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1 Capuchin monkeys (*Cebus apella*) are sensitive to others' reward:

2 An experimental analysis of food-choice for conspecifics.

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23

24

Abstract

25

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

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

48

## Introduction

49

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

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

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

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

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

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

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

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

118 However, Visalberghi and Anderson (2008) argued that the chimpanzee  
119 proposers should have no motivation to play fairly if the responder chimpanzees  
120 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 phylogenically 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

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

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

188

189 Apparatus

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191

Figure 1

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

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

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

216

217 Procedure

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219

Figure 2 and Table 1

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

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

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

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

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

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

265 Three experimental parameters were of interest: (i) the presence or absence of  
266 the recipient, (ii) the social rank of the recipient and (iii) the food value for the operator.  
267 Regarding the first parameter, in the alone condition (the recipient-absent condition),  
268 food was delivered in front of the recipient's cage in the same way as in the faced  
269 condition (the recipient-present condition) and it was removed by the experimenter after  
270 10 s. For the second parameter, the recipient was either the dominant monkey (Heiji) or  
271 the subordinate monkey (Theta). For the third parameter, in the middle-value food  
272 condition, the operator obtained a piece of middle-value food regardless of container  
273 that was chosen. In the high-value food condition, the operator obtained a piece of  
274 high-value food regardless of container choice. In both conditions, the recipient-side  
275 food was either high- or low-value food (see Figure 2). Left-right placement of foods on  
276 the recipient's side was counterbalanced.

277 Each test session consisted of 10 trials. Each operator received 20 faced  
278 (recipient-present) sessions and 20 alone (recipient-absent) sessions, in total 40 sessions.  
279 These two types of sessions were run every other day, one session per day. The  
280 recipients participated in two sessions every other day. The dominant and subordinate  
281 recipients were alternated every 10 sessions. The placement of food was changed after  
282 20 sessions. Table 1 shows a summary of the experimental design.

283

#### 284 Analysis

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

289 presence/absence of the recipient, food value for the operator (high- vs. middle-value)  
290 and session (5 pairs) as factors, using generalized linear mixed models (GLMM; Schall  
291 1991) implemented using the MIXED procedure in SPSS version 12.0, for the dominant  
292 and subordinate recipient. We treated the three factors as fixed and the operator (4  
293 individuals) as a random factor. The generalized linear mixed models allow both fixed  
294 and random terms to be fitted, thus taking into account repeated sampling.

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

300

## 301 Results

302 -----

303 Figures 3 (a, b)

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305 Figure 3 shows the total number of operator choices for the high-value food  
306 container in the dominant recipient condition (Figure 3a) and the subordinate recipient  
307 condition (Figure 3b). In the dominant recipient condition, no main effect or interaction  
308 was significant, although two operators, Zilla and Zinnia, showed a consistent tendency  
309 to choose the low-value container. On the other hand, in the subordinate recipient  
310 condition, the main effects of the presence or absence of the recipient ( $F_{1,57} = 8.251, p =$   
311  $0.006$ ) was significant. No other main effects or interactions were significant.

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

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

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

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

322

323

## Discussion

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

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

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

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

359

360

## Experiment 2

361

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

370

## 371 Method

### 372 Subjects and apparatus

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

374

### 375 Procedure

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

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

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384

## Results

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Figures 4 (a, b)

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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.

396

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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.

400

401

402

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).

403

404

405

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.

406

## Discussion

407

408

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

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

432

433 Experiment 3

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

439

440 Method

441 Subjects

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

444

445 Apparatus

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Figure 5

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

452

453 Procedure

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

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

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

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## Results

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Figures 5 (a, b)

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

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

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## Discussion

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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.

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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

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

543         The monkeys reacted differentially depending upon the two recipients'  
544 dominance ranks. We suspect that social rank may be an important factor influencing  
545 food-sharing in this species. Primates are highly sensitive to the social hierarchy and  
546 adjust their behavior accordingly in competitive situations. For instance, chimpanzees  
547 change their strategies to obtain food depending upon their social rank relative to their  
548 competitor's in experimental situations (Hare et al. 2000). However, the present results  
549 do not necessarily imply that capuchins share food with the social rank of the partner in  
550 mind; we used only one dominant and one subordinate monkey as the recipient.  
551 Individual relationships between operator and recipient may have played a role. This  
552 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

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

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

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

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

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

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

627

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Table Captions

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

789

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

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### Tables

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Operator	Session			
	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

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Table 1

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**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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Table 2

Figure Captions

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

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

837

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

844

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

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852

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

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

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Figures



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Figure 1a

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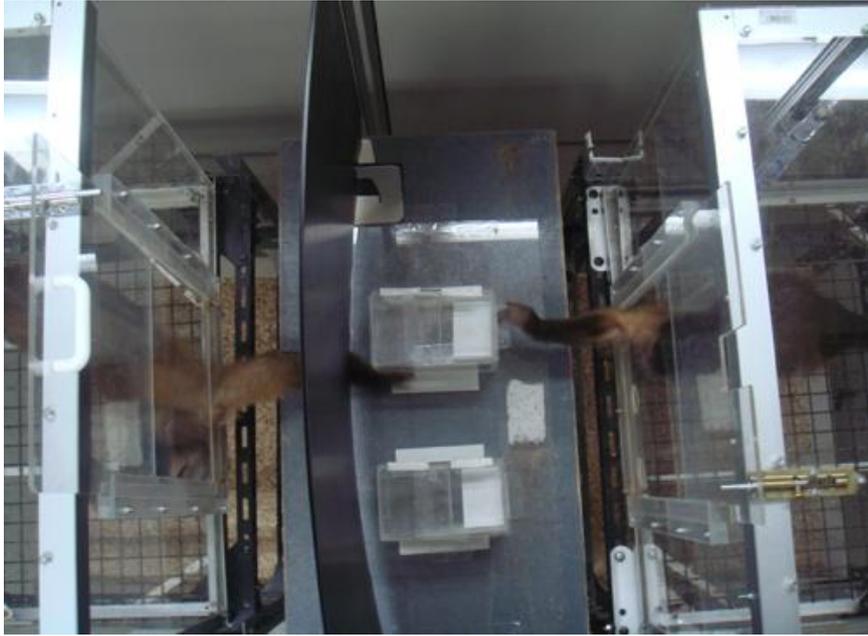
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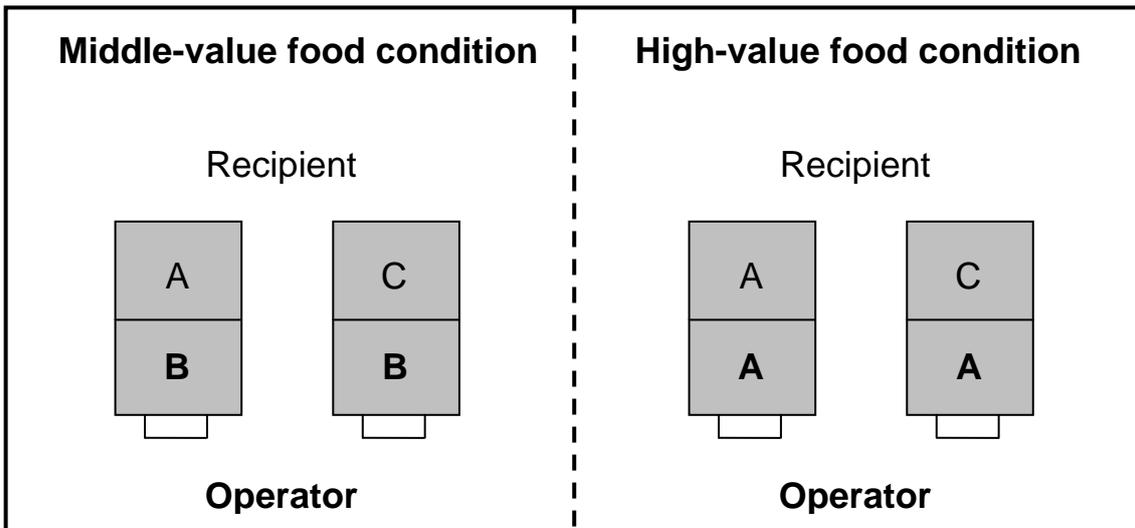
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Figure 1b



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Figure 2

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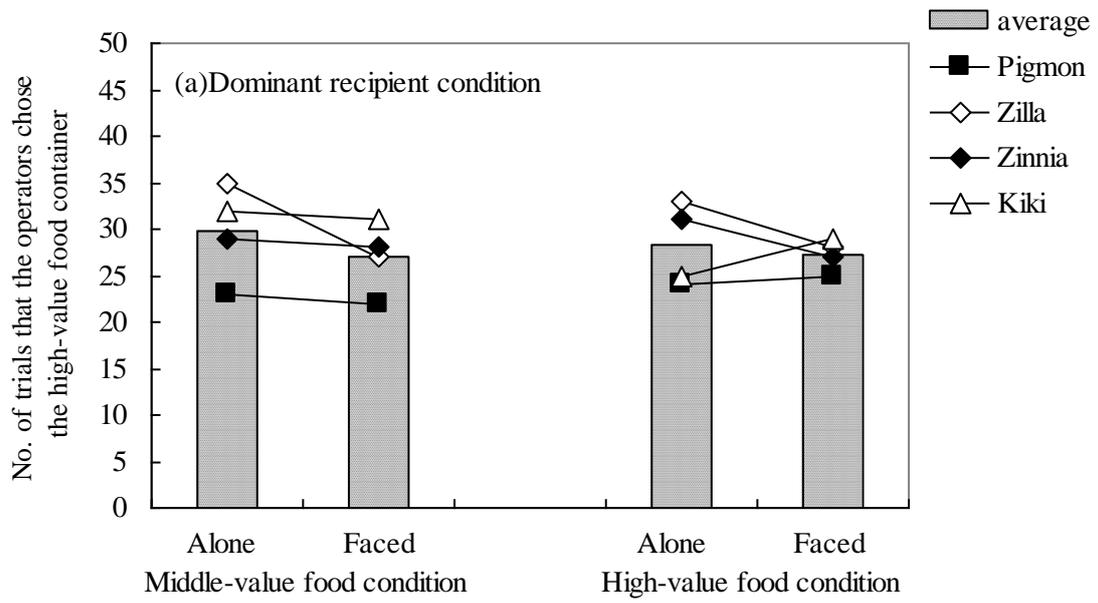
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Figure 3a

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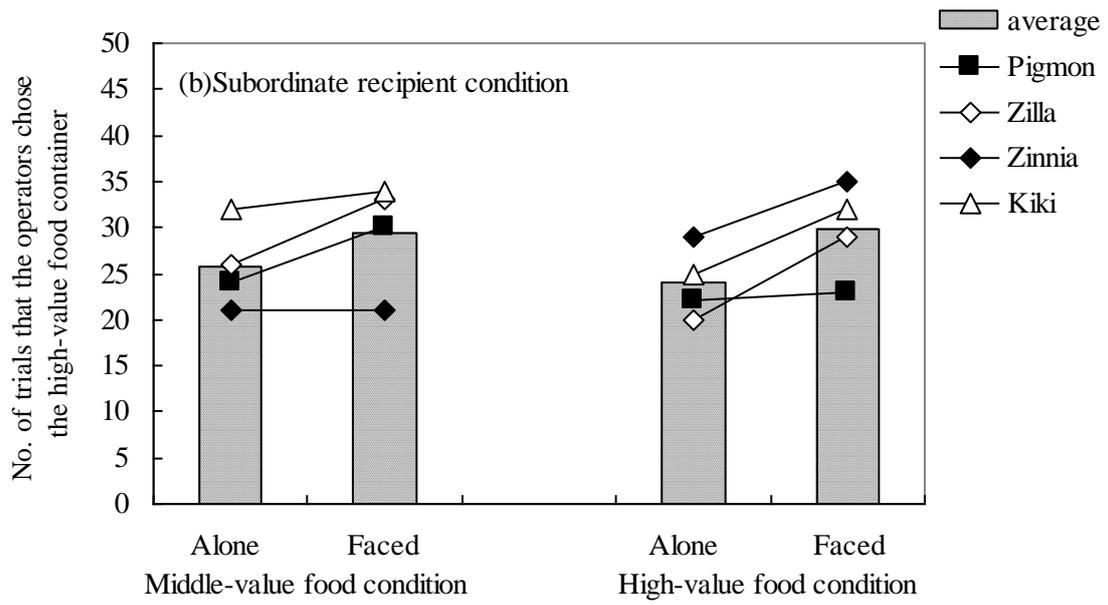


Figure 3b

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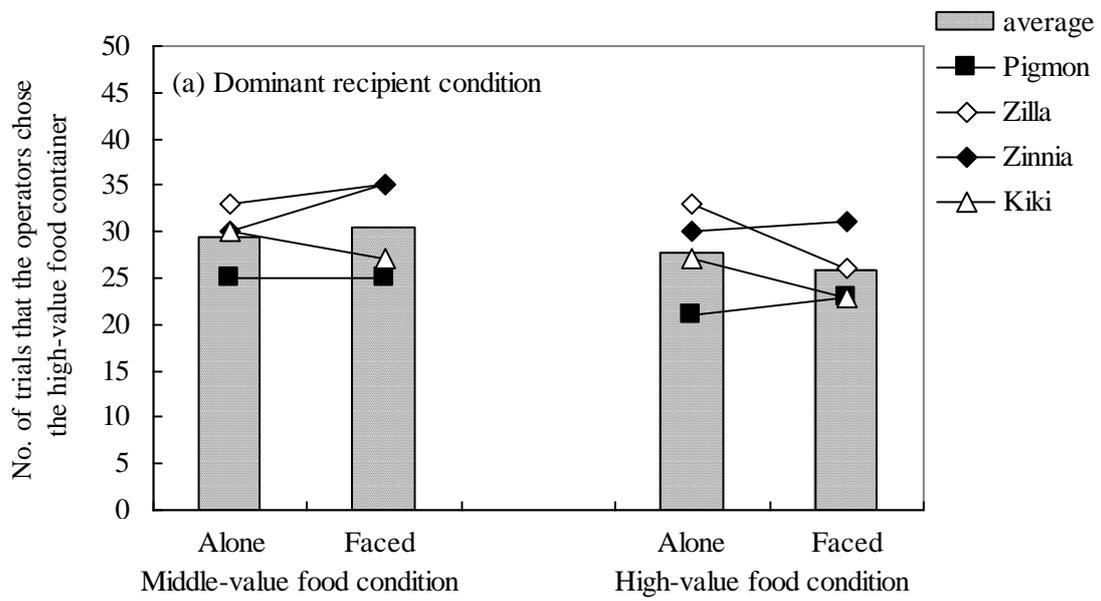
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Figure 4a

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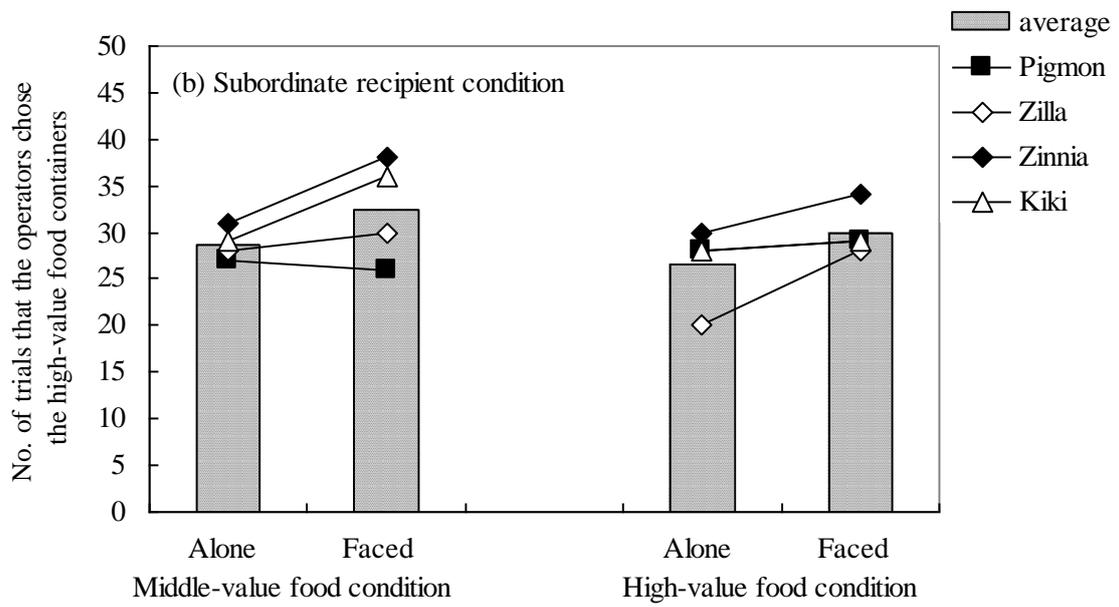
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Figure 4b

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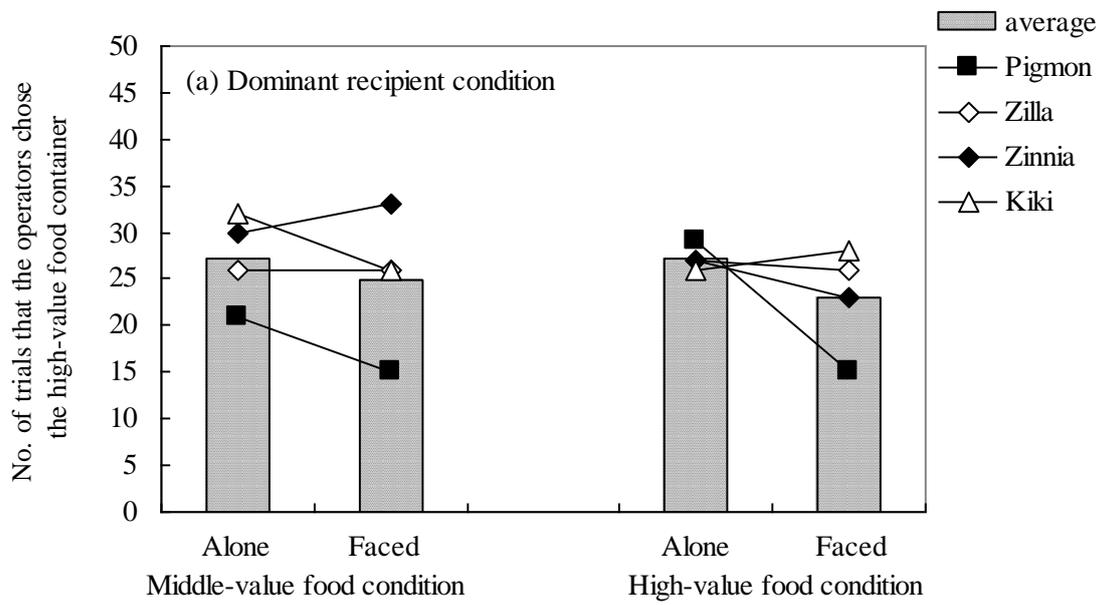


Figure 5a

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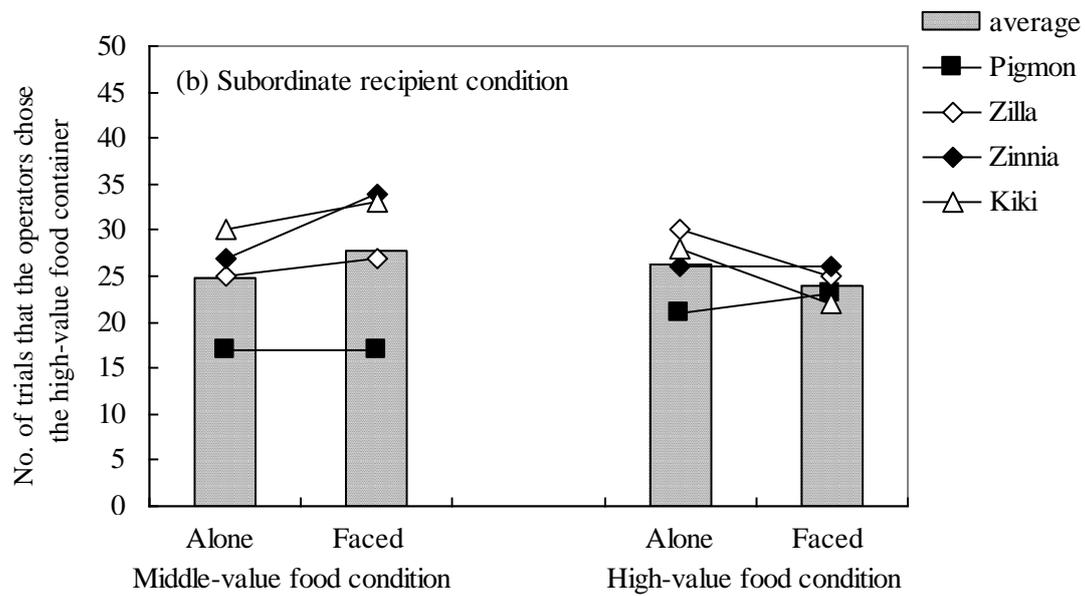
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Figure 5b

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