends. In the experiment, we gave the subjects the same choice 20 times, divided over two consecutive days with ten trials on each day in order to retain the monkeys' motivation. We consider the trials independent of each other, since the monkeys did not consistently pull on one side. Moreover, the subjects did not differ significantly in their side preference between the first ten trials and the second ten trials (Wilcoxon signed-rank test $T^+ = 51$, $n = 19$, $P = 0.719$). Consequently, an initial side preference on a day did not influence the remaining trials of that day. Finally, all animals completed all trials and were generally very motivated, since they always took the food.

Measures and data analysis

The dyadic prosociality experiment

To measure prosociality, we compared the proportion of times the subject chose the tray at the partner side in the test condition with the proportion of times the subject chose the tray at the nonpreferred side in the control condition. We then calculated a prosocial tendency (Pt) by subtracting the proportion of times the subject chose the tray at the nonpreferred side in the control condition from

the proportion of times the subject chose the tray at the partner side in the test condition. A positive prosocial tendency thus shows prosocial behavior, whereas a negative prosocial tendency shows “asocial” behavior, since the tested individual actually withholds a reward from its partner. However, the maximum theoretical value of P_t that an individual can attain depends on its individual degree of side bias in the control condition, and consequently comparisons between individuals are impossible. Therefore, we calculated a corrected prosocial tendency (P_t'), in which we controlled for the strength of each individual's side bias in the control condition. We calculated the corrected prosocial tendency (P_t') differently for animals that increased and for animals that decreased their original side bias in the test, since if we want to claim that animals are asocial, we also need to correct this asocial tendency for the maximum theoretical asocial value, which is different from, i.e., the opposite of, the maximum theoretical prosocial value:

If $P_t > 0$,

$P_t' = P_t / (\text{the proportion of times the subject chose the tray at the preferred side in the control condition})$.

If $P_t < 0$,

$P_t' = P_t / (\text{the proportion of times the subject chose the tray at the nonpreferred side in the control condition})$.

Since relationship quality is a fixed measure, we regressed the corrected prosocial tendency of the subject on the relationship quality with its partner. However, previous analysis showed a very strong effect of the subject's rank on its prosocial tendency (Massen et al. 2010a). Therefore, to analyze the effect of relationship quality, we used a multiple regression in which we controlled for the rank of the subject. Residuals of each of these linear regression models did not differ significantly from a normal distribution.

To test for a possible effect of the proximity of the subject to its partner, we measured the proportion of time the subject spend in either area a, b or c of its compartment (Fig. 1). It should, however, be noted that the subjects were able to pull in both trays from any place within the compartment.

Finally, we measured all affiliative (i.e., lip smacking and eye-lifting) and aggressive (i.e., open mouth threats, “pointing,” and serial grunts) behavior (Angst 1974) of the subjects towards their partner, to measure whether this was predictive of their prosocial tendency.

To assess the effect of proximity, affiliation, and aggression of the subject on its prosocial tendency, we used Spearman's correlation coefficient (ρ).

The triadic choice experiment

To measure a preference to give to a particular individual (e.g., friend or nonfriend), we compared the proportion of choices for the corresponding tray with the subject's initial

side preference, which we established in the control condition of the dyadic prosociality experiment. Since these data were not normally distributed, we used Wilcoxon signed-rank tests for these analyses. To control for the relative dominance position of the subjects, and to test for a possible interaction effect of this relative dominance position with the main effect, we used repeated-measures analysis of variance (ANOVA). Since our data consisted of proportions, we used an arcsin $\sqrt{}$ transformation to normalize our data and to allow for such analyses.

To test for possible effects of the proximity of the subject to its partners, we measured the proportion of time the subject spend in either area a, b or c of its compartment (Fig. 1).

Finally, we measured all affiliative (i.e., lip smacking and eye-lifting) and aggressive (i.e., open mouth threats, pointing, and serial grunts) behavior (Angst 1974) of the subjects towards their partners to establish whether this was predictive of their choice.

To assess the effect of proximity, affiliation, and aggression of the subject on its prosocial tendency, we used Spearman's correlation coefficient (ρ).

Our sample size is rather small. Therefore, whenever we use Wilcoxon signed-rank tests, we provide the T^+ value instead of the Z value. Moreover, reported P values of Wilcoxon signed-rank tests are exact P values (Mundry and Fischer 1998). All reported P values are two tailed. We consider α of 0.05–0.10 as a trend and $\alpha \leq 0.05$ as a significant effect.

Results

The dyadic prosociality experiment: effect of relationship quality

We first tested whether the corrected prosocial tendency of an animal was due to the quality of its relationship with its partner. However, after controlling for the subject's dominance rank, we did not find a significant effect of relationship quality on the subject's corrected prosocial tendency towards their non-kin partners ($t = -0.674$, $\beta = -0.007$, $n = 20$, $P = 0.510$), and also no significant effect of relationship quality on the subject's corrected prosocial tendency towards their kin partners ($t = 1.601$, $\beta = 0.026$, $n = 10$, $P = 0.153$).

Alternatively, it can be argued that subjects do not make a deliberate choice, but pull most often the tray on the side they are sitting (Jaeggi et al. 2010). Therefore, we tested whether the corrected prosocial tendency of an animal was due to its proximity to its partner. We first correlated the corrected prosocial tendency with the proportion of time the subjects spend in the area of their compartment closest

to their partner. However, we did not find a relation between the subject's proximity to their partner and their corrected prosocial tendency (non-kin: Spearman's $\rho = 0.363$, $n = 20$, $P = 0.115$; kin: Spearman's $\rho = 0.101$, $n = 10$, $P = 0.782$). Moreover, we tested whether the time the subjects spend in the area of their compartment furthest away from their partner influenced their prosocial behavior; again we did not find a relation between the subject's distance to its partner and their corrected prosocial tendency (non-kin: Spearman's $\rho = 0.175$, $n = 20$, $P = 0.459$; kin: Spearman's $\rho = 0.049$, $n = 10$, $P = 0.893$).

Lastly, subjects and their partner never showed any aggressive behavior, and only four cases of affiliative behavior were scored in the dyadic prosociality test. Consequently, we performed no analyses on these behaviors.

The triadic choice experiment

To test whether long-tailed macaques preferentially choose to give to their friends, we compared the proportions of choices to give to the friend with the subject's initial side preference, established in the control condition of the dyadic prosociality experiment. The subject's preference for the tray on the side of its friend indeed tended to differ from the initial side (Wilcoxon signed-rank test $T^+ = 137.5$, $n = 19$, $P = 0.089$) (Fig. 2). This trend suggests that long-tailed macaques may prefer giving to their friends when given the choice between a friend and a nonfriend.

Since it has been shown that dominants and subordinates differ in their prosocial tendencies (Massen et al. 2010a), we investigated whether the subject's relative dominance position affected its choice in this experiment. Therefore, we split the data in subjects that ranked below both their

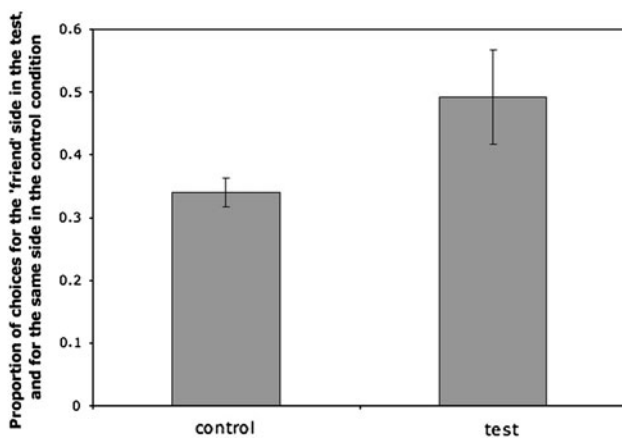


Fig. 2 Mean \pm standard error of the mean (SEM) proportion of choices of subjects ($n = 19$) to give to their friends in the test, and mean \pm SEM proportion of choices of the subjects for the tray on the same side in the control condition

partners ($n = 7$) and subjects that ranked above both their partners ($n = 8$), while omitting the data for those subjects that ranked between their partners ($n = 4$). Thereafter, we tested the effect of these relative rank positions on the choices these individuals made between friend and nonfriend. A repeated-measures ANOVA showed, however, only a slight and nonsignificant interaction of the subject's relative dominance position on the choice between friend and nonfriend ($F = 3.454$, $n = 15$, $P = 0.086$). Moreover, this analysis also showed no main effect of choices for a friend ($F = 2.107$, $n = 15$, $P = 0.170$), suggesting that, in contrast to the previous analysis, individuals do not preferentially choose their friends.

Instead of benefiting their friends, subjects may prefer to benefit the most dominant of their partners, since prosocial behavior towards dominants may appease them or may result in receiving rank-related benefits from these dominants in the future (Seyfarth 1977; Noë et al. 1991). Therefore, we tested the subject's preference to give to the most dominant of their partners. We found that the preference of the subject to give to the most dominant of their partners did not differ significantly from their initial side preference (Wilcoxon signed-rank test $T^+ = 100.5$, $n = 19$, $P = 0.837$). Again we also tested the effect of the subject's relative dominance position on this choice, i.e., subjects that ranked below both their partners ($n = 7$) and subjects that ranked above both their partners ($n = 8$), while omitting the data for those subjects that ranked between their partners ($n = 4$). A repeated-measures ANOVA of the subjects' choices for the highest ranking partner compared with the choices for the corresponding side in the control condition showed a main effect ($F = 11.027$, $n = 15$, $P = 0.006$), and showed a strong interaction of the subjects choice with its own dominance position (ranking either below or above both partners) ($F = 5.426$, $n = 15$, $P = 0.037$) (Fig. 3). Post hoc analyses showed that only the subjects that rank below both their partners have a significant preference to give to the highest ranking of both partners (Wilcoxon signed-rank test $T^+ = 28$, $n = 7$, $P = 0.016$), and that those subjects that outrank both their partners do not show such a preference (Wilcoxon signed-rank test $T^+ = 23$, $n = 8$, $P = 0.539$) (Fig. 3).

Alternatively, subjects may not make a deliberate choice, but pull most often the tray on the side they are sitting (Jaeggi et al. 2010). Therefore, we correlated the proportion of choices to give to each partner with the proportion of time they spend closest to that partner. However, we did not find a significant correlation between the proportion of choices for either side and the proportion of time spent on the corresponding side; i.e., when they preferentially sit on the right side of their compartment, they do not preferentially pull the right tray, and vice versa (Spearman's $\rho = 0.040$, $n = 19$, $P = 0.872$).

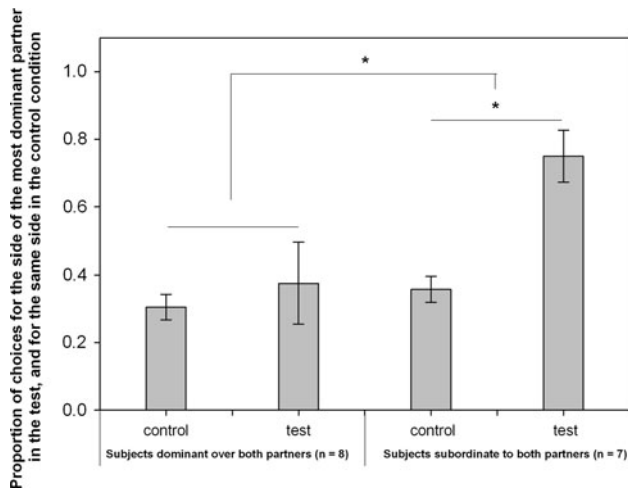


Fig. 3 Mean \pm SEM proportion of choices of subjects to give to the most dominant partner in the test, and mean \pm SEM proportion of choices for the tray on the same side in the control condition, for subjects that outrank both their partners (*left* $n = 8$) and subjects that are subordinate to both their partners (*right* $n = 7$). * $P < 0.05$

Lastly, subjects and their partners never showed any aggressive behavior and only three cases of affiliative behavior were scored in the triadic choice test. Consequently, we performed no analyses on these behaviors.

Discussion

From long-term observational studies it was expected that some animals, like humans, are more prosocial towards their friends than towards their nonfriends. In this study we report on two experiments that test this hypothesis. While in the dyadic prosociality experiment we did not find an effect of relationship quality on the prosocial tendency of long-tailed macaques, in the triadic choice experiment we found that subjects differentiate between partners based on relative dominance position.

Earlier work suggested an important role for dominance rank in prosocial behavior of long-tailed macaques (Massen et al. 2010a). Whereas dominants benefit others, subordinates actually withhold their partner access to food. This effect may have obscured or overruled the effect of relationship quality in the dyadic prosociality experiment. However, we chose the subjects and their partner to represent a wide array of both relationship qualities and dominance rank positions. Moreover, when we tested for the effect of relationship quality on prosociality, we controlled for the effect of dominance rank. Therefore, the lack of an effect of relationship quality on prosociality probably represents an existing pattern of long-tailed macaque behavior in the experimental situation.

In the triadic choice experiment, we found in one test an indication that subjects tend to prefer giving to their friends, yet this effect was absent in a second analysis controlling for relative dominance position. These results can be interpreted in two ways. First, an effect of friendship may be absent, similar to the results in the dyadic prosociality experiment. Consequently, relationship quality does not determine long-tailed macaque behavior in the short-term setting of an experiment. Alternatively, the effect may be weak and can only be assessed when a large number of individuals is tested. Still, this means that, in a short-term setting, friendship has only a minor effect on prosociality in long-tailed macaques.

In contrast, we found that the subject's relative dominance position did affect its behavior towards its partners: individuals that are lower in rank than both their partners have a significant preference to give to their highest ranking partner, while subjects that outrank both their partners do not show such a preference. These results are in line with previous research on primates that report that subordinates provide services preferably to dominants (Seyfarth 1977; Noë et al. 1991). Presumably this prosocial attitude towards high-ranking individuals is to gain future tolerance or support. However, subordinate individuals are generally not likely to behave prosocially to their partner (Massen et al. 2010a). Therefore, an alternative explanation of their preference to give to the more dominant of two partners is that this preference reflects a competitive attitude; i.e., if subordinates give to someone, they avoid giving to animals that within the normal group setting would be their direct competitors (i.e., animals close in rank to themselves). In contrast, dominants will not need such a competitive attitude, because they are already dominant. Since their position does not depend on their choices in the experiment, they may not differentiate based on dominance position between the two possible partners. Thirdly, in the triadic choice experiment subjects can exert partner choice. Subordinates may not be willing to give in a dyadic setting, where they can choose to withhold food, but may choose to provide the most dominant partner when they have to provide, but also have a choice between two partners. Unfortunately, our experimental setup did not allow us to differentiate between these three hypotheses.

Finally, the preference of individuals that are lower in rank than both their partners to give to the most dominant of the two partners also suggests that these subordinate long-tailed macaques are able to assess rank differences between others (i.e., third-party relations), and consequently this result confirms earlier work on long-tailed macaques (Dasser 1988) and other primate species (vervet monkeys, *Cercopithecus aethiops*: Cheney and Seyfarth 1980; hamadryas baboons, *Papio hamadryas*: Bachmann and Kummer 1980; chacma baboons, *P. cynocephalus*:

Cheney et al. 1995; bonnet macaques, *M. radiata*: Silk 1999).

Alternatively, it can be argued that choices to give or to give to a particular partner are not deliberate, but merely a consequence of the typical sitting location of an animal (Jaeggi et al. 2010). However, the subject long-tailed macaques in our tests were able to pull both trays from any place within their compartment. Moreover, their proximity or distance to their partner in the dyadic prosociality and in the triadic choice experiment is not predictive of their choice to give or of their choice to give to a particular partner in the two experiments. Therefore, we conclude that the choices these macaques made were not a consequence of their spatial proximity to their partners. Furthermore, their affiliative behavior and their aggressive behavior were also not predictive of the prosocial tendency of the subjects. Therefore, when they deviate from the control situation, they seem to express a preference to provide for this particular partner.

The results from our two experiments, showing no or only weak effects of “friendship” on prosocial behavior, contrast with long-term behavioral studies where friends benefit each other. Long-tailed macaques can act both prosocially and asocially (Massen et al. 2010a), therefore these experiments can demonstrate both behavioral tendencies. However, these experimental settings differ in some crucial features from group settings. First, long-tailed macaques are a despotic species. Therefore, they may consider dominance more important than relationship quality in an experimental setting. This may explain the behavior of long-tailed macaques in general in the dyadic (Massen et al. 2010a) and of the subordinate long-tailed macaques in the triadic experiment that we report here. Moreover, the effect of dominance position on prosocial behavior was not determined in prosociality tests in chimpanzees, another rather despotic species (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008). Although speculative, this may explain the absence of prosocial behavior in these studies. Second, long-term observations show that long-tailed macaque friendship is based on a long-term interchange of beneficial interactions and not so much on direct exchanges of benefits (Massen 2010). Therefore, it may not be necessary to confirm friendship by benefiting the other at every possible occasion. However, a tendency to benefit friends would still be expected, but was not conclusively found. Third, although in the triadic choice experiment the subject could choose between two partners, the subject was not free to follow its own preferences, since we determined which monkeys were tested together. Partner choice is considered a crucial feature of social exchanges (Noë et al. 1991; de Vos et al. 2001). The current experiments may actually only measure behavioral tendencies. In a natural setting, behavior benefiting another

individual may not so much be caused by behavioral tendencies once near an individual, but instead by partner choice. This suggests that the effect of partner choice should be considered in future testing.

Prosocial behavior has now been established in several animal species (ravens: Heinrich 1988; jackdaws: de Kort et al. 2006; chimpanzees: Warneken et al. 2007; common marmosets: Burkart et al. 2007; capuchin monkeys: de Waal et al. 2008; Lakshminarayanan and Santos 2009; rooks: Scheid et al. 2008; bonobos: Hare and Kwetuenda 2010; long-tailed macaques: Massen et al. 2010a). However, these species have different socioecological group structures, and this may affect the benefits derived from prosocial behavior. While prosocial behavior can be regarded as one type of behavior, its function may differ according to these socioecological structures. First, prosocial behavior may be adaptive when it is directed at related individuals, following the rules of kin selection (Hamilton 1964). Several studies indeed show that individuals are prosocial towards kin and more prosocial towards kin than towards non-kin (Burkart et al. 2007; de Waal et al. 2008; Massen et al. 2010a; but see also Yamamoto and Tanaka 2010). Second, prosocial behavior may lead to reciprocal relations. However, most studies on prosocial behavior do not allow for such relations to arise in the experimental setup, because only one individual can benefit another. A study on chimpanzees (Yamamoto and Tanaka 2010) that did allow for reciprocal relations to arise, however, did not find prosocial behavior of chimpanzees. Lastly, prosocial behavior may function as image building (Moore 1984; de Waal 1989) resulting in indirect reciprocity (Alexander 1987). This may be especially important in species that have a hierarchical group structure or in species where individuals can meet each other irregularly (e.g., fission–fusion species). A previous study on long-tailed macaques (Massen et al. 2010a) and a study on rooks (Scheid et al. 2008) indeed showed a clear effect of a dominance hierarchy on prosocial behavior: High-ranked individuals use their prosocial behavior as a signal of their status. However, whether in fission–fusion species prosocial behavior is used to signal a positive attitude in the presence of unfamiliar individuals or after reencountering known individuals has not yet been tested. In sum, the functions of prosocial behavior can be various, and with only few tests on several different species, the discussion about its function remains vibrant and alive.

To conclude, observational studies provided the suggestion that long-tailed macaques will be more prosocial towards their friends than towards their nonfriends. However, the two conducted experiments yielded no conclusive support for this hypothesis. In the dyadic prosociality experiment, prosociality was not related to relationship quality. Moreover, subjects only tended to prefer to give to

their friends when they have the choice between a friend and a nonfriend. In contrast, subordinate long-tailed macaques show a competitive attitude and avoid giving to close competitors, but instead give to the highest ranking individual. Therefore, relative dominance rank seems to be a more important factor than relationship quality in directing prosocial behavior of long-tailed macaques.

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