Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: An experimental analysis of food-choice for conspecifics.

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Abstract

Whether non-human primates have other-regarding preference and/or inequity aversion has been under debate. We investigated whether tufted capuchin monkeys are sensitive to others' reward in various experimental food sharing settings. Two monkeys faced each other. The operator monkey chose one of two food containers placed between the participants, each containing a food item for him/herself and another for the recipient. The recipient passively received either high- or low-value food depending on the operator's choice, whereas the operator obtained the same food regardless of his/her choice. The recipients were either the highest- or lowest-ranking member of the group, and the operators were middle-ranking. In Experiment 1, the operators chose the high-value food for the subordinate recipient more frequently than when there was no recipient, whereas they were indifferent in their choice for the dominant. This differentiated behavior could have been because the dominant recipient frequently ate the low-value food. In Experiment 2, we increased the difference in the value of the two food items so that both recipients would reject the low-value food. The results were the same as in Experiment 1. In Experiment 3, we placed an opaque screen in front of the recipient to examine effects of visual contact between the participants. The operators' food choice generally shifted toward providing the low-value food for the recipient. These results suggest that capuchins are clearly sensitive to others' reward and that they show other-regarding preference or a form of inequity aversion depending upon the recipients and the presence of visual contact.

Keywords: other-regarding preference, inequity aversion, food sharing, social sensitivity, capuchin monkeys

Introduction

Humans have developed remarkably cooperative behaviors. We often do good to others without expecting any return when we see people in need, even if they are unrelated strangers, and we frequently cooperate with people we may never meet again (Fehr and Fischbacher 2003). Frequent and apparently altruistic cooperation is an extremely impressive characteristic of human society.

Cooperation in nonhumans has often been explained by sharing of genes among participants (kin selection: Hamilton 1964). However, it sometimes occurs among unrelated participants; several nonhuman primates have been demonstrated to show elaborate cooperative behaviors [chimpanzees (*Pan troglodytes*): Boesch 2003; Boesch and Boesch 1989; Crawford 1937; Povinelli et al. 1992, capuchin monkeys (*Cebus apella*): Brosnan et al. 2006; de Waal 2000; de Waal and Berger 2000; de Waal and Davis 2003; Hattori et al. 2005; Mendres and de Waal 2000; Visalberghi et al. 2000, cotton-top tamarins (*Saguinus oedipus*): Cronin et al. 2005; Hauser et al. 2003]. This suggests that human-like cooperation has traceable evolutionary roots.

In the evolution of cooperation, the concern for the welfare of others (other-regarding preference) appears to have played a key role. Individuals are able to ensure future beneficial cooperative interaction if they are sensitive to the partners' benefit or loss and can compare their own effort and reward with others'. Brosnan and de Waal (2004) argued that it is unlikely that sensitivity to others' benefit appeared *de novo* in humans. Rather, it probably evolved over a series of simpler, intermediate steps in nonhuman primates. In Brosnan and de Waal (2003), brown capuchin monkeys apparently eschewed imbalance of reward and effort between participants in token exchanges with a human experimenter (inequity aversion: IA). IA implies a mismatch

detected between the balance of one's own effort and reward with those of other individuals (Fehr and Schmidt 1999). The monkeys willingly exchanged tokens for a piece of cucumber in the baseline, but when they witnessed their partner receiving better food (a grape) for the same token in the inequity test (IT), they started to refuse to exchange or to accept the food. Such refusals increased when the partner received a grape without exchanging the token, in an effort control test. Brosnan et al. (2005) replicated these tests in chimpanzees. The chimpanzees' exchange behaviors were consistent with inequity aversion, although they did not appear to respond to the discrepancy between their own effort and others'. This may be because the chimpanzees were able to return the tokens with a gesture that was too simple to be seen as requiring effort on their part.

Several researchers have suggested that simpler cognitive mechanisms might explain the results of these studies. Henrich (2004) argued that rejecting the cucumber is inconsistent with IA because it increases, not decreases, inequality. Wynne (2004) argued that the comparable refusal rate in IT and the food control test in which food accumulated in an adjacent empty cage in Brosnan and de Waal (2003) might suggest that the monkeys mistakenly expected to obtain the preferred food. In support of this view, Dubreuil et al. (2006) showed that monkeys were less motivated to obtain the low-preferred food when they saw the preferred food than when they did not. Dubreuil et al. concluded that the refusals were not due to inequity aversion but to heightened motivation for getting the preferred food caused by seeing it (the greed hypothesis). Moreover, Roma et al. (2006) suggested that the experience of receiving a preferred food led to frustration when the monkeys then received ordinary food. In their study, they found that monkeys rejected cucumber more often after having received grapes

(the frustration hypothesis). For apes, Bräuer et al. (2006) proposed the food expectation hypothesis: seeing another individual receiving a preferred food creates the expectation of receiving the same food in the observer. In support, the apes, particularly chimpanzees, begged more often when the conspecific obtained the preferred food.

On the other hand, Dindo and de Waal (2007) reported that no IA effect occurred when they fed the monkeys without any task. They suggest that some labor is necessary to show IA. In addition, van Wolkenten et al. (2007) showed that capuchin monkeys are sensitive to their own effort. van Wolkenten et al. also countered many of the alternative hypotheses, such the greed and frustration accounts, by using a task-oriented experiment in which IA was confirmed.

None of the studies mentioned above allowed the subjects to control the partners' reward. But four experimental studies investigated whether chimpanzees are sensitive to others' food reward when they can control both their own and the others' reward (Jensen et al 2006; Jensen et al. 2007a; Jensen et al. 2007b; Silk et al 2005). In particular, Jensen et al. (2007a) investigated whether chimpanzees would reject a selfish proposal of a share of food by the partner or accept it in a modified version of the ultimatum game. In the ultimatum game, a human responder will typically refuse to play if the proposer offers too small a share. However, the responder chimpanzees did accept such selfish proposals by the proposer chimpanzees as long as they received food. Furthermore, the proposers offered shares with only their own food reward in mind. These results may suggest that chimpanzees are insensitive to others' welfare.

However, Visalberghi and Anderson (2008) argued that the chimpanzee proposers should have no motivation to play fairly if the responder chimpanzees willingly accept all types of offers. Visalberghi and Anderson stated that it is too early

121 to conclude that chimpanzees are indifferent to others' reward. In addition, Warneken et
122 al. (2007) reported that chimpanzees spontaneously assist both humans and conspecifics,
123 regardless of reward prospects. It is still an open question to what extent nonhuman
124 primates are in fact sensitive to others' welfare.

125 In this study, we investigated in several experimental conditions whether tufted
126 capuchin monkeys are sensitive not only to their own food reward but also to that of
127 others. We set up situations so that only the operator monkey was able to control the
128 recipient's food and the recipient passively received food without any effort. Their role
129 was fixed throughout the present study not to confound the effects of frustration and
130 inequity (see Roma et al. 2007; Silberberg et al. 2009). The monkeys faced each other
131 across two food containers. The recipient received either high- or low-value food
132 depending on the operator's choice, whereas the operator obtained the same food
133 regardless of their food container choice. First, we assessed simply whether capuchin
134 monkeys would be sensitive to others' food reward. We hypothesized that if the
135 monkeys were sensitive to others' food reward, they would change their food choice
136 according to the presence or absence of a recipient. Second, we also examined whether
137 the social rank of the recipient would affect the operator monkeys' choice, by using a
138 dominant monkey and a subordinate monkey as recipients. This is because social rank
139 has an important influence on behavior of animals living in complex societies. For
140 example, chimpanzees change strategies to obtain food depending upon their social rank
141 relative to a competitor in the experimental situation (Hare et al. 2000). Third, we
142 investigated whether satisfaction level with the food reward would influence the
143 operators' food choices by comparing middle- and high-value foods as the operators'
144 reward. This is because prosocial behavior often seems to be accompanied by a sense of

145 satisfaction. It has been demonstrated that capuchin monkeys are sensitive to food
146 quality (Anderson et al. 2008; de Waal 2000). Finally, we investigated whether visual
147 contact between the operator and the recipient, allowing interactions such as begging
148 and eye gaze, would influence the operators' food-choice, by blocking visual contact
149 between them.

150 Capuchin monkeys are phyletically more distant from humans than
151 chimpanzees are. However, they demonstrate various characteristics that seem to be
152 essential for having other-regarding preferences. For example, they are tolerant to the
153 extent that the other individuals including subordinates are allowed to retain food items
154 or they receive some share of resources. This creates a baseline level of expectation of
155 equity that makes individuals more likely to react to inequitable situations (Brosnan
156 2006; de Waal 1996). Capuchins may also share meat obtained by a group hunt
157 (Fedigan 1990; Perry and Rose 1994). Additionally, they have shown highly
158 cooperative behaviors in experimental situations as mentioned above (Brosnan et al.
159 2006; de Waal 2000; de Waal and Berger 2000; de Waal and Davis 2003; Hattori et al.
160 2005; Mendres and de Waal 2000; Visalberghi et al. 2000). Sharing food, sensitivity to
161 unfairness and successful cooperation seem to be products of the tolerance engendered
162 by close social relationships (van Wolkenten et al. 2007).
163
164 Experiment 1
165
166 Method
167 Subjects
168 Subjects were six tufted capuchin monkeys (*Cebus apella*), housed together in

a group of seven at the Graduate School of Letters, Kyoto University. Heiji (Male) and Zilla (Female) were 13 years old, Kiki (Female) and Theta (Female) were 11 years old, Pigmon (Male) was 9 years old and Zinnia (Male) was 6 years old. All subjects except Zinnia, who was born to Heiji and Zilla in the laboratory, were born in a social group at the Primate Research Institute, Kyoto University. The dominance hierarchy among these monkeys was very stable, confirmed through daily observations. Heiji was the alpha male, whereas Theta was ranked as the most subordinate in the group. These two individuals served as recipients. The operator monkeys were ranked between Heiji and Theta; the relative ranks of these individuals were not clear. Their role was fixed throughout the present study.

All had experienced a variety of laboratory tests such as operant discrimination (Fujita 2004; Fujita and Giersch 2005), tool use (Fujita et al. 2003), deception (Fujita et al. 2002), cooperation (Hattori et al. 2005), social knowledge (Anderson et al. 2004; Anderson et al. 2008; Hattori et al. 2007; Hattori et al. in press; Kuroshima et al. 2002; Kuroshima et al. 2003; Kuroshima et al. 2008), mirror-image stimulation (Paukner et al. 2004), and video-image stimulation (Anderson et al. 2009). The monkeys were not food deprived but received a portion of their daily rations during testing and the remainder in their home cage after testing each day. Kiki was pregnant during Experiment 1 and gave birth after the completion of the experiment.

Apparatus

Figure 1

Two experimental cages, 60 cm (W) x 45 cm (D) x 55 cm (H), made of transparent acrylic board with a wire-mesh floor were placed facing each other across a wooden table, 80 cm (W) x 39 cm (D) x 74 cm (H) (Figure 1). An operator monkey was placed in one cage which had three round openings (3.5 cm in diameter) aligned horizontally in the front panel. These openings were 6 cm apart and 10.5 cm above the floor. A recipient monkey was placed in the other cage which had a front panel opening of 24 cm (W) x 3 cm (H). This opening was positioned centrally and 8.5 cm above the floor. Each cage was set on a metallic pedestal of 65 cm (W) x 56 cm (D) x 74cm (H).

Two identical food containers, 9.5 cm (W) x 16 cm (D) x 10.5 cm (H), made of transparent acrylic boards were placed 12cm apart on the wooden table between the two cages (Figure 1). The containers had a drawer, 9 cm (W) x 8 cm (D) x 3.5 cm (H) in the operator side, 6 cm from the bottom. When pulled, the drawer, containing a food item, slid out to within reach of the operator monkey and this also dispensed a food to the recipient by hitting a dropper board attached behind the drawer. The containers were placed either 10 cm or 14cm from the operator, determined by the latter's arm length. The operator was allowed to pull only one drawer at a time. The recipient had no means of operating the drawer, and hence was only a passive recipient of food. A large transparent screen, 50 cm (W) x 28 cm (H), was placed against each cage to prevent the monkeys from handling the food containers during intertrial intervals and the baiting process.

All tests were recorded with two digital video cameras (Sony, DCR-TRV27), one located behind the recipient monkey to record the operator's behavior and the other located behind the operator monkey to record the recipient's behavior.

Procedure

Figure 2 and Table 1

Food preference test. We conducted a food preference test to determine appropriate rewards for the operator monkeys. First, their preferences among a raisin, an SPS pellet (a monkey food provided by the Oriental Yeast company) and a piece of green pepper were tested. We simultaneously presented 1 piece of two kinds of food placed 18 cm apart on a board measuring 50 cm (W) x 28 cm (L) for a few seconds, then moved the board toward the subject. The monkey was allowed to choose one food item. The positions of food alternated every trial. The test was repeated for 12 trials for each different pair of food. If the monkey did not show any clear preferences, we added a piece of an apple (high-value) and a piece of a sweet potato (middle-value) and re-tested. We thus obtained three food items that were differentially preferred (10 choices out of the 12 trials) for each monkey, as follows (high-, middle-, and low-value, respectively): apple, pellet, and green pepper for Pigmon and Zilla ; apple, sweet potato, and green pepper for Zinnia ; raisin, pellet, and green pepper for Kiki.

Preliminary training. Before testing, the operator monkeys were familiarized with the test apparatus in the absence of the recipient monkey. They were individually trained to pull the drawer, learning by trial and error to obtain a food item (SPS pellet) in the drawer. The operators then learned to choose between the two containers and pull the drawer within 30 s. At this stage we baited only the operator’s side. When the screen was removed, the operator could choose one of the two containers. As soon as one drawer was pulled the screen was reinstalled to prevent pulling the other drawer. If the

operator did not choose within 30 s, the trial was terminated. This training continued until they succeeded in 10 consecutive trials.

In the next stage of training, we placed two pieces of food in the containers, one in the operator's side and the other in the recipient's side, but the operator could obtain only the food in the operator's side. When the operator pulled the drawer, the food on the recipient's side dropped in front of the vacant cage, out of the operator's reach. The food also was left there for about 10 s so that the operator could learn that the recipient-side food was inaccessible. This training continued until operators showed no interest in the delivered recipient-side food for 5 consecutive trials.

Finally, the operators were habituated to the presence of a recipient in the other cage. The containers were baited as before. When the operator pulled the drawer, 1 food item became available for the operator and the other was dispensed for the recipient. This training continued until the operators stopped threatening the recipient when the latter took the delivered food for 5 consecutive trials. In all, preliminary training took 10 days (10 trials per day) to complete.

Test. The experimenter placed a transparent screen against the front panel of each cage. She then baited the two food containers. Following this, as soon as the operator looked toward the containers, the experimenter removed both screens simultaneously and the trial started. Whichever container the operator chose, it resulted in the same kind of food as reward. On the other hand, the recipient received either high- or low-value food depending upon the operators' choice. The trial ended either as soon as the recipient picked up the food, or 10 seconds after the operator's choice. During the intertrial interval of 30 s, the experimenter removed any leftover foods and set the containers up for the following trial.

Three experimental parameters were of interest: (i) the presence or absence of the recipient, (ii) the social rank of the recipient and (iii) the food value for the operator. Regarding the first parameter, in the alone condition (the recipient-absent condition), food was delivered in front of the recipient's cage in the same way as in the faced condition (the recipient-present condition) and it was removed by the experimenter after 10 s. For the second parameter, the recipient was either the dominant monkey (Heiji) or the subordinate monkey (Theta). For the third parameter, in the middle-value food condition, the operator obtained a piece of middle-value food regardless of container that was chosen. In the high-value food condition, the operator obtained a piece of high-value food regardless of container choice. In both conditions, the recipient-side food was either high- or low-value food (see Figure 2). Left-right placement of foods on the recipient's side was counterbalanced.

Each test session consisted of 10 trials. Each operator received 20 faced (recipient-present) sessions and 20 alone (recipient-absent) sessions, in total 40 sessions. These two types of sessions were run every other day, one session per day. The recipients participated in two sessions every other day. The dominant and subordinate recipients were alternated every 10 sessions. The placement of food was changed after 20 sessions. Table 1 shows a summary of the experimental design.

Analysis

The experimenter recorded the operators' choice of food container on each trial, later reconfirmed from the videotapes. The reliability between real-time observations and the video analysis was 100%. The frequency of the operator choices for the high-value container was examined in two separate 3-way ANOVAs with

presence/absence of the recipient, food value for the operator (high- vs. middle-value) and session (5 pairs) as factors, using generalized linear mixed models (GLMM; Schall 1991) implemented using the MIXED procedure in SPSS version 12.0, for the dominant and subordinate recipient. We treated the three factors as fixed and the operator (4 individuals) as a random factor. The generalized linear mixed models allow both fixed and random terms to be fitted, thus taking into account repeated sampling.

In addition, we recorded the recipients' eating and begging behaviors. We classified their eating behaviors into 3 categories (ate, picked up but did not eat, did not pick up) and their begging behaviors into 4 categories (waited on the side of the high-value container, extended arm toward the high-value container [pointing gesture], touched the high-value container, pounded on the front panel of the cage).

Results

Figures 3 (a, b)

Figure 3 shows the total number of operator choices for the high-value food container in the dominant recipient condition (Figure 3a) and the subordinate recipient condition (Figure 3b). In the dominant recipient condition, no main effect or interaction was significant, although two operators, Zilla and Zinnia, showed a consistent tendency to choose the low-value container. On the other hand, in the subordinate recipient condition, the main effects of the presence or absence of the recipient ($F_{1, 57} = 8.251$, $p = 0.006$) was significant. No other main effects or interactions were significant.

Both recipients ate the high-value food whenever it was given, but they did not

always eat the low-value food; only the dominant recipient often did so (in 69.13% of trials) and the subordinate recipient refused to even pick it up(in 62.25% of trials). On the other hand, the operators never refused to make a choice and they always ate their food reward.

Table 2 shows the percentage of the recipient's begging behaviors. The dominant recipient showed begging behaviors (in 74.5% of trials) almost twelve times more often than subordinate recipient (in 6% of trials).

The individual data of the total number of operator choices for the high-value food container is presented in Table S1 in Electronic Supplementary Material.

Discussion

In Experiment 1, we examined whether capuchin monkeys were sensitive to others' food reward and whether relative social rank and food value of the operator would affect this sensitivity. The operators chose the high-value food container significantly more often in the presence of a recipient than when alone if the recipient was subordinate. In contrast, they chose randomly between the containers in the dominant recipient condition. The presence or absence of a recipient had no effect on the operator's choice, although some operators showed a tendency to choose the low-value container when the recipient was a dominant monkey. These results suggest that capuchin monkeys have other-regarding preferences and seem to show prosocial food choice toward the subordinate, but not the dominant recipient.

Here, the results raise two questions. First, why did the operator monkeys give the high-value food to the subordinate monkey more often than to the dominant monkey, even though the latter begged for the high-value food more frequently? One possibility

is that the operators might have hoped to usurp the food on the recipient side only when the recipient was subordinate, even though they had been extensively trained to understand the restrictions imposed by the food containers. If so, they should have chosen the high-value container more often when there was no recipient than when the subordinate recipient was present, since it would seem easiest to usurp the food in the former condition. However, they did not do this. Another possible answer is that the operators avoided the container near which the dominant recipient begged. But, if so, they should have chosen the low-value container more often in the presence of the dominant recipient than when there was no recipient. Again, however, they showed no such tendency. These results imply that the operators understood both the functioning of the food containers and the situation. In addition, the operators showed no aggression to the subordinate recipient when the latter ate the high-valued food, suggesting that the operators knew that they were unable to usurp the recipient-side food.

Our second question is why the operators' choice did not change as a function of the presence or absence of the dominant recipient. One possible answer is that the operators were simply less attentive to the dominant's food, given the zero probability of being able to usurp it. However, we think that this is unlikely because, as mentioned above, the operators were well trained to understand the food containers. Another possibility is that the difference between the dominant recipient' behaviors towards high- and low-value food was not salient; both recipients always ate the high-value food, whereas only the dominant recipient ate often the low-valued food. We addressed this possibility in the next experiment.

Experiment 2

Experiment 2 was a replication of Experiment 1 using food items with extremely high- or low-value for all subjects. We asked whether the recipients' disparity in response toward the low-value food might have influenced the operators' food choice in Experiment 1, by equalizing the recipients' response toward the low-value food. In Experiment 1, only the dominant recipient often ate the low-value food (green pepper). The operators' prosocial food choice for the subordinate recipient might have been a consequence of this disparity. To eliminate this possibility we therefore used a piece of parsley, which no monkey ate, as the low-value food.

Method

Subjects and apparatus

The subjects, their roles, and the apparatus were the same as in Experiment 1..

Procedure

Test procedure was the same as in Experiment 1, except for new food items, selected on the basis of the following food preference test.

Food preference test. We assessed the subjects' preference for new food items in the same manner as in Experiment 1. The newly selected combinations of foods were a peanut (high-value), SPS (middle-value), and a few leaves of parsley (low-value). All the monkeys, including the dominant, showed the same order of preference and avoided parsley.

Results

Figures 4 (a, b)

Figure 4 shows the total number of operator choices for the high-value container in the dominant recipient condition (Figure 4a) and the subordinate recipient condition (Figure 4b). As in Experiment 1, we analyzed these data using GLMM separately for dominant and subordinate recipients. In the dominant recipient condition, only the main effect of food value was significant ($F_{1, 57} = 4.795$, $p = 0.033$). No other main effects or interactions were significant. On the other hand, in the subordinate recipient condition, the main effect of presence or absence of recipient was significant ($F_{1, 57} = 5.610$, $p = 0.021$), but no other main effects or interactions were significant.

Both recipients almost never ate the low-value food made available by the operators; the dominant recipient ate it in 2.63% of all trials and the subordinate recipient never ate it. In addition, they refused to even pick it up in more than 90% of all trials.

Table 2 shows the percentage of the recipient's begging behaviors. The dominant recipient showed begging behaviors more often than subordinate recipient (in 95.75% and 61.25% of all trials, respectively).

The individual data of the total number of operator choices for the high-value food container is presented in Table S2 in Electronic Supplementary Material.

Discussion

In Experiment 2, we investigated whether the recipients' disparity in response toward the low-value food might have influenced the operators' food choice in

Experiment 1, by equalizing the recipients' response toward the low-value food. Overall, the results of Experiment 2 replicated those of Experiment 1 even though the dominant monkey again begged more than the subordinate monkey, as Experiment 1. In the subordinate recipient condition, the operators continued to choose the high-value food more often when the recipient was present, with food value failing to influence their choice of container. In contrast, in the dominant recipient condition, the operators' food choice was again unaffected by the presence of the dominant recipient, but was influenced by the food value for the operator. That is, the operators chose the high-value food more often in the middle-value food condition than in the high-value food condition. However, the absence of an interaction between the presence or absence of the recipient and the food value for the operator suggests that the food value for the operator failed to influence their choice of the container for the recipients. These results suggest that the difference in the operators' choice with regard to the recipients in Experiment 1 was not due to the fact that only the dominant recipient often ate the low-value food. Instead, they may have purposely chosen the two containers indifferently. Conceivably, they might have inferred that spiteful behavior with regard to the dominant recipient might result in punishment upon return to the home cage, even though they may not have liked to see the dominant recipient eating the high-value food. The operators behaved more generously - choosing the high-value food container - with regard to the subordinate than to the dominant, suggesting that capuchin monkeys may behave preferentially prosocially for socially inferior individuals. This intriguing possibility should be tested in future by using various combinations of dominant and subordinate recipients.

Experiment 3

In Experiment 3, we asked whether blocking visual contact between subjects would influence the operators' food container choice. The aim of this manipulation was to eliminate effects of behavioral cues (e.g. begging gestures) by the recipients, as these might have influenced the operators' behavior in Experiments 1 and 2.

Method

Subjects

The subjects and their roles were the same as in Experiments 1 and 2. Kiki was pregnant during Experiment 3 and gave birth shortly after the experiment.

Apparatus

Figure 5

The same apparatus as in Experiments 1 and 2 was used. An opaque screen measuring 80 cm (W) x 50 cm (H) was introduced as a means of blocking visual contact between the operator and the recipient (Figure 1b).

Procedure

We followed the procedure used in Experiment 2, except for the introduction of the opaque screen between the recipient's cage and the food containers. The screen was set 4.5cm from the floor level of the cage, so that the operator was able to see only the

recipient's hand reach for the food delivered by the operator's choice. The operator could not make eye contact with the recipient or see any begging or pointing (extending arms toward the food) by the latter. Likewise the recipient was unable to see the food in the containers or the operator. In this situation, recipients showed almost no begging behaviors.

At the start of the test sessions the operator and recipient were allowed to see each other before the opaque screen was put in place. At the start of control sessions the operator saw that there was no recipient present. Once in position, the opaque screen remained there throughout the sessions.

Results

Figures 5 (a, b)

Figure 5 shows the total number of the operator choices for the high-value food container in the dominant recipient condition (Figure 5a) and in the subordinate recipient condition (Figure 5b). As in Experiments 1 and 2, we analyzed these data using the GLMM separately for the dominant and the subordinate recipients. In the dominant recipient condition, the main effect of the presence or absence of the recipient was significant ($F_{1, 57} = 4.466$, $p = 0.039$). No other main effects or interactions were significant. In contrast, in the subordinate recipient condition, no main effects or interactions reached significance.

The individual data of the total number of operator choices for the high-value food container is presented in Table S3 in Electronic Supplementary Material.

Discussion

In Experiment 3, we asked whether blocking visual contact between subjects would influence the operators' food container choice. Blocking visual contact between the operator and the recipient led to a general shift in the operators' choice toward providing low-value food for the recipients. Now the operators gave the low-value food more often when the dominant recipient was present than when he was absent. On the other hand, they behaved randomly with regard to the subordinate recipient and whether or not she was present. This shift may be due to the lack of begging behavior by the recipients, which was often observed in Experiments 1 and 2. These results might suggest that capuchin monkeys do not show other-regarding preference in the absence of their conspecifics' begging behaviors and/or visibility of their choices of food for the partners. But, as seen in Table 2, although operators received less begging by the subordinate recipient than by the dominant recipient in Experiments 1 and 2 they chose the high-value food container more frequently for the subordinate recipient. Therefore, we do not think that such simplistic visual cues alone facilitated the operators' prosocial food choice. Also, it is possible that the operators showed inequity aversion to the recipients more easily when they were not seen than when they were seen by the recipients.

Of particular interest, one of the operators, Pigmon, dramatically changed his behavior toward the dominant monkey in Experiment 3. In Experiments 1 and 2, his choice of the containers appeared random regardless of the presence of the recipient or the latter's dominance rank. However, in Experiment 3 in which there was no visual contact between the subjects, Pigmon started to choose the low-value food container in

505 the presence of the dominant recipient significantly more often than when there was no
506 recipient. His ‘spiteful’ food choices for the dominant recipient in Experiment 3 suggest
507 the possibility that capuchin monkeys may show inequity aversion to others when visual
508 contact between them is blocked.
509
510 General discussion
511 We investigated whether capuchin monkeys are sensitive to rewards received
512 by conspecifics. The operator monkeys chose one of two containers which provided
513 high- or low-value food for recipient monkeys. In Experiment 1, the operators showed
514 other-regarding preference and prosocial food choice by providing high-value food for a
515 socially subordinate recipient. In contrast, they appeared indifferent to the presence of a
516 dominant recipient. In Experiment 2, we used food items that were extremely prized or
517 disliked by all the monkeys. The operators showed virtually the same choice pattern as
518 in Experiment 1. However, in Experiment 3, when visual contact between operator and
519 recipient was blocked by an opaque screen, operators switched to giving the low-value
520 food to the recipients, particularly to the dominant. The satisfaction level with the food
521 reward influenced the operators’ food choices to others in no experiments. These results
522 suggest that capuchin monkeys are sensitive to others’ food rewards and that they
523 change their food choice strategies depending on the social rank of the recipient. This is
524 consistent with the finding that capuchin monkeys choose partners with whom to
525 spontaneously share food (de Waal 1996).
526 The ‘greed hypothesis’ and social facilitation arising from the presence of the
527 recipient fail to account for the operators’ differential container choices. First, as noted
528 earlier, an account based on the greed hypothesis presumes that operators did not

understand the structure and functioning of the food containers and that they mistakenly expected to be able to obtain the food on the recipient's side. If this had been the case, they should have chosen the high-value food container more often than the low-value food container regardless of the presence and identity of the recipient. Moreover, if they had not understood how the food containers worked, they should have changed their choice across sessions; however, within-experiment change did not occur. The abrupt changes in behavior when visual contact between operator and recipient was blocked also contradict this view. We are confident that they understood the structure and functioning of the food containers. Second, if the presence of the recipient simply got the operators' attention and the operators chose the food container nearest to the recipient, the high-value container should have been chosen preferentially regardless of presence or rank of the recipient. However, the operators clearly changed their choice depending upon the recipient. Therefore, we do not think that simple social facilitation can account for the operators' choices.

The monkeys reacted differentially depending upon the two recipients' dominance ranks. We suspect that social rank may be an important factor influencing food-sharing in this species. Primates are highly sensitive to the social hierarchy and adjust their behavior accordingly in competitive situations. For instance, chimpanzees change their strategies to obtain food depending upon their social rank relative to their competitor's in experimental situations (Hare et al. 2000). However, the present results do not necessarily imply that capuchins share food with the social rank of the partner in mind; we used only one dominant and one subordinate monkey as the recipient. Individual relationships between operator and recipient may have played a role. This should be tested using various combinations of operators and recipients.

553 The prosocial choice by the operators for the subordinate recipient might not
554 seem advantageous; in fact, "flattery" into the dominant individual might seem to be a
555 more functional strategy. However, capuchin monkeys are known to donate food to
556 conspecifics (de Waal 1996); this has also been observed in our capuchin colony,
557 involving unrelated individuals (Hattori, unpublished video recording). Other species
558 known to actively give food to unrelated individuals are chimpanzees (de Waal 1996;
559 see Bethell et al. 2000; Nissen and Crawford 1932) and, according to recent work,
560 common marmosets (*Callithrix jacchus*) (Burkart et al. 2007), who also tolerate others
561 taking food from their mouth (Kasper et al. 2008). Thus, Burkart et al. stated that
562 other-regarding preferences are not unique to humans and may evolve without
563 sophisticated socio-cognitive abilities such as theory of mind. Additionally, some
564 researchers suggest that other-regarding preferences might be found in species that rely
565 on cooperative strategies, such as cooperative breeding (Clutton-Brock 2002; Silk et al.
566 2005). Capuchin monkeys are not cooperative breeders, unlike common marmosets and
567 humans. However, infant capuchins are sometimes nursed by females that are not their
568 biological mothers. This phenomenon, called "allonursing" is a genus-typical
569 phenomenon. Tufted capuchin monkeys relatively frequently show allonursing in the
570 wild (Baldovino and Di Bitetti 2008) and captivity (Fragaszy et al. 2004). Baldovino
571 and Di Bitetti (2008) suggests that allonursing in tufted capuchin monkeys has a social
572 function and it does not mainly aim at providing milk to infants. Most recently,
573 Lakshminarayanan and Santos (2008) reported that capuchin monkeys are sensitive to
574 others' welfare in a similar experimental food-sharing situation. These facts support our
575 results that capuchin monkeys have other-regarding preferences and suggest that they
576 may in cases give high-value food to the subordinate recipient, but not to the dominant

individual, more often than when there is no recipient at all.

In Experiment 3, blocking visual contact between the subjects resulted in the operators generally shifting toward giving the low-value food to the recipients. This was particularly marked for the dominant recipient. This might suggest that capuchin monkeys control their food choice in the visible presence of the recipient. In addition, begging by recipients may play a role in controlling the behavior of the operator. Stevens (2004) reported that begging increased the frequency of food sharing in chimpanzees and squirrel monkeys (*Saimiri boliviensis*). Capuchin monkeys have been shown to recognize even subtle attentional states of humans suggested by open or closed eyes (Hattori et al. 2007) and to change their behavior as a function of the state of human eyes in food requesting tasks (Hattori et al. in press). Thus it seems likely that they can adjust their behavior not only in response to direct begging but to subtle changes in behavior of a potential recipient. Most recently, de Waal et al. (2008) found that capuchin monkeys behave prosocially to others but their choices become strikingly selfish in a blocked-view condition. This study supports our data that capuchin monkeys do not show other-regarding preference in the absence of their conspecifics' begging behaviors and/or visibility of their choices of food for the partners when the visual contact between monkeys are blocked.

In contrast to the present findings in a New World monkey species, chimpanzees have been repeatedly shown to be indifferent to others' food rewards (Jensen et al. 2006; Jensen et al. 2007a; Jensen et al. 2007b; Silk et al. 2005). However, all of those results were obtained in situations where the subject chimpanzees were seen by their partners. In the absence of altruism, in such situations behaving indifferently to the partner may be the best solution for the subjects to avoid later punishment by the

partner. Additionally, they have been shown to recognize others' perspectives in competitive situations (Hare et al. 2000) and to recognize attention in humans signalled by the eyes (Hostetter et al. 2007). Therefore, it is premature to conclude that chimpanzees are truly indifferent to the others' reward before they are tested in situations where they are not seen by their partners. Moreover, Warneken and Tomasello (2006) demonstrated that chimpanzees show instrumental helping (toward goals) for a human experimenter even if they can't receive any benefit for helping. Warneken et al. (2007) showed that chimpanzees have the capacity to use a newly acquired skill to help a conspecific as well and they help him/her spontaneously and repeatedly, even in a novel situation when no reward is expected and no previous rewarding could have trained them to act accordingly. Consequently, it is clear that chimpanzees are sensitive to others in some situations.

Finally, we found that capuchin monkeys behaved "spitefully" toward the dominant recipient when they were visually blocked from him. Although this behavior might suggest a form of inequity aversion, a more sophisticated form of inequity aversion is the one caused by a mismatch in the cost/benefit ratios between self and others. In the present study the cost was not manipulated, so we can not conclude that monkeys have inequity aversion. van Wolkenten et al. (2007) showed that capuchin monkeys are also sensitive to their own effort and responded to inequity by modifying the subjects' effort to obtain food. However, those authors did not manipulate the partners' effort; the partners always received food without any effort. Therefore, they did not show that the subject monkeys were sensitive to their partners' effort. Thus, it is still an open question whether capuchins are capable of recognizing others' effort and comparing the cost/benefit relationship between self and others. Nonetheless, our

findings that capuchin monkeys show other-regarding preferences and that they change their food sharing flexibly is a new contribution to the field.

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Table Captions

Table 1 The test sequence of each experiment. Each cell shows the dominance of the recipient/food value for the operator. These experimental parameters were combined and conducted in a counterbalanced order across the operators.

Table 2 The percentage of the recipient's begging behaviors. There were 4 kinds of begging behaviors; 1) waiting on the side of the high-value food container, 2) extending arms toward the high-value food container [pointing gesture], 3) touching the high-value food container, 4) pounding the front panel of the cage.

Tables

	Session			
Operator	1~10	11~20	21~30	31~40
Pigmon	Subordinate/Middle	Dominant/Middle	Subordinate/High	Dominant/High
Zilla	Dominant/Middle	Subordinate/Middle	Dominant/High	Subordinate/High
Zinnia	Dominant/High	Subordinate/High	Dominant/Middle	Subordinate/Middle
Kiki	Subordinate/High	Dominant/High	Subordinate/Middle	Dominant/Middle

Table 1

Exp.1

Heiji						Theta					
Middle						Middle					
behavior	did not beg	waited	pointed	touched	pounded	behavior	did not beg	waited	pointed	touched	pounded
operator						operator					
Pigmon	20	26	30	10	14	Pigmon	80	6	6	8	0
Zilla	8	32	32	12	16	Zilla	96	4	0	0	0
Zinnia	50	18	6	4	22	Zinnia	96	0	4	0	0
Kiki	12	58	8	10	12	Kiki	100	0	0	0	0
High						High					
behavior	did not beg	waited	pointed	touched	pounded	behavior	did not beg	waited	pointed	touched	pounded
operator						operator					
Pigmon	24	46	6	8	16	Pigmon	100	0	0	0	0
Zilla	30	40	16	0	14	Zilla	98	0	0	2	0
Zinnia	36	18	10	22	14	Zinnia	90	10	0	0	0
Kiki	24	32	6	2	36	Kiki	92	2	0	6	0

Exp.2

Heiji						Theta					
Middle						Middle					
behavior	did not beg	waited	pointed	touched	pounded	behavior	did not beg	waited	pointed	touched	pounded
operator						operator					
Pigmon	0	0	8	22	70	Pigmon	44	2	48	6	0
Zilla	2	8	20	6	64	Zilla	24	20	50	6	0
Zinnia	14	6	40	6	34	Zinnia	8	2	84	6	0
Kiki	0	12	54	20	14	Kiki	30	14	52	4	0
High						High					
behavior	did not beg	waited	pointed	touched	pounded	behavior	did not beg	waited	pointed	touched	pounded
operator						operator					
Pigmon	0	12	48	8	32	Pigmon	32	18	50	0	0
Zilla	4	20	22	6	48	Zilla	2	2	78	18	0
Zinnia	8	22	2	2	66	Zinnia	92	2	4	2	0
Kiki	6	14	8	4	68	Kiki	78	2	14	6	0

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829 Table 2

Figure Captions

Figure 1 The experimental setup in Experiments 1, 2 (a) and 3 (b).

Figure 2 The placement of food for the operator and the recipient in each condition in all experiments. “A” denotes the high-value food, “B” the ordinary food and “C” the low-value food.

Figure 3 The total number of operator choices for the high-value food container in the dominant recipient condition (a) and in the subordinate recipient condition (b) in Experiment 1. The x axis shows the experimental condition and the y axis shows the total number of choices. The left pair of bars in each figure is for the middle-value food condition and the right pair of bars is for the high-value food condition. Symbols denote individuals. Each bar and each symbol is based on 50 trials.

Figure 4 The total number of operator choices for the high-value food container in the dominant recipient condition (a) and in the subordinate recipient condition (b) in Experiment 2. The x axis shows the experimental condition and the y axis shows the total number of choices. The left pair of bars in each figure is for the middle-value food condition and the right pair of bars is for the high-value food condition. Symbols denote individuals. Each bar and each symbol is based on 50 trials.

Figure 5 The total number of operator choices for the high-value food container in the

dominant recipient condition (a) and in the subordinate recipient condition (b) in Experiment 3. The x axis shows the experimental condition and the y axis shows the total number of choices. The left pair of bars in each figure is for the middle-value food condition and the right pair of bars is for the high-value food condition. Symbols denote individuals. Each bar and each symbol is based on 50 trials.

878 Figures

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880 Figure 1a

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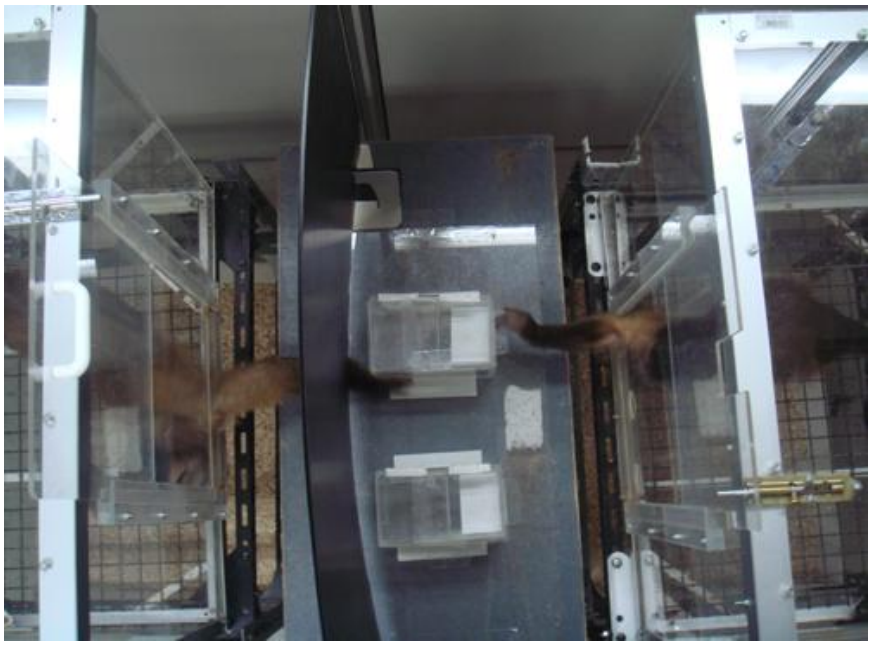


Figure 1b

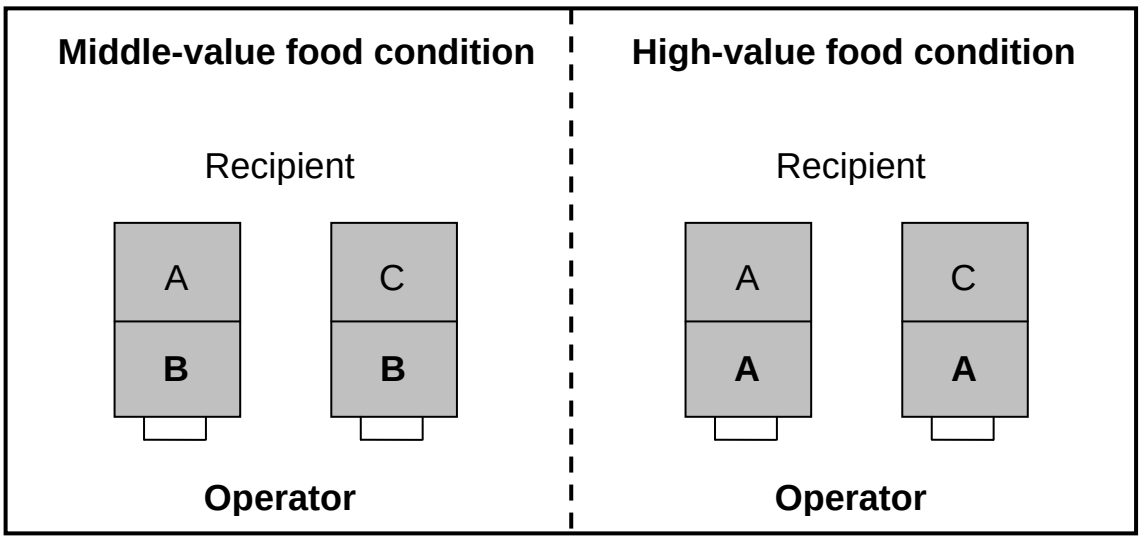

Middle-value food condition
Recipient
A
B
C
B
Operator
High-value food condition
Recipient
A
A
C
A
Operator

Figure 2

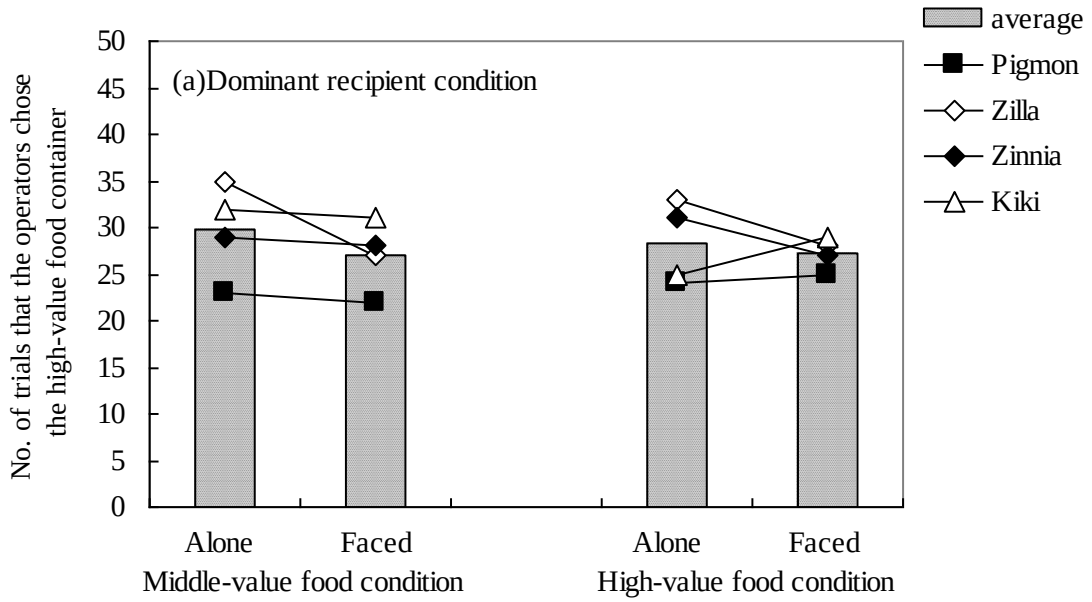

(a)Dominant recipient condition
No. of trials that the operators chose the high-value food container
50
45
40
35
30
25
20
15
10
5
0
Alone
Faced
Alone
Faced
Middle-value food condition
High-value food condition
average
Pigmon
Zilla
Zinnia
Kiki

Figure 3a

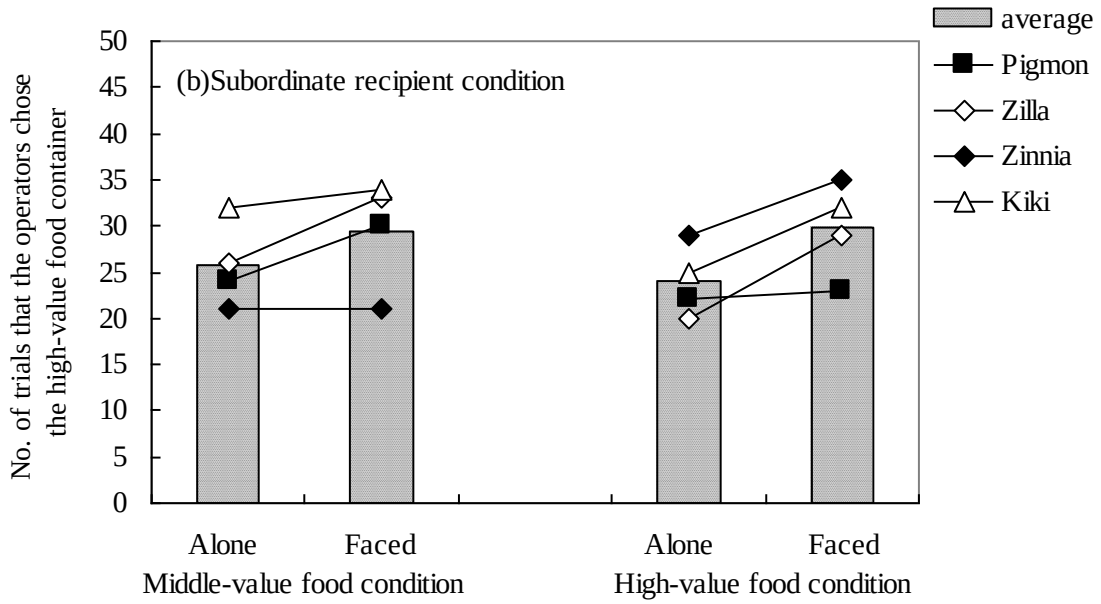

(b)Subordinate recipient condition
No. of trials that the operators chose the high-value food container
50
45
40
35
30
25
20
15
10
5
0
Alone
Faced
Alone
Faced
Middle-value food condition
High-value food condition
average
Pigmon
Zilla
Zinnia
Kiki

Figure 3b

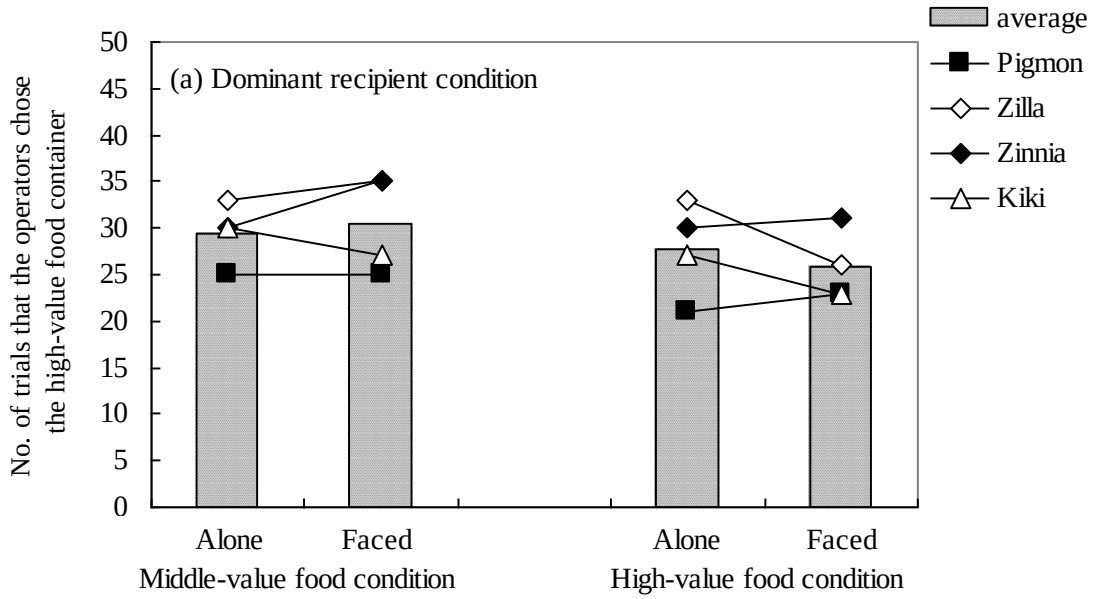

(a) Dominant recipient condition
No. of trials that the operators chose the high-value food container
50
45
40
35
30
25
20
15
10
5
0
Alone
Faced
Alone
Faced
Middle-value food condition
High-value food condition
average
Pigmon
Zilla
Zinnia
Kiki

Figure 4a

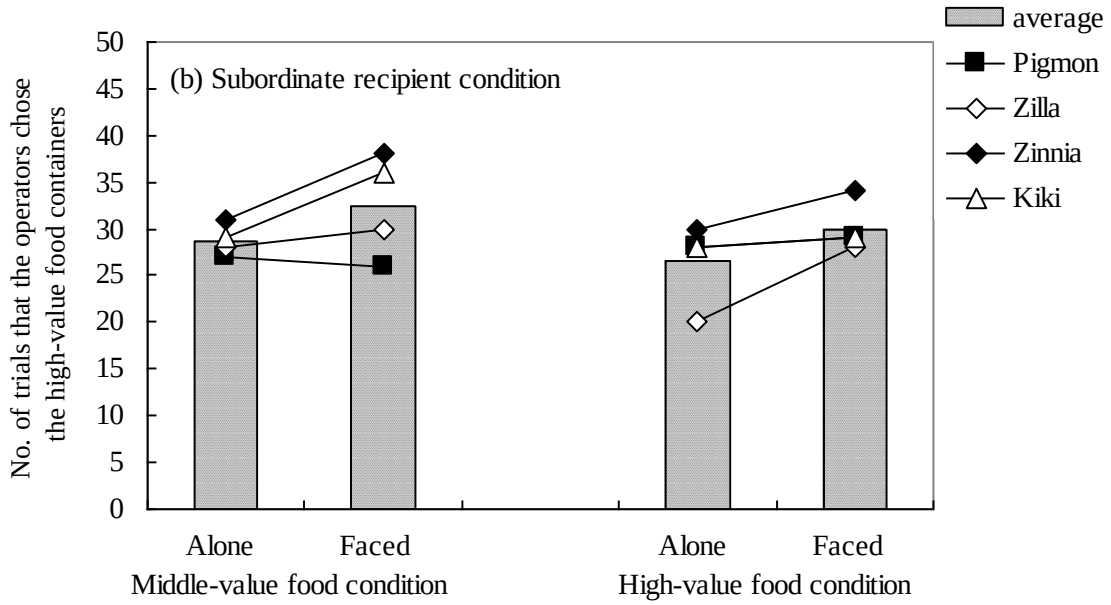

(b) Subordinate recipient condition
No. of trials that the operators chose the high-value food containers
50
45
40
35
30
25
20
15
10
5
0
Alone
Faced
Alone
Faced
Middle-value food condition
High-value food condition
average
Pigmon
Zilla
Zinnia
Kiki

Figure 4b

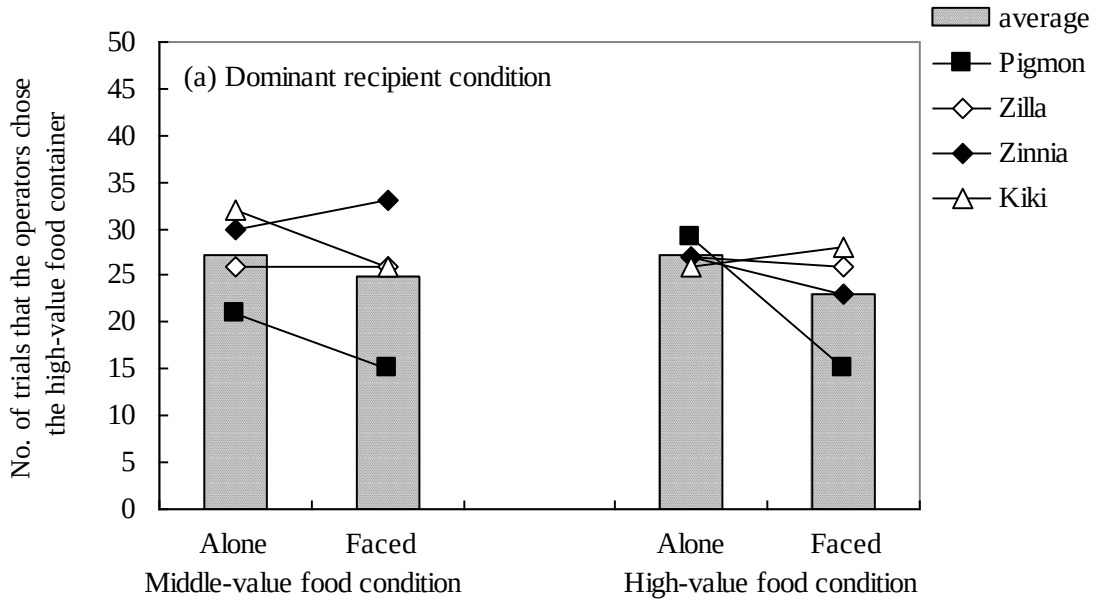
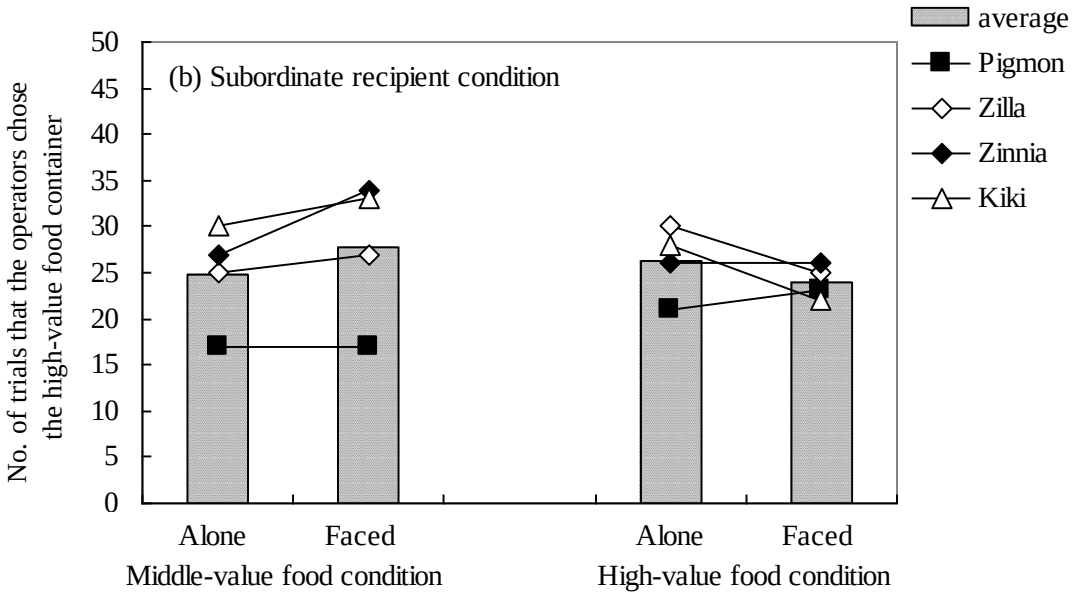

(a) Dominant recipient condition
No. of trials that the operators chose the high-value food container
50
45
40
35
30
25
20
15
10
5
0
Alone
Faced
Alone
Faced
Middle-value food condition
High-value food condition
average
Pigmon
Zilla
Zinnia
Kiki

Figure 5a



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998 Figure 5b

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