

No Costly Prosociality Among Related Long-Tailed Macaques (*Macaca fascicularis*)

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Altruism, benefiting another at a cost to the donor, may be achieved through prosocial behavior. Studies of nonhuman animals typically investigate prosocial behavior with paradigms in which the donor can choose to give a recipient a food item, and the choice does not affect the donor's reward (which is either present or absent). In such tasks, long-tailed macaques (*Macaca fascicularis*) show prosocial behavior, especially toward kin. Here, we tested captive long-tailed macaques with related recipients in an alternative task, in which the donor had to give up a preferred reward to benefit the recipient; that is, they had to choose a lower valued reward for themselves to provide food to their kin. Overall, the macaques did not provide their kin with food. The task forced the donor to balance its prosocial behavior with its selfish choice for a higher value reward, a balance that turned out to favor selfish motives. Consequently, our study shows that a prosocial tendency is not sufficient to elicit costly prosocial behavior in long-tailed macaques. Subsequently, we feel that tasks in which the donor must choose a lower value reward to benefit another individual may allow the titration of the strength of prosocial behavior, and thus provides interesting possibilities for future comparative studies.

Keywords: altruism, other-regarding preferences, inequity aversion, kin selection, prosocial choice task

Altruism, benefiting another individual while incurring a cost, remains a scientific enigma. Evolutionary models indicate that altruistic behavior can be selected for when related individuals are benefited (kin selection; Hamilton, 1964) or when others reciprocate the benefiting behavior at a later point in time (reciprocal altruism; Trivers, 1971). Whereas these cost–benefit payoffs for selection are relatively clear, it remains to be established how these ultimate rules can be achieved within proximate behavioral rules. A practical approach to investigate proximate processes is to look at behavioral outcomes to determine when animals may exhibit

prosocial behavior, for example, behaving to provide another individual with a reward. Such prosocial behavior was long considered a uniquely human capacity (Fehr & Fischbacher, 2003). This has recently been called into question with research on various other species (reviewed in Cronin, 2012) using so-called *instrumental helping tasks* (e.g., Warneken, Hare, Melis, Hanus, & Tomasello, 2007) or, alternatively, a task in which a donor may choose to provision a conspecific at no cost to itself, a so-called *prosocial choice task* (cf. Cronin, 2012). In this task, donors may generally choose between two options: one that provides a conspecific recipient with food (prosocial choice) and one that does not (nonsocial choice). We studied a choice task in which the donor had to choose against its own interest, in a so-called *costly prosociality task*.

In a typical prosocial choice task, the donor receives the same reward irrespective of its choice (Cronin, 2012), and this is named the *prosocial setting* (Schwab, Swoboda, Kotrschal, & Bugnyar, 2012). One often-used task is the food-pulling task. In this task, the donor is presented with a choice between so-called prosocial (providing a reward to the recipient) and nonsocial (not providing a reward to the recipient) choices while all food rewards are visible. There are two versions of this task that are treated as similar (cf. Burkart & Rueth, 2013): (1) Donors can provision recipients by choosing the bar that contains a reward for the recipient in favor of the one that does not provide the recipient with a reward: 1–1 provides both donor and recipient food; 1–0 provides the donor food, but not the recipient (e.g., Silk et al., 2005). (2) The donor can choose the bar on the side of the recipient versus the side with an empty compartment: 1–1 provides both donor and recipient food; 1–(1) provides the donor food, but the other reward goes to the empty compartment (e.g., Jensen, Hare,

This article was published Online First May 11, 2015.

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We thank the animal caretakers and the Animal Science Department of the Biomedical Primate Research Centre for their continued dedication to the welfare of the monkeys. We thank Megan Lambert for proofreading and three anonymous reviewers for helpful comments on an earlier version of this manuscript. We are grateful to the funding agencies that made this research possible: a PRIMOCID grant from EUPRIM-Net under EU Contract RII3-026155 of the Sixth Framework Programme (PRIMOCID-207) and a stand-alone grant of the Austrian Science Fund (P26806), both to Jorg J. M. Massen.

This study was carried out in accordance with the legal requirements of the Netherlands. This research was approved by the Animal Ethical Committee of the Biomedical Primate Research Centre with Protocol DEC#656.

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Call, & Tomasello, 2006). The 1–1/1–0 and 1–1/1–(1) notations follow those of Burkart and Rueth (2013).

Several primates, rats, and one corvid species showed prosocial behavior in such tasks (bonobos, *Pan paniscus*: Hare & Kwetuenda, 2010; Long–Evans (brown) rats, *Rattus norvegicus*: Hernandez-Lallement, van Wingerden, Marx, Srejjic, & Kalenscher, 2015; capuchin monkeys, *Cebus apella*: Lakshminarayanan & Santos, 2008; long-tailed macaques, *Macaca fascicularis*: Massen, van den Berg, Spruijt, & Sterck, 2010; jackdaws, *Corvus monedula*: Schwab et al., 2012). In contrast, there are also studies in which donors did not show prosocial behavior (chimpanzees, *Pan troglodytes*: Amici, Visalberghi, & Call, 2014; House, Silk, Lambeth, & Schapiro, 2014, Study 2; Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008; other apes, capuchin, and spider monkeys, *Ateles geoffroyi*: Amici et al., 2014; cotton-top tamarins, *Saguinus oedipus*: Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009; Stevens, 2010, but see Cronin, Schroeder, & Snowdon, 2010; human children, *Homo sapiens*: Burkart & Rueth, 2013; and ravens, *Corvus corax*: Di Lascio, Nyffeler, Bshary, & Bugnyar, 2013). However, in tasks in which food was not visible but a token was exchanged that benefits only the donor or both the donor and its recipient, chimpanzees (Horner, Carter, Suchak, & de Waal, 2011) and capuchin monkeys (de Waal, Leimgruber, & Greenberg, 2008) chose prosocially (but see Amici et al., 2014). In all of these tasks, the donor typically chooses between two options that yield the same reward for the donor, and when the donor chooses prosocially, the donor and recipient receive the same reward. Although the donor has to act, which may be considered a cost, it always gains a reward. Therefore, these results do not require costly prosociality from the donor, only that it takes benefits for its recipient into account.

To test for altruism in the evolutionary sense, the donor has to incur a cost, as tested in a costly prosociality task, and this has been named the *altruistic setting* (cf. Schwab et al., 2012). In principle, donors can incur two types of costs: (1) the donor has to *work* to benefit the recipient, but the donor does not benefit from its choice because it gains no or a low-quality reward; or (2) the donor has to *choose against its own interest* by giving up a high-quality reward for a lower quality one to benefit the recipient. A number of studies reported prosocial behavior in the altruistic setting in which the donor has to work to benefit the recipient: The donor obtains no reward and can make a prosocial choice (donor–recipient: 0–1) or a nonsocial choice (0–0). The costs for the donor involve the act of pulling or exchanging a token. When this was tested with a pulling device where the donor could not obtain a reward, common marmosets (*Callithrix jacchus*; Burkart, Fehr, Efferson, & van Schaik, 2007), capuchin monkeys (Lakshminarayanan & Santos, 2008), and children (Burkart & Rueth, 2013) were prosocial. However, chimpanzees (House et al., 2014, Study 2; Jensen et al., 2006) and cotton-top tamarins (Cronin et al., 2009; Stevens, 2010) were not prosocial in this task. This may have resulted from the reluctance of the donors to pull when no reward was available. Indeed, when both the prosocial and altruistic settings were tested in the same study, donors were less likely to pull in the altruistic setting (Cronin et al., 2009; House et al., 2014; Jensen et al., 2006; Stevens, 2010). In addition, in a token exchange task, capuchins acted prosocially when they obtained equal-quality food themselves; yet, they were not prosocial when they received a lower quality reward than their recipients (de Waal

et al., 2008). Moreover, behavior in the prosocial setting does not necessarily predict behavior in the altruistic setting. Whereas capuchin donors were similarly prosocial in the prosocial and altruistic settings, in a token exchange task, they were less likely to show prosocial behavior in the altruistic than in the prosocial setting (de Waal et al., 2008). In contrast, chimpanzees and cotton-top tamarins behaved in a similar nonsocial manner in both the prosocial and altruistic setting, whereas children (Burkart & Rueth, 2013) and chimpanzees in a different study (House et al., 2014; Study 1) were prosocial in an altruistic setting, but not in a prosocial setting. Therefore, behavior in the prosocial setting does not seem to predict behavior in the altruistic setting.

To date, we know of only a few studies that have examined an altruistic setting in which the donor had to choose against its own interest to benefit the recipient. There are three versions of this task: To act prosocially, the donor has to choose (a) no reward over a reward to benefit the recipient (0–1 provides the recipient food, but not the donor; 1–0 provides the donor food, but not the recipient, e.g., chimpanzees, “attention trials”: Silk et al., 2005; jackdaws: Schwab et al., 2012); or (b) the donor has to share the rewards with the recipient (e.g., bonobos: Hare & Kwetuenda, 2010; Tan & Hare, 2013); or (c) the donor can choose between a bar that delivers to a recipient’s compartment versus an empty compartment, and the reward distribution is such that the bar on the recipient’s side provides the donor with low-quality food and the recipient with high-quality food (LQ–HQ), whereas the bar on the other side provides the donor high-quality food, but the low-quality reward goes to the empty compartment, HQ–(LQ). Jackdaws, especially in mixed-sex dyads, provide the recipient with food, even if they have to give up food to do so. Similar to the marmosets and capuchin monkeys, however, the distribution of food did not influence the donors’ behavior because the jackdaws were similarly prosocial in a task in which the donor received a reward regardless of its choice (Schwab et al., 2012) and bonobos also provided the recipient when the donor could not obtain food (Tan & Hare, 2013). In similar “attention trials,” chimpanzees, however, did not provide their partner with food (Silk et al., 2005). Altogether, evidence for prosocial behavior in an altruistic setting is mixed, but it has been documented in some species.

In altruistic settings, the donor typically does not receive a reward, and two processes may affect the donor’s behavior: (a) the fact that the donor does not receive a reward and (b) the fact that the donor obtains less than its recipient. First, when a donor obtains no reward, it will need a clear incentive to act in a task. This incentive may be provided by the emotions elicited from rewarding its recipient (de Waal, 2008). Alternatively, the act of pulling itself may be rewarding (e.g., long-tailed macaques: Dekleva, van den Berg, Spruijt, & Sterck, 2012; Gumert, Kluck, & Malaivijitnond, 2009; Leca, Gunst, & Huffman, 2007). Second, when an individual obtains less than its recipient, inequity aversion (IA) may reduce its willingness to work (Brosnan & de Waal, 2003; Brosnan, Houser, et al., 2010). Indeed, a donor that has to “work” for its food is less willing to accept the reward when it receives a reward of lower quality than its partner, whereas a donor that is provided with food (i.e., does not have to “work”) does not have a reduced willingness to eat a low-quality reward (chimpanzees: Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; long-tailed macaques: Massen, van den Berg, Spruijt, & Sterck, 2012). Therefore, IA could preclude working for a low-quality reward

when the recipient obtains high-quality food. However, in IA tests, the donor never refuses all food it has to work for, and the donor obtains at least some rewards (e.g., capuchin monkeys: Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007; chimpanzees: Brosnan, Talbot, et al., 2010; long-tailed macaques: Massen et al., 2012). Whereas testing for costly prosocial behavior without any reward for the donor may be very taxing, testing with rewards of different quality, where the donor obtains a low-quality reward when providing its recipient with a high-quality reward, guarantees that donors have an incentive to act and may allow for some choosing the low-quality reward despite IA. To our knowledge, this has not been tested thus far in primates or any other animal species.

Long-tailed macaques can act prosocially to benefit others in a prosocial setting, particularly if those individuals are related to the donor (Massen, Luyten, Spruijt, & Sterck, 2011; Massen et al., 2010). In addition, high-ranking animals benefit others, whereas low-ranking animals behave asocially and withhold the recipient rewards. However, in these studies, the animals did not incur a cost because they obtained the same reward irrespective of whether they made a prosocial or nonsocial choice. Therefore, although long-tailed macaques show prosocial behavior toward kin, which from an ultimate perspective follows the predictions of kin selection (Hamilton, 1964), it is not clear whether they will also show prosocial behavior when it is costly. Moreover, long-tailed macaques show IA (Massen et al., 2012); yet, even when they have to work very hard and the reward distribution between themselves and the recipient is unequal, they still work to obtain some food. Therefore, testing for prosocial behavior in an altruistic setting in which the donor has to choose a low-quality reward to benefit a kin recipient may yield evidence for costly prosociality in this species, especially when considering the competing demands of prosociality and equity (Brosnan, Houser, et al., 2010).

In this research, we aimed to determine whether long-tailed macaques would show prosocial behavior toward kin in an altruistic setting. We measured whether the macaques would act prosocially when their prosocial behavior was costly with a LQ–HQ/HQ–(LQ) task, in which they would have to forgo a high-quality reward and choose a low-quality reward to benefit their kin recipient with high-quality food, whereas a choice for the high-quality reward would make the additional low-quality food available to an empty compartment.

Method

Subjects and Housing

The behavioral experiment was conducted with individuals from a captive social group of long-tailed macaques (*Macaca fascicularis*; the “Haas” group) housed at the Biomedical Primate Research Center in Rijswijk, the Netherlands. The group consisted of three adult males and 14 adult females (>3 years old) and five juvenile males and three juvenile females (<3 years old). During the training period, three infants were born. In total, we tested 16 donors, of which 15 were adult (two males, 13 females), and one was a juvenile male (2 years).

All the macaques were born in captivity, and some of them had previously participated in other behavioral experimental research that was unrelated to the current study. At the Biomedical Primate

Research Center, the group was housed in a large indoor–outdoor enclosure. The inside enclosure consisted of three parts, all 2.85 m high, with a total surface area of 48 m². A high corridor in the front part of the cage connected these three parts. This corridor (height: 0.8 m; breadth: 0.8 m; l:4.56 m) was located at a height of 1.8 m, and was used for the experimental setup (see below). The outside enclosure also consisted of three parts, all 3.1 m high, with a total surface area of 260 m². All parts, both inside and outside, were connected to each other by one or two openings. The inside enclosure had sawdust bedding; the outside enclosure had sand. All parts of the enclosure contained numerous platforms and permanent environmental enrichment consisting of fire hoses, tires, ladders, and a swimming pool. In addition, enrichment-containing food was provided at least every week (Vernes & Louwse, 2010). The macaques were fed monkey chow, complemented by fresh fruit, vegetables, or bread on a daily basis. Water was available ad libitum.

Dominance Hierarchy

Observational data of agonistic behavior were collected ad libitum throughout the training period. Behaviors included the unidirectional silent bared teeth display and unprovoked make room as submissive behaviors, as well as the open mouth threat as dominance behavior (Angst, 1974). The dominance hierarchy, determined with these data using Matman 1.1 (de Vries, 1995, 1998; de Vries, Netto, & Hanegraaf, 1993), was significantly linear (linearity index h' : 0.3053, $p = .012$). Individuals older than 2 years of age were assigned a dominance rank ranging from 1 for the most dominant individual to 19 for the lowest ranking individual (see Table 1).

Relationship Characteristics of Tested Dyads

The 16 donors and recipients (see Table 1) were chosen on the basis of knowledge about their kin relations to other group members and on their willingness to participate in the training. Kin relations were assessed through maternal pedigree. Donors were paired with a closely related recipient, and pairs were either maternal siblings, a mother with her offspring, or an offspring with its mother. To avoid reciprocal behavior, recipient and donor never exchanged roles. Nevertheless, donors could be the recipients for other donors. Some recipients had this role one or two times, and not all donors also served as recipients (see Table 1). The nonnatal alpha male did not participate in the study because he had no maternal kin in the group.

Experimental Setup

Testing took place inside in the corridor. For the experimental setup, the corridor was subdivided into three smaller test compartments (I, II, and III) by means of four slides (see Figure 1). The two outer slides were opaque, whereas the two slides in the middle were transparent. A custom-designed test apparatus was placed in front of the corridor covering the length of Compartments I, II, and III (see Figure 1) at a height equal to the height of the corridor's bottom. The test apparatus consisted of a large board (0.65 m × 1.6 m) with two sliding bars (0.3 m × 0.8 m) mounted on it. On each end of these two sliding bars a transparent cup for rewards was attached, giving a total

Table 1

Donor Identity, Dominance Rank, and Age; Recipient Identity and Dominance Rank; and Kin Relationship and Sex Combination of Each Donor–Recipient Dyad

Donor	Dominance rank	Age (years)	Recipient	Dominance rank ^a	Relationship	Sex combination	Control (preferred food of 20)	Test (preferred food of 20)	Prosociality	Prosociality (0–1)
Za	2	6	Se	13	Offspring–mother	Male–female	15	17	–0.1	0
Li	3	11	Co	6	Sibling	Female–female	19	17	0.1	1
Er	4	22	Li	3	Mother–offspring	Female–female	18	19	–0.05	0
Fr	5	7	Co	6	Offspring–mother	Female–female	19	20	–0.05	0
Co	6	14	Se	13	Sibling	Female–female	16	11	0.25	1
Ge	7	4	Op	12	Sibling	Male–female	20	20	0	0
Ta	8	2	Fr	5	Offspring–mother	Male–female	18	19	–0.05	0
An	9	7	Ic	11	Offspring–mother	Female–female	18	19	–0.05	0
Ba	10	4	Ni	14	Offspring–mother	Female–female	17	19	–0.1	0
Ic	11	15	Ge	7	Mother–offspring	Female–male	17	14	0.15	1
Op	12	6	An	9	Sibling	Female–female	19	20	–0.05	0
Se	13	16	Ic	11	Sibling	Female–female	14	17	–0.15	0
Ni	14	12	Su	16	Sibling	Female–female	19	15	0.2	1
Ro ^b	15	26	Su	16	Mother–offspring	Female–female	17	17	0	0
Su	16	15	Er	4	Sibling	Female–female	15	18	–0.15	0
Ch	19	17	Ro	15	Sibling	Female–female	17	18	–0.05	0
Ro ^c	15	26	Su	16	Mother–offspring	Female–female	10	11	–0.05	0

Note. The donor's performance in the control (number choices of preferred food) and test (number choices of preferred food) conditions. The donor's prosociality as a continuous measure and as a dichotomous measure.

^a Lower values represent a higher dominance position. ^b Roswitha chose between cucumber + banana and cucumber. ^c Roswitha chose between cucumber and banana; the latter measures were not used in the data analyses.

of four cups (see Figure 1). A pulling handle was attached to each sliding bar that could be operated only from Compartment II. The donor was always placed in Compartment II. Both pulling handles were offered at an equidistant position from Compartments I and III during testing (cf. Amici et al., 2014). The transparent slides allowed the donor to have visual access to both the left and the right neigh-

boring test compartments. The donor could pull only one of the two handles per trial and it received only one reward. The experimenter unobtrusively kept the nonchosen sliding bar in place. The reward in an outer cup was only accessible for a possible recipient sitting either in Compartment I or III.

Training

The macaques were first trained to voluntarily come to the corridor and to be separated from their group members. All macaques that habituated to the separation procedure were trained to sit alone in one of the test compartments for up to 10 min without showing any signs of anxiety. In the following training phase, the macaques were trained to pull the handles of the test apparatus and to distinguish between right and left by baiting only one side while sitting alone in Compartment II. This was done by placing rewards on either the left or the right sliding bar in a randomized order. Once the macaque distinguished between left and right, that is, when the macaque pulled the rewarded sliding bar in 10 out of 10 trials, the macaque proceeded to the next training phase. Here, we trained the macaques with a recipient that received the same reward as the donor with a 1–1/0–(0) task. Before the actual testing, each macaque had been trained both as donor and as recipient, and thus had experience in both donating and receiving rewards, that is, with the consequences of each choice both from the perspective of the actor and the receiver. To avoid reciprocity during the tests, the donor–recipient combinations of the training phase were different from those during testing.

Food Preference Test

Prior to testing, the food preference of each donor was tested in 30 trials, divided over 3 consecutive days (10 trials per day). In

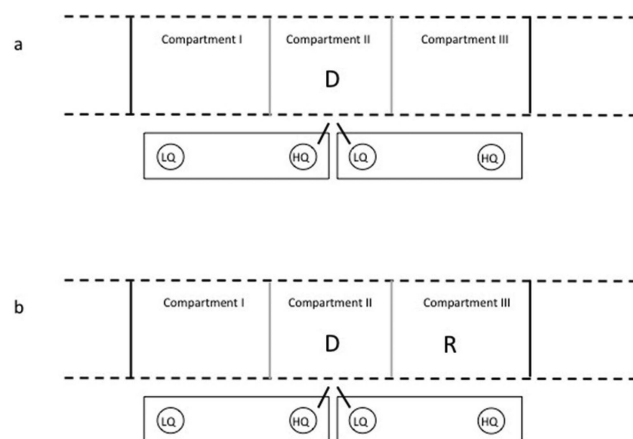


Figure 1. Schematic view of the corridor in the home cage and test apparatus. The three test compartments of the corridor, I, II, and III, are indicated. Solid black lines represent opaque borders, solid gray lines represent transparent slides, and dashed lines represent wire mesh. The position of the two sliding bars, the position of the four transparent cups for the food rewards, and the distribution of the reward quality (LQ = low-quality reward; HQ = high-quality reward) are indicated. (a) Control situation: Only the donor (D) is present. (b) Test situation: Donor (D) and recipient (R) are present; the recipient could also be located in Compartment I. Not to scale.

each trial, the macaque had the choice between two different food items presented roughly 20 cm apart on a black surface (A4 size). The position (left or right) of the two food items in each trial was randomized. In this study, an overall preference of 80% or above was assumed to reflect a preference for a certain food item. The food items tested were peanut versus cucumber, cut into equally sized pieces. All individuals had a preference for peanut (high-quality reward) over cucumber (low-quality reward) with the exception of one individual: Roswitha. For her, the peanut was substituted with a slice of banana; in the food preference test, she preferred banana over cucumber. However, this preference was not evident in the control test (see Table 1) and a preference was found only when one reward was quantitatively larger than the other, that is, banana + cucumber (high-quality reward) versus cucumber (low-quality reward). Therefore, results of Roswitha based on this quantitative contrast were used in further analyses.

Control and Test Condition

The macaques were tested with a LQ–HQ/HQ–(LQ) task (see Figure 1), the bar on the recipient's side provided the donor with low-quality food and recipient with high-quality food (LQ–HQ), whereas the bar on the other side, HQ–(LQ), provided the donor high-quality food, but the low-quality reward went to the empty compartment. Control and test condition each consisted of 20 trials divided over 2 days (10 per day), with a maximum of 5 days between sessions. Equally sized food rewards of high and low quality were used in both control and test conditions. The donor was allowed to pull only one handle per trial and subsequently collect the reward.

In the control condition, the donor was sitting alone in test Compartment II with no recipient present in Compartment I or III. For the two cups in front of Compartment II, the position of the high-quality reward and the low-quality reward was semirandomized and balanced. Both sliding bars contained a high- and a low-quality reward. The sliding bar that presented a high-quality reward in front of Compartment II had a low-quality reward in front of the adjacent outer compartment (I or III), the sliding bar that presented a low-quality reward in front of Compartment II had a high-quality reward in front of the other adjacent outer compartment (III or I; see Figure 1a). This prevented the choice being based on the summed value of the rewards.

In the test condition, a recipient was placed in one of the neighboring test compartments, I or III (see Figure 1b). The position of recipient was balanced between left and right to account for a potential side preference of the donor on each of the 2 testing days: On Day 1, the recipient was placed either left or right for the first five trials, and thereafter on the opposite side for the last five trials; on Day 2, the starting position of the recipient was always the opposite of Day 1. Starting positions of the recipients on the first testing days were (counter-) balanced over the 16 donors. The low-quality reward in front of Compartment II was always placed on the same side as the recipient, and the preferred high-quality reward was placed on the side of the empty compartment. The two outer cups in front of Compartments I and III were baited in the same way as in the control condition, that is, dependent on the position of the low-quality and high-quality reward in the cups in front of Compartment II (see Figure 1b). Thus, for the

donor to provide the recipient with a reward, the donor had to pull in the handle, which provided it with a low-quality reward.

Measures and Analyses

To test for prosociality, we compared donors' preference for pulling the bar containing the high-quality reward in the control condition with their preference for pulling that bar in the test condition. Prosocial behavior was assumed when donors had a significantly lower preference for this bar in the test condition compared with the control condition, that is, when they would forgo a high-quality reward and choose a low-quality reward to benefit their kin recipient.

The effects of the relationship characteristics (i.e., dominance, dominance distance, type of family relationship, and sex combination) on behavior were determined. We used dominance rank number as a proxy for dominance. Dominance distance was calculated by subtracting the recipient's dominance rank number from that of the donor. The dominance rank number of the donor was higher than its recipient in nine dyads and lower in seven dyads. Two types of family relationships were tested: The donor and its recipient were pairs of offspring and mother ($n = 8$) or siblings ($n = 8$). Two types of sex combinations were tested: The donor and its recipient were both females ($n = 12$) or consisted of a male and female ($n = 4$). No male–male dyads were formed because of the low number of males in the group. We balanced the different relationship characteristics relative to each other as much as possible.

Analyses were conducted in SPSS 20, and alpha was set to .05. All tests were two-tailed.

Results

General Behavior in the Task

In the control condition, the donors pulled significantly more of the high-quality than the low-quality reward (binomial test, one-tailed: $Se: p = .058$; for all other individuals significant), corroborating the food-preference tests prior to the experiment. Only one individual had a significant side preference ($Su: 15$ out of 20 pulls were left; binomial test, two-tailed: $p = .042$). We found no learning/order effects given that a comparison of the first 10 and last 10 trials in both the control (Wilcoxon's signed-rank matched pair test: $z = -1.417, p = .20$) and the test conditions (Wilcoxon's signed-rank matched pair test: $z = -0.924, p = .48$) did not differ significantly.

Prosocial Behavior

We tested whether the macaques were more likely to forgo the preferred high-quality food reward in the test condition, providing the recipient with food, than in the control condition. Donors always pulled a tray and ate the reward, both in the control and test conditions. The recipient, when provided with a reward, also always ate it. However, there were no significant differences between macaques' preferences in the control and test conditions (Wilcoxon's signed-rank matched pair test: $z = -0.39, p = .67$; see Figure 2), indicating that they did not behave prosocially. In addition, the data were analyzed separately to determine individual prosocial preferences. For 14 individuals, no significant effect was

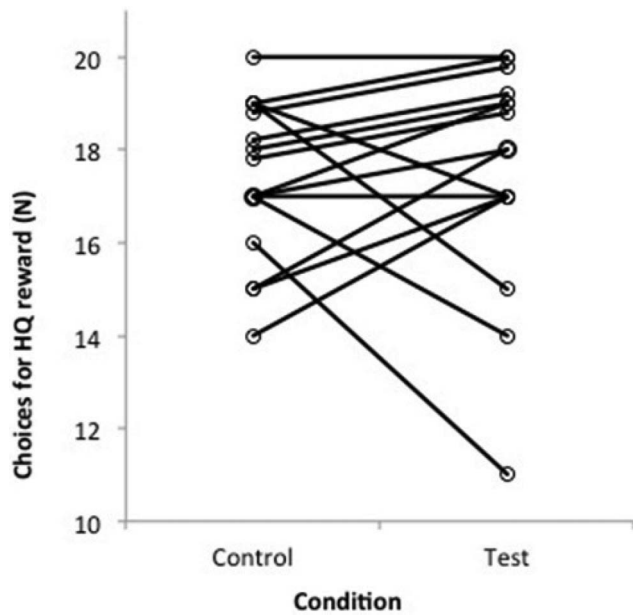


Figure 2. Number of times (out of 20 trials) that each donor pulled the high-quality (HQ) reward in the control and test situations.

found either way, and two individuals showed a nonsignificant tendency to have a prosocial preference and provided their recipient with food (Fisher's exact test: Co: $p = .07$; Ni: $p = .08$). These two individuals had a middle and low dominance rank (Co: rank 6; Ni: rank 14; see Table 1).

Prosocial Behavior and Relationship Characteristics

We also investigated whether differences in prosocial behavior were influenced by relationship characteristics (i.e., dominance, dominance distance, type of family relationship, and sex combination). The behavior in the test relative to the control situation was binary categorized as prosocial (the donor more often gave up a high-quality reward in the test than in the control condition) and nonsocial (the donor did not more often give up a high-quality reward in the test than in the control condition; see Table 1). When investigating the effect of these characteristics, none had an effect on the probability of a prosocial choice; that is, we did not find any significant differences between prosocial and nonsocial individuals with regard to dominance rank (Mann-Whitney test: $N_1 = 12$, $N_2 = 4$, $U = 20$, exact $p = .86$) and dominance distance (Mann-Whitney test: $N_1 = 12$, $N_2 = 4$, $U = 18$, exact $p = .52$), nor could being prosocial or nonsocial be predicted by family relationship (χ^2 cross-table: $\chi^2 = 0.00$, $df = 1$, exact $p = 1.00$) or sex combination (χ^2 cross-table: $\chi^2 = 1.33$, $df = 1$, exact $p = .57$) of the dyad.

Discussion

When donors had to choose a low-quality reward to deliver food to their kin recipient, long-tailed macaques did not provide their kin with food. This indicates that these macaques are not readily willing to bear a cost to provide food to a relative, although such null results should not immediately be interpreted as proof of

nonexistence. However, previous studies on long-tailed macaques (Massen et al., 2011; Massen et al., 2010), albeit on different individuals, showed that long-tailed macaques are able to behave prosocially toward kin in this task. The only parameter that varied between this and these previous tasks was the cost of being prosocial. Therefore, this behavioral experiment provides an indication that in long-tailed macaques evidence of prosocial tendencies without costs to the donor does not predict costly prosocial behavior.

In the altruistic setting of the LQ-HQ/HQ-(LQ) task, long-tailed macaques showed a clear preference for the high-quality reward. However, their lack of prosocial behavior is not due to an impossibility to behave prosocially: The donors had ample possibilities to forgo a preferred reward, even if only a few times, to provide the recipient with food. When tested on an individual basis, two individuals indeed tended to be prosocial, whereas all others were not. This suggests that prosocial tendencies in long-tailed macaques are weak and are typically found when they bear no cost for the donor.

In our previous studies, the task with no costs to the donor, 1-1/1-(1), led to prosocial behavior toward kin (Massen et al., 2010). Therefore, we tested donors with close kin only. Nevertheless, this did not result in prosocial behavior. Moreover, we did not find a difference in behavior depending on the type of kin relationship: Whether donor and recipient were siblings (relatedness coefficient $r = .25$), mother and offspring, or offspring and mother ($r = .5$) did not affect their behavior. In addition, sex combination did not affect it either. It should be noted, however, that because almost all individuals showed the same nonsocial behavior, there was little to no variation to be explained by these factors. Nevertheless, these results contrast with the results of jackdaws, where donors paired with a bird of the other sex made prosocial choices in the altruistic condition, possibly reflecting mate choice (Schwab et al., 2012). However, partner choice did not affect behavior of the long-tailed macaques because they were tested with kin and because mate choice is rather fluid in this promiscuous species (Overduin-de Vries, Olesen, de Vries, Spruijt, & Sterck, 2013) in contrast to the lifelong pair bonds formed by jackdaws.

In our previous study, dominant donors were prosocial, whereas subordinate donors withheld food and were asocial (Massen et al., 2010). We interpreted the prosocial behavior of dominant donors as a costly signal of dominance (Zahavi, 1977). However, in the current study, in which providing really had a cost to the donor, we did not find an effect of dominance on behavior, countering this interpretation. Moreover, the two macaques that showed a nonsignificant tendency to be prosocial were middle- and low-ranking. Instead, dominants may behave prosocially when their dominance is partly dependent on the "goodwill" of the others in the group. Moreover, in contrast to our previous study, we did not find that subordinate donors were asocial and withheld food. Also at the individual level, none of the donors was significantly asocial. However, the strong preferences during the control experiment made it almost impossible for most individuals to behave significantly asocially because of a ceiling effect, that is, preferences for the bar containing the preferred reward were already almost 100%, leaving little room for an increase.

In our study, donors obtained a lower quality reward than the recipients when pulling prosocially; yet, almost never did so. Therefore, the LQ-HQ/HQ-(LQ) task seems to reflect the com-

peting demands of prosociality and IA (Brosnan, Houser, et al., 2010). Indeed, IA may have reduced the number of prosocial choices; yet, we did not expect it to prevent it given that in IA tests individuals are still willing to accept part of the low-value rewards (Brosnan & de Waal, 2003). Yet, in our LQ–HQ/HQ–(LQ) task, a prosocial donor both had to choose against its own food preference and had to overcome IA; therefore, with this task, it is not possible to tease apart what caused donors to choose selfishly. These double “costs” will be prevented in a LQ–LQ/HQ–(LQ) task: A prosocial choice does result in a lower quality reward for the donor, but not in a reward that is lower in quality than that of its recipient.

The lack of evidence for costly prosociality in long-tailed macaques is similar to results with cotton-top tamarins (Cronin et al., 2009; Stevens, 2010), capuchins (de Waal et al., 2008), and chimpanzees (Jensen et al., 2006), but contrasts with the results found in common marmosets (Burkart et al., 2007), capuchin monkeys (Lakshminarayanan & Santos, 2008), jackdaws (Schwab et al., 2012), chimpanzees (House et al., 2014, Study 1), and children (Burkart & Rueth, 2013). The difference with other studies may result from differences in relationship quality, social organization, and the task. It is surprising that in macaques mothers do not provide for kin, although they do support them in risky and potentially costly conflicts (Chapais, Savard, & Gauthier, 2001; Kawai, 1958; Thierry, 2007). Therefore, relationship quality does not seem fully decisive. However, results are consistent with the lack of alloparental care in macaque species (Burkart et al., 2014). Alternatively, the difference between the current study on prosocial behavior in long-tailed macaques and previous studies on prosocial behavior may result from the task itself. In both the prosocial and altruistic setting in which the donor has to work, sensitivity to the reward of the other is prominent (but see Burkart & Rueth, 2013). However, the choice to pull does not entail a real cost to the donor, even in the altruistic setting in which the donor has to work yet obtains no food. Therefore, these tasks probably test for prosocial rather than altruistic tendencies per se. In contrast, a task in which the donor has to choose against its own interest, such as in the LQ–HQ/HQ–(LQ) task of the current study, donors are tested for both their sensitivity to the reward of the other and sensitivity to the reward for themselves. Its outcome reflects the balance between willingness to provide for another (i.e., prosocial preferences) and willingness to give up rewards. In the current task, we employed qualitative differences between the rewards; yet, their valuation may not be equal between individuals and is difficult to measure. Quantitative differences between the rewards may allow for establishing the relative difference in reward at which the donor will show costly prosocial behavior provided that it can distinguish this difference in quantities. Therefore, the paradigm we used in this study enables tests of costly prosociality and allows the titration of the strength of costly prosociality, which in turn may determine the presence of altruistic behavior by changing the relative value of the rewards.

Previously, we showed that long-tailed macaques exhibit prosocial behavior, particularly to kin, in a task in which their choices did not incur costs (Massen et al., 2010). In the current study, however, they did not provide their kin with food when they had to give up a high-value reward to do so. Consequently, our results indicate that prosocial preferences alone are not sufficient to exhibit altruistic behavior in this species.

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Received October 21, 2014

Revision received March 3, 2015

Accepted March 4, 2015 ■