Title	I acknowledge your help: capuchin monkeys' sensitivity to others' labor.
Author(s)	Takimoto, Ayaka; Fujita, Kazuo
Citation	Animal cognition (2011), 14(5): 715-725
Issue Date	2011-09
URL	http://hdl.handle.net/2433/148016
Right	The final publication is available at www.springerlink.com
Type	Journal Article
Textversion	author

I acknowledge your help: capuchin monkeys' sensitivity to others' labor

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Our society is sustained by wide-ranging cooperation. If individuals are sensitive to others' gains and losses as well as the amount of labor, they can ensure future beneficial cooperative interaction. However, it is still an open question whether nonhuman primates are sensitive to others' labor. We asked this question in tufted capuchin monkeys in an experimental food-sharing situation by comparing conditions with labor by two participants equalized (Equal labor condition) or unequalized (Unequal labor condition). The operator monkey pulled the drawer of one of two food containers placed between two monkeys, each containing a food for him/herself and another for the recipient monkey. The recipient 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. In Unequal labor condition, the operator first had to pull the handle of the board to which the containers were glued, and then pull the drawer of one of the containers, while the recipient received food with no labor. In Equal labor condition, the recipient had to pull the handle of the board so that the operator could operate a container. Results showed that operators chose the high-value food container for recipients more often than when the recipient was absent only in Equal labor condition. This suggests that capuchin monkeys are sensitive to others' labor and actively give food to a partner who has helped them to complete a task. (237 words)

Introduction

Human social organization depends on cooperation with others (Boyd and Richerson 2005). Cooperation yields greater benefits than those that can be achieved by individual effort alone. Human cooperation appears to be maintained in part by prosocial orientations and a concern about inequity.

Cooperation is in fact widespread in nonhumans (see Dugatkin 1997). In particular, several species of nonhuman primates have been demonstrated to show elaborate cooperative behaviors in the laboratory [e.g., chimpanzees (*Pan troglodytes*): Crawford 1937; Hirata and Fuwa 2007; Melis et al. 2006ab, capuchin monkeys (*Cebus apella*): Brosnan et al. 2006; de Waal and Berger 2000; Hattori et al. 2005, cotton-top tamarins (*Saguinus oedipus*): Cronin et al. 2005, 2008]. This may suggest that human-like cooperation has traceable evolutionary roots.

Individuals are able to ensure future beneficial cooperative interaction, on the ground that they are not only sensitive to gains and losses but also able to compare their own effort and reward with others', that is, they have inequity aversion (IA). IA 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. The monkeys willingly exchanged tokens for a piece of cucumber at first, but they started to refuse the exchange or to accept the food after witnessing their partner receiving better food (a grape) for the same token. Such refusals increased when the partner received a grape without exchanging the token. Brosnan et al. (2005) and Brosnan et al. (2010b) replicated these results in chimpanzees (but see Bräuer et al. 2009), although they did not appear to respond to the discrepancy between their own

effort and others'.

In this regard, however, several researchers have suggested that simpler cognitive mechanisms might explain the results of these studies (see Bräuer et al. 2006; Dubreuil et al. 2006; Henrich 2004; Silberberg et al. 2009; Roma et al. 2006; Wynne 2004). For example, Roma et al. (2006) argued that the apparent aversion to inequity shown by Brosnan & de Waal (2003) might be explained by frustration due to an individual's past experience with greater rewards (but see Brosnan & de Waal 2006). On the other hand, Dindo and de Waal (2007) reported that no IA effect occurred when they gave free rewards to the monkeys as Bräuer et al. (2006), Dubreuil et al. (2006) and Roma et al. (2006) tasks, in which both the subject and the partner just determined whether they would accept a reward offered by the human experimenter without any labor. That is, they suggest that some labor is necessary to show IA. In addition, van Wolkenten et al. (2007) countered many of the alternative hypotheses, such as the greed and frustration accounts, by using a task requiring labor in both the subject and the partner in which IA was confirmed. Recently, however, Bräuer et al. (2009) failed to reproduce the findings of Brosnan et al. (2005) in great apes using the same procedure. Thus, the extent of IA in cooperative nonhuman primates remains open to debate.

Therefore, first, it must be investigated whether cooperative nonhuman primates have essential components to have IA, that is, sensitivity to others' reward and their labor. Most of recent relevant studies with various primates have focused only on sensitivity to others' rewards, that is, other-regarding preferences, which underlie prosociality in humans (see de Waal and Suchak 2010). Several studies explicitly designed to look for prosocial preferences in chimpanzees found no evidence that they behave in ways that benefit their partners, even when it costs them nothing; that is, they

were indifferent to others' rewards (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008, Yamamoto & Tanaka 2010). On the other hand, capuchin monkeys have showed sensitivity to others' rewards and other-regarding preferences in experimental food-sharing tasks (Lakshminarayanan & Santos 2008, Takimoto et al. 2010), a token exchange task (de Waal et al. 2008) and a bar-pull task (Brosnan et al. 2010a). Among other New World monkeys, common marmosets spontaneously provide food to nonreciprocating and genetically unrelated individuals (Burkart et al. 2007). Moreover, cottontop tamarins show sensitivity to others' rewards and a stronger reaction to inequity when they complete a task than when they do not (Neiworth et al. 2009; but see Cronin et al. 2008, 2009; Stevens 2010). It has been proposed that other-regarding preferences might be found in species that rely on cooperative strategies, such as cooperative breeding (Clutton-Brock 2002). Most recently, however, Brosnan et al. (2010b) showed that chimpanzees were more likely to refuse a high-value grape when another chimpanzee got a lower-value carrot than when the other chimpanzee also received a grape. In other words, chimpanzees avoided inequity which was advantageous for them, and showed other-regarding preference. Additionally, Melis et al. (in press) reported that chimpanzees helped their conspecifics obtain even food items, that is, the presence of food did not constrain chimpanzees' tendency to help others. Moreover, Hare & Kwetuenda (2010) reported that bonobos (*Pongo pygmaeus*) preferred to release a partner from an adjacent room and eat together instead of eating all the food alone. Together these studies suggest that sensitivity to others' rewards, in particular other-regarding preferences, is not unique to cooperative breeders but may be seen broadly among cooperating nonhuman primates.

By comparison, there are very few studies on nonhuman primates' sensitivity

121 to others' labor. In de Waal & Berger (2000), pairs of capuchin monkeys were required
122 to combine efforts to pull a tray with food. The capuchins more successfully cooperated
123 when presented with a tray baited for both monkeys than when presented with a tray
124 baited for only one. Moreover, significantly more pieces of food were shared after
125 successful cooperation trials than after solo-effort trials. A greater portion of food
126 transfers after cooperation were of a tolerant nature. However, an increase in proximity
127 between the monkeys could have led to more food sharing as a byproduct, rather than as
128 the intention of the operator. Moreover, it remains unclear whether experience of
129 partners' cooperative labor leading to food would influence possessors' subsequent food
130 sharing. Capuchin monkeys also showed sensitivity to their own effort and responded to
131 inequity by modifying their effort to obtain food (van Walkenten et al. 2007). That is,
132 capuchins increasingly refused a token or food when the effort required to obtain a
133 reward increased. However, it was not clear if the subject monkeys were sensitive to
134 their partners' effort because the partner monkey always received food without any
135 effort. Thus, it is still an open question whether nonhuman primates are capable of
136 recognizing others' effort and of comparing the cost/benefit relationship between self
137 and others.

138 In the present study, we investigated whether capuchin monkeys are sensitive
139 to others' labor and its disparity between the participants (the operator and the recipient).
140 We changed the amount of each participant's labor required to obtain food in an
141 experimentally induced cooperative food-sharing situation. We expected situations that
142 required labor in both participants to facilitate their sensitivity to others' reward and
143 labor. The operators were able to give either high- or low-value food to recipients. The
144 operators received the same high-value food regardless of their choices. Therefore, the

operators' choice of the high-value container for the recipient should indicate intentional giving of the high-value food and allow us to rule out giving as a by-product of the operator obtaining his/her own food. We also investigated whether experience of recipients' cooperative labor leading to food would influence operators' subsequent food choices by setting two Unequal labor conditions and conducting each Unequal labor condition before and after Equal labor condition.

We manipulated the following 3 experimental parameters: the presence of the recipient (Faced or Alone condition), the recipient's social rank (Dominant or Subordinate recipient condition), the subjects' labor (Unequal labor 1, Equal labor or Unequal labor 2 condition). In Unequal labor 1 and 2 conditions, the operator first had to pull the handle of the board on which the two food containers were glued and then pull the drawer of one of the containers, while the recipient obtained food without any labor. In contrast, Equal labor condition was a cooperative food sharing situation in which the recipient first had to pull the handle of the board in order to reposition the containers so that the operator could select one by pulling the drawer. If operators are sensitive to others' labor and can compare it with their own, they should preferentially choose the high-value container in Equal labor condition, but not in Unequal labor 1 and 2 conditions, of Faced, not Alone, conditions. In addition, once operators had experience of recipients having to work in order to receive rewards, the operators may become frustrated if the recipients obtain rewards without any labor (Unequal labor 2 condition). If the sight of the previously helpful partner now free-riding is negative for the operator, he/she should choose the high-value container more frequently in Unequal labor 1 condition than Unequal labor 2 condition.

Tufted capuchin monkeys are phyletically more distant from humans than

chimpanzees are, but they are suitable for such work in view of suggested IA (Brosnan and de Waal 2003; Brosnan et al. 2010a; Fletcher 2008; van Wolkenten et al. 2007) and robust prosociality (Brosnan et al. 2010a; de Waal et al. 2008; Lakchminarayanan and Santos 2008; Takimoto et al. 2010) of this species. Furthermore, capuchins are tolerant to the extent that they actively share high-value food especially with subordinates (Takimoto et al. 2010). This social background creates a baseline level of expectation of equity that makes individuals more likely to react to inequitable situations (Brosnan 2006; de Waal 1996). Anderson (2007) suggested that more tolerant primates are more likely to show cooperation, and capuchin monkeys show some elaborate cooperative behaviors, linked to reciprocity and food sharing, both in the wild and in captivity (see de Waal and Suchak 2010).

Method

Participants

Participants 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 15 years old, Kiki (female) and Theta (female) were 13 years old, Pigmon (male) was 11 years old and Zinnia (male) was 8 years old. All subjects except Zinnia, who was born to Heiji and Zilla in the laboratory, were born and raised in a social group at the Primate Research Institute, Kyoto University. The dominance hierarchy among these monkeys was very stable, confirmed through daily observations and occasional pairwise dominance tests using food competition. Heiji was the alpha male, while Theta was the most subordinate in the group. These two individuals served as recipients. In decreasing order of dominance, the others, who served as operators,

were ranked as follows: Pigmon, Zinnia, Zilla, and Kiki.

All monkeys had experienced a variety of laboratory tests on topics such as operant discrimination (Fujita 2004; Fujita and Giersch 2005), tool use (Fujita et al. 2003; Fujita et al. in press), deception (Fujita et al. 2002), cooperation (Hattori et al. 2005), social knowledge (Anderson et al. 2004; Anderson et al. 2005a,b; Anderson et al. 2008; Anderson et al. 2010; Hattori et al. 2007; Hattori et al. 2010; Kuroshima et al. 2002; Kuroshima et al. 2003; Kuroshima et al. 2008; Morimoto and Fujita in press), 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 and gave birth during the experiment, but she failed to care for the baby and so her baby was hand-raised; Kiki therefore continued to participate in the study.

Apparatus

Figures 1a and 1b

Two experimental cages, 60 cm (W) x 45 cm (D) x 55 cm (H), made of transparent acrylic 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 from each other and 10.5 cm from 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 from 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 were placed 12cm apart on a transparent acrylic board, 58cm(W)x 30cm(D), on the wooden table between the two cages (Figure 1). The containers could slide along two metallic rails 58cm apart on a white plastic board, 58cm (W) x 41cm (D). The containers had a drawer, 9 cm (W) x 8 cm (D) x 3.5 cm (H) at 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 food to the recipient by hitting a dropper board attached behind the drawer. The operator was allowed to pull only one drawer at a time. The recipient had no means of operating the drawer, and hence was a passive recipient of food.

The precise placement of the containers and the handle of the board on which the containers were fixed varied as a function of the labor conditions. For Unequal labor 1 and 2 conditions the containers were set out as shown in Figure 1a. The containers were placed out of reach of the operator, but the handle (W20cm×D0.5cm×H4cm) was either 10 cm or 14cm from the operator, determined by the operator's arm length. Thus the operator could pull the containers to within reach. For Equal labor condition the containers were set out as shown in Figure 1b. Now, the handle was within reach of the recipient (either 12 cm or 14 cm depending on the recipient). Additionally, the containers were moved 22 cm nearer to the operator's box, so that the operator could not pull on a drawer due to inadequate space.

A transparent screen, 50 cm (W) x 28 cm (H), was placed against each cage to prevent the monkeys from handling the containers during inter-trial intervals and the

241 baiting process.

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

245

246 Procedure

247

248 **Food preference test**

249 We conducted a food preference test to determine appropriate food rewards for
250 all participants. Their preference between a piece of peanut and a few leaves of parsley
251 was tested by a two-choice task. All of them showed a clear preference for the peanut
252 over the parsley (12 choices out of the 12 trials). We thus decided to use peanut as a
253 high-value food reward and parsley as a low-value reward in this experiment.

254

255 **Preliminary training**

256 The 4 operator monkeys had been trained to operate the food containers in the
257 previous study (Takimoto et al. 2010). Therefore, they had learned that they were able
258 to obtain food in the drawer of the container by pulling it within 30 seconds. They also
259 had learned that the recipient monkey was able to collect food without any labor by the
260 operator's pulling. Moreover, they had learned that they were able to obtain only their
261 own food, not the food dropped on the recipient's side irrespective of the
262 presence/absence of the recipient (see Takimoto et al. 2010 for details).

263 In the preliminary training for operators before testing, all 4 operators were
264 individually trained to obtain food by completing the sequence of pulling the handle of

the board and operating one of the two food containers. They were trained until they performed these operations within 30 sec at 80% level in five consecutive sessions (1 session = 12 trials). Each operator participated in this training a session per day. This training required between 5 and 11 days.

In the preliminary training for recipients before testing in Equal labor condition, both recipients were individually trained to obtain a chance to receive food by pulling the handle of the board to enable the operator's pulling the drawers, in the absence of the operator. The experimenter pulled the drawer of the food container in place of the operator, which prevented the recipient's experience of the interaction with the particular operator in the training from influencing the test results. The recipients were trained until they started the operation within 30 sec at 80% level in five consecutive sessions (1 session = 12 trials). Each recipient participated in this training a session per day. This training required 7 sessions.

Test

Figure 2

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. The operator chose one of two food containers and pulled the drawer of the container. The operator received the same high-value food whichever container he/she chose, whereas the recipient received either high- or low-value food

289 depending upon the operator's choice. The trial ended when the recipient picked up the
290 food or in 10 sec after the operator's choice. During the inter-trial interval of 30 s, the
291 experimenter removed any leftover food and set the containers up for the next trial.
292 As described earlier, we varied three experimental parameters: (i) presence of
293 the recipient, (ii) social rank of the recipient and (iii) labor of the two individuals (the
294 operator and the recipient). Regarding the first parameter, in Alone condition
295 (recipient-absent), food was delivered in front of the recipient's cage as in Faced
296 condition (recipient-present), but it was removed by the experimenter after 10 s. For the
297 second parameter, the recipient was either the dominant (Heiji) or the subordinate
298 monkey (Theta). For the third parameter, in Unequal labor 1 and 2 conditions, the
299 operator obtained food by completing the sequence of pulling the handle of the support
300 board followed by opening the drawer; thus the operator had to complete 2 actions in
301 order to obtain food, whereas the recipient received food without any labor. In Equal
302 labor condition, first, the recipient pulled the handle of the support board in order to
303 enable the operator to pull the drawer of a container and then the operator pulled one of
304 the two containers. In other words, both operator and recipient contributed one action to
305 obtain food for each. In Alone condition of Equal labor condition, however, the
306 experimenter pulled the handle of the board in place of the recipient.
307 Subjects were tested in the following sequence: first, Unequal labor 1, second,
308 Equal labor, and third, Unequal labor 2 conditions in the ABA design. The reason why
309 we set two Unequal labor conditions and conducted each Unequal condition before and
310 after Equal condition was that we investigated whether the experience of others' labor
311 leading to food in Equal labor condition would influence the operators' subsequent food
312 choices. In all three conditions, the reward in the recipient side was either high- or

low-value food (see Figure 2). Left-right placement of food on the recipient's side was counterbalanced.

Experimental design

Each test session consisted of 10 trials. Each operator received 30 Faced (recipient-present) sessions and 30 Alone (recipient-absent) sessions. These two types of sessions were run alternatingly, one session per day. All operators started with the Alone condition. The recipients participated in two sessions every other day when Faced conditions were tested. The dominant and subordinate recipients were alternated every 10 sessions. The subjects' labor was changed after 20 and 40 sessions. All operators participated in this sequential order: Unequal labor 1, Equal labor and Unequal labor 2 condition.

Analysis

The experimenter recorded the operator's choices of container and any begging behaviors by the recipient on each trial. The records were confirmed from the videotapes later.

First, we examined the average frequency of operator choices for the high-value container in three separate two-way repeated ANOVAs with the presence of the recipient and social rank of the recipient (dominant/subordinate) as factors for the subjects' labor conditions. Additionally, we examined the average difference in frequency of operator choices for the high-value container between the Faced and Alone conditions in a two-way repeated ANOVA with the subjects' labor and the social rank of the recipient as factors.

Second, we measured recipient begging behaviors for the high-value food container, including after operator choices for the low-value food container, as a possible indicator of frustration. Each average ratio of those behaviors was examined in a two-way repeated ANOVA with the social rank of the recipient and labor as factors.

All analyses were conducted using SPSS version 17.0. The Bonferroni correction was applied for post-hoc comparisons.

Results

Figures 3a, 3b, 3c

Figure 3 shows the average number of operator choices for the high-value food container in Unequal labor 1 (Figure 3a), Equal labor (Figure 3b) and Unequal labor 2 conditions (Figure 3c). In Unequal 1 and 2 conditions, no main effect or interaction was significant. However, in Equal labor condition the main effect of presence of the recipient was significant [$F_{1, 3}$=45.485, p=0.007]. No other main effect or interaction was significant. The difference in the average number of operator choices for the high-value food container between Faced and Alone conditions is presented in Figure S1 in Electronic Supplementary Material. This subtracted value is hereafter referred to as the operators' generosity score. The main effect of the labor was significant [$F_{2,6}$=14.211, p=0.005]. Post-hoc comparisons revealed a significant difference only between Equal and Unequal labor 2 conditions [p=0.035]. No other main effects or interactions were significant.

Figure 4

Figure 4 shows the average ratio of recipient begging behaviors for the high-value food container. The main effect of the labor was significant [$F_{2,6}$=35.025, p=0.000]. Post-hoc comparisons revealed significant differences between Unequal labor 1 and Equal labor conditions [p=0.030], and Equal and Unequal labor 2 conditions [p=0.028]. However, there was no difference between Unequal 1 and 2 conditions. No other main effect or interaction was significant.

Figure 5

Figure 5 shows the average ratio of recipient begging behaviors for the high-value food container after operators chose the low-value food container. This ratio is hereafter referred to as the recipients' frustration score. The main effect of the labor was significant [$F_{2,6}$=14.541, p=0.005]. Post-hoc comparisons revealed a significant difference only between Equal and Unequal labor 2 conditions [p=0.010]. Moreover, although the main effect of recipient's social rank was not significant, there was a significant interaction between social rank of recipient and labor [$F_{2,6}$=7.110, p=0.026]. This interaction means that, only in Unequal labor 1 condition, the dominant recipient more frequently begged for the high-value food container after operators chose the low-value food container than the subordinate recipient, though there was no difference between the ratios of both recipients' begging behaviors in the other labor conditions.

Both the operators and the recipients ate the high-value food whenever it was given, whereas the recipients almost always refused to receive the low-value food

regardless of the subjects' labor conditions. The average ratio of recipient receiving the low-value food is presented in Figure S2 (a: Dominant recipient condition / b: Subordinate recipient condition) in Electronic Supplementary Material.

Discussion

In the present study, operator monkeys chose the high-value food container significantly more often when a conspecific recipient was present (Faced condition) than absent (Alone condition) only when the recipients helped them to operate the containers (Equal labor condition), irrespective of the social rank of the recipient. On the other hand, when operators alone had to work for food while recipients received food without any labor (Unequal labor 1 and 2 conditions), operators did not change their food sharing strategies as a function of the presence or social rank of the recipient. Additionally, they chose the high-value container for both recipients significantly more often in Equal labor condition than in Unequal labor 2 condition. These results clearly show that capuchin monkeys are sensitive to others' labor and may change how they distribute rewards depending upon others' contribution to the task. Moreover, operators were more likely to give their partner the low-value food in Unequal labor 2 compared to Unequal labor 1 condition, though not significantly so. Thus, the data imply a weak contrast effect based on whether the partner had to help previously. In other words, the operators may have been frustrated by witnessing recipients receiving food without any labor, after experiencing the same helpful partner.

In de Waal & Berger (2000), food sharing could have been a byproduct of increased proximity between the monkeys, rather than an intention of the operator. This account fails to apply to our study, since the operator monkeys had to make a

409 dichotomous choice, and there was no increased proximity between operator and
410 recipient. The operators in the present study made choices that were at chance level
411 when the partner did not need to help, but actively tried to benefit their partner when
412 he/she did help.

413 Brosnan et al. (2010b) reported that the chimpanzees responded similarly when
414 the partner obtained the same reward as they did for 'free' versus when both individuals
415 had to exchange to receive the reward. This finding is in accord with Fontenot et al.
416 (2007) and van Wolkenten et al. (2007), which showed capuchins' failure to respond to
417 differences in effort only. Such studies in which each individual's task was independent
418 indicate that difference in effort alone is insufficient to evoke a response to inequity. On
419 the other hand, Brosnan et al. (2006) investigated how capuchins would react to
420 inequitable rewards by a joint task, as our study, which required the individuals to pull a
421 bar together in order to receive food. They reported that capuchins' cooperation success
422 depended not on the equity of the reward distribution, but on the equity of the partner's
423 behavior. In other words, equitable capuchin dyads in which the individuals regularly
424 alternated taking the higher-value reward in an unequal distribution were more than
425 twice as successful as less-equitable dyads. Studies in which each individual's task was
426 dependent, as Brosnan et al. (2006) and our study, suggest that perceived effort is more
427 crucial in joint tasks for capuchin monkeys. This suggestion seems consistent with the
428 idea that reciprocity appears crucial for participants to maintain cooperation in food
429 sharing situations. Indeed, capuchin monkeys, like chimpanzees, are capable of
430 contingent reciprocity in an alternating condition (Hattori et al. 2005), though it may be
431 difficult for them to succeed by spontaneous alternation of donor and recipient roles
432 (capuchin monkeys: Pelé et al. 2010; chimpanzees: Yamamoto & Tanaka 2009). Future

studies should ask whether reciprocity facilitates capuchins' prosocial food sharing by exchanging their role in order to test the effect of reciprocity for their prosociality.

One possible explanation for our results in Equal condition is that the recipients waited to manipulate the apparatus until the operator was standing in front of the high-value container. This could have led to the outcome we see, in which high-value rewards are pulled more in the equal labor condition. However, we do not think this explanation applies in our case, as recipients in fact almost always pulled the handle of the support board as soon as the screen was removed. That is, recipients did not work with precise timing. Conceivably, the recipients' begging behaviors might be a form of harassment claiming the operators to share high-value food. Stevens (2004) reported that begging behaviors (harassment) can play a significant role in food sharing in chimpanzees and squirrel monkeys. In our previous study (Takimoto et al. 2010), blocking visual contact between the operator and the recipient resulted in the operators generally shifting toward giving the low-value food to the recipients, so the latter's begging behaviors may have sustained more prosocial food sharing by operators. If this applied to the present study, recipients should have shown more begging behaviors in Equal labor condition than in Unequal labor 1 and 2 conditions; however, the opposite trend was observed in fact. This result suggests that operator choices of the high-value food for recipients were not just a reaction to recipients' begging signals.

In our previous study (Takimoto et al. 2010), the same operator monkeys chose the high-value food container for the subordinate recipient more frequently than when the recipient was absent, even though the recipient received food without any labor. In the present study, however, they did not choose the high-value container for recipients more than when they were alone in Unequal labor conditions. This may be because of a

457 difference in the operators' own labor to obtain food. Previously (Takimoto et al. 2010),
458 operators had only to pull the handle of the drawer of the container to obtain food, that
459 is, only one action was required of them. On the other hand, in Unequal labor conditions
460 of the present study, double actions were required of operators: pulling the handle of the
461 board and pulling the drawer of the selected container. Therefore, in Unequal labor
462 conditions, rather, it was expected the operators should have show inequity aversion by
463 choosing the high-value container significantly less frequently in the presence of the
464 recipient than in his/her absence if capuchin monkeys are sensitive to others' labor.
465 Contrary to this hypothesis, the operators failed to show such a tendency in Unequal
466 labor conditions, though they were slightly below chance in giving high-value food in
467 Unequal labor 2 condition.

468 However, this result does not necessarily mean lack of inequity aversion in
469 capuchin monkeys. Capuchins are not only suggested to have inequity aversion in
470 previous studies (Brosnan & de Waal 2003; Brosnan et al. 2010a; Fletcher 2008;
471 Takimoto et al. 2010; van Wolkenten et al. 2007) but also shown robust other-regarding
472 preferences in experimental tasks involving food-sharing (Lakshminarayanan & Santos
473 2008, Takimoto et al. 2010), token exchange (de Waal et al. 2008) and bar-pulling
474 (Brosnan et al. 2010a). Therefore, it appears difficult for them to maintain perfect equity
475 in every interaction because it is also hard to produce prosocial behavior without some
476 degree of inequity tolerance (Brosnan et al. 2010a). In fact, the evolution of human
477 society and economic growth are often accompanied by inequality (Aghion et al. 1999),
478 leaving open the possibility that prosocial motivations must entail inequity tolerance if
479 they are to result in extensive cooperation.

480 Recipients continued to cooperate by repositioning the food containers, even

though this might not necessarily lead to the high-value food for them in the equal labor condition. This may have been because the operators chose the high-value food container for both recipients in 65-70% of trials, probably enough to maintain the recipients' motivation to continue cooperating, given the species' natural social tolerance. Capuchin monkeys are reported to donate food to conspecifics (de Waal 1996); such active giving of food has also been observed in our group, involving unrelated individuals (Hattori, unpublished video recording). Capuchin monkeys are not cooperative breeders, unlike common marmosets and cottontop tamarins, although they show allonursing (Baldovino and Di Bitetti 2008, Fragaszy et al. 2004). Moreover, our capuchins also have lived together for over 8 years. Cronin et al. (2009) reported that cottontop tamarins (*Saguinus oedipus*) who were housed together for at least 5 years continued to cooperate under unequal rewards, but they were sensitive to reward distributions and cooperated most often when both individuals receive rewards either simultaneously or over repeated interactions. Brosnan et al. (2005) showed that chimpanzees with long-term relationships were more tolerant of inequitable reward distributions.

We also found that recipients showed more begging behaviors for the high-value food container after operator choices for the low-value container especially in Equal labor condition compared to Unequal labor 2 condition, but not Unequal labor 1 condition. In other words, the recipient's experience of helping the operator on the task in Equal labor condition reduced their begging behaviors after operator choices for the low-value container in the unequal labor 2 condition, even though Unequal 1 and 2 conditions were identical. This result suggests that not only operators but also recipients are sensitive to their own as well as others' reward and labor and can adjust their

behaviors flexibly in a cooperative food sharing situation, that is, recipients may not expect to receive the high-value food without any labor, and experience frustration by not receiving the high-value food after their experience of being rewarded in return for helping others. Indeed, Lakshminarayanan and Santos (2009) reported that capuchins easily inhibit the tendency to reach directly for food in an object retrieval task, successfully employing an alternative reaching strategy that allows them to achieve good retrieval performance. Additionally, we have demonstrated that capuchins are capable of delaying of gratification by waiting until additional food items had accumulated before reaching for the food, thereby increasing the total amount obtained (Anderson et al. 2010), changing their requesting actions flexibly in response to changes in the experimenter's attention (Hattori et al. 2010) and modifying their own behaviors according to a conspecific's emotional expressions (Morimoto and Fujita in press). All of these relevant studies convergingly support capuchins' sensitivity to others' behavior and behavioral flexibility.

In conclusion, this is the first study to have shown that capuchin monkeys, not only operators but also recipients, are sensitive to others' labor and behave flexibly based on their own experience in a cooperative food sharing situation. More specifically, operator monkeys actively distributed better food to the recipient if he/she helped them to access rewards in the joint task. Our study indicates that perceived effort may be more crucial in joint tasks for capuchin monkeys and shows that joint tasks are particularly useful to explore the origin of inequity aversion in nonhuman primates. However, it is still unknown whether capuchins are aware of the amount of others' effort and whether they compare the cost/benefit relationship between self and others. Future work may vary the amount of recipient labor with the operator labor kept

529 constant.

530

531 **Acknowledgement**

532 This study was supported by the Research Fellowships of the Japan Society for the
533 Promotion of Science (JSPS) for Young Scientists (No. 21264 to Ayaka Takimoto), the
534 Grant-in-Aid for Scientific Research (No. 20220004 to Kazuo Fujita) from JSPS, and
535 by the Japan Ministry of Education, Culture, Sport, Science, and Technology (MEXT)
536 Global COE Program, D-07, to Kyoto University. The subject monkeys were originally
537 provided by the Cooperation Research Program from the Primate Research Institute,
538 Kyoto University, with Tetsuro Matsuzawa as the counterpart. We also gratefully
539 acknowledge Hika Kuroshima and James R. Anderson, for various suggestions on our
540 manuscript.

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720

Table

Table 1 The test sequence in each experiment. Each cell shows the social rank of the recipient. This procedure was conducted in a counterbalanced order across the operators.

session	1~10	11~20	21~30	31~40	41~50	51~60
labor	Unequal 1		Equal		Unequal 2	
operator	recipient					
Pigmon	Subordinate	Dominant	Subordinate	Dominant	Subordinate	Dominant
Zilla	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate
Zinnia	Dominant	Subordinate	Dominant	Subordinate	Dominant	Subordinate
Kiki	Subordinate	Dominant	Subordinate	Dominant	Subordinate	Dominant

Table 1

Figures

Figure 1 The experimental setup in Unequal labor condition (a) and Equal labor condition (b). In Unequal labor condition (a), the operator had to first pull the handle of the support board and then pull the drawer of one container. The recipient received food passively. In Equal labor condition (b), the recipient had to pull the handle of the board in order to enable the operator to operate the drawer of a container. Then, the operator pulled the drawer of one container.

Figure 2 The placement of food for the operator and the recipient in each condition in all experiments. “H” denotes the high-value food and “L” denotes the low-value food.

Figure 3 The average number of operator choices for the high-value food container in Unequal labor 1 condition (a), in Equal labor condition (b) and in Unequal labor 2 condition (c). The x axis shows the experimental condition and the y axis shows the average number of choices. The left pair of bars in each figure is for Dominant recipient condition and the right pair of bars is for Subordinate recipient condition. Symbols denote individuals. Each bar and each symbol is based on 10 trials (= the number of trials per session).

Figure 4 The average ratio of recipient begging behaviors for the high-value food container in Dominant and Subordinate recipient conditions. The x axis shows the experimental condition and the y axis shows the average ratio of recipient begging behaviors. The left half of bars is for Dominant recipient condition and the right half of bars is for Subordinate recipient condition. Symbols denote individuals whom recipients

788 begged for the high-value food (operators). Each bar and each symbol is based on 10
789 trials (= the number of trials per session).
790
791 **Figure 5** The average ratio of recipient begging behaviors for the high-value container
792 after operator choices for the low-value food container in Dominant and Subordinate
793 recipient conditions. The x axis shows the experimental condition and the y axis shows
794 the average ratio of recipient begging behaviors. The left half of bars is for Dominant
795 recipient condition and the right half of bars is for Subordinate recipient condition.
796 Symbols denote individuals whom recipients begged for the high-value food (operators).
797 Each bar and each symbol is based on 10 trials (= the number of trials per session).
798
799
800

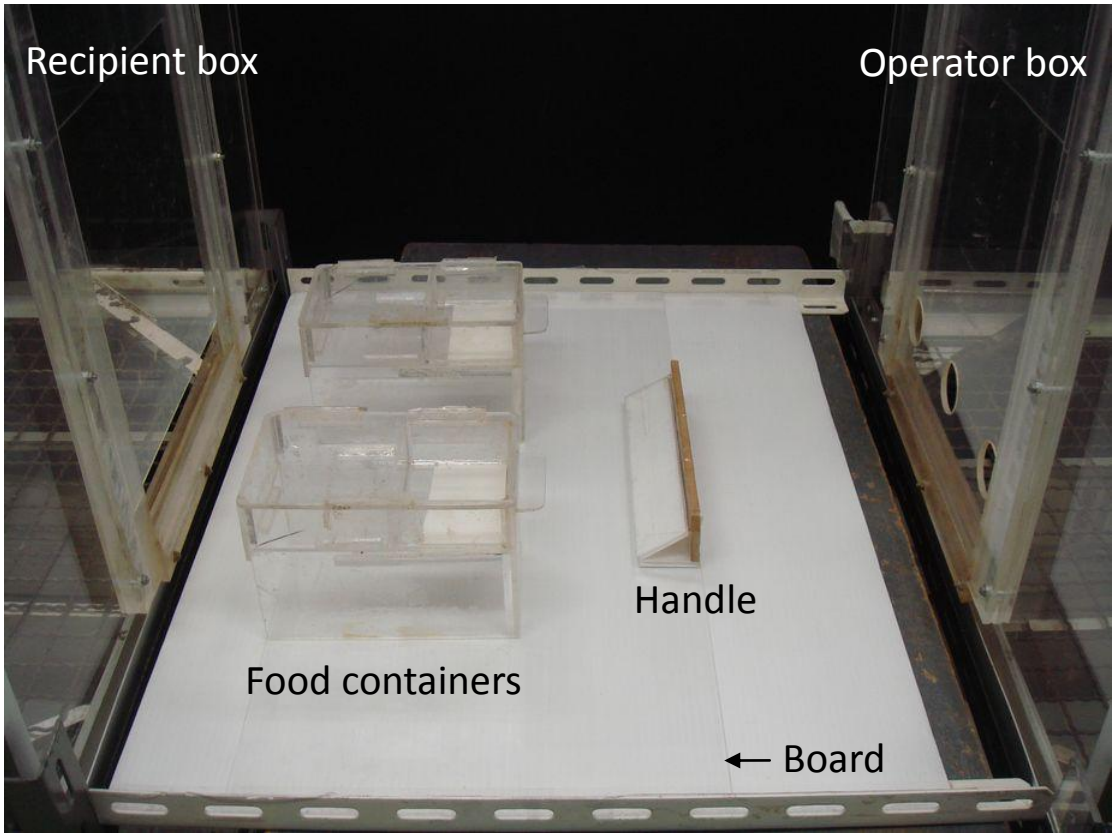
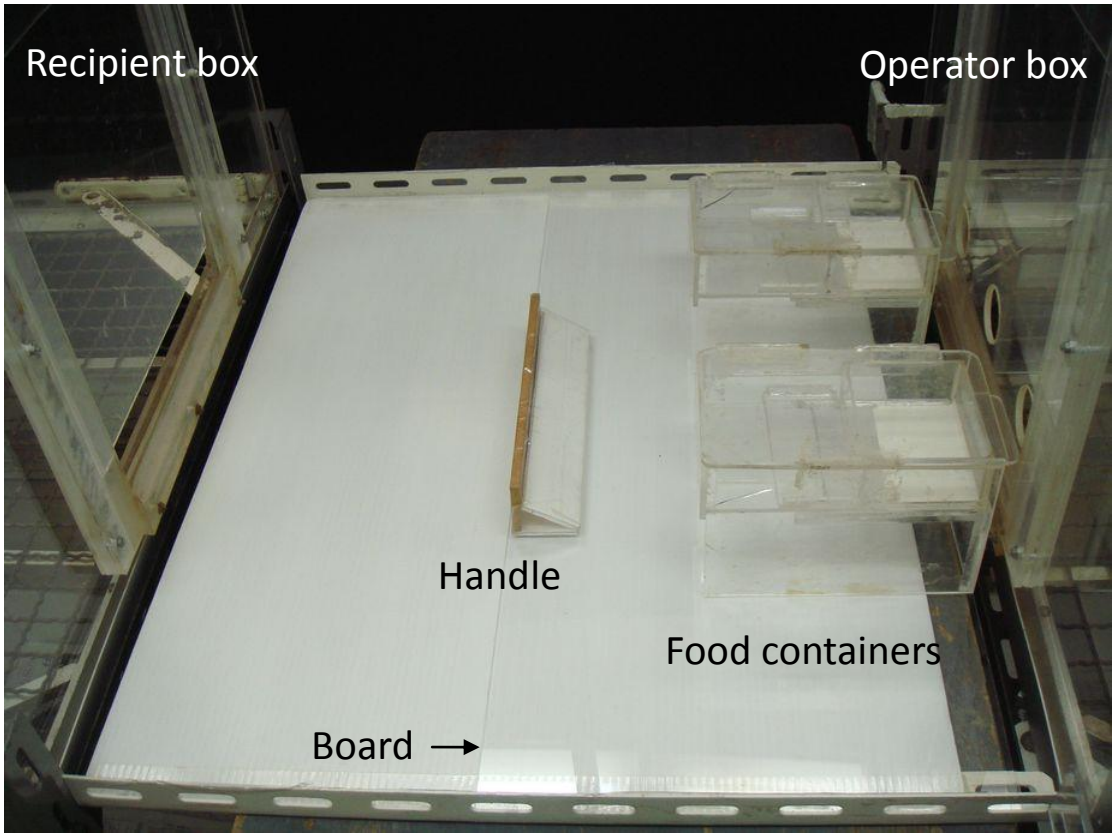


Figure 1a



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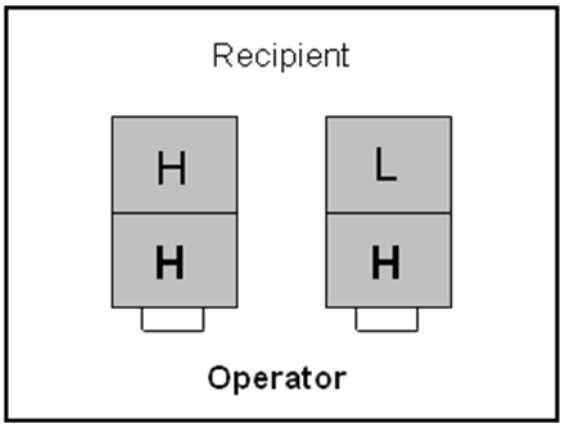


Figure 2

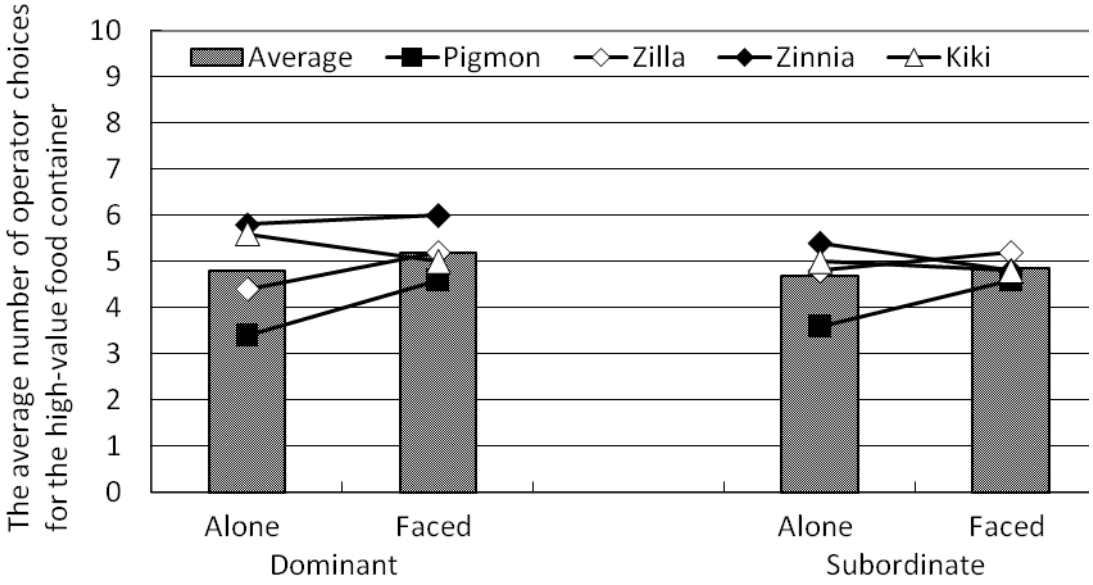

The average number of operator choices for the high-value food container
10
9
8
7
6
5
4
3
2
1
0
Average
Pigmon
Zilla
Zinnia
Kiki
Alone
Faced
Dominant
Alone
Faced
Subordinate

Figure 3a

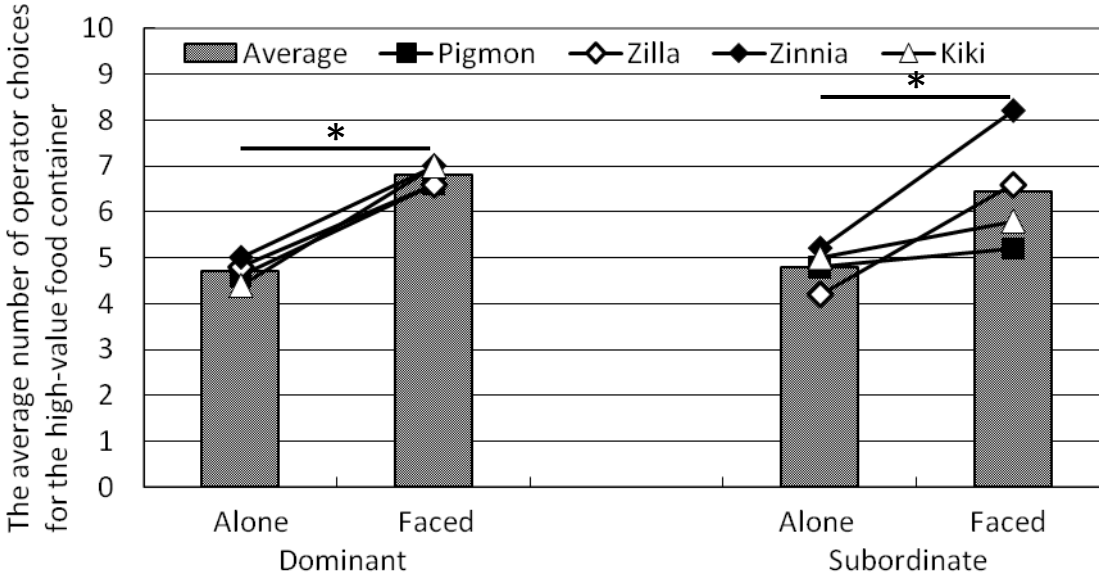

The average number of operator choices for the high-value food container
10
9
8
7
6
5
4
3
2
1
0
Average
Pigmon
Zilla
Zinnia
Kiki
*
*
Alone
Faced
Dominant
Alone
Faced
Subordinate

Figure 3b

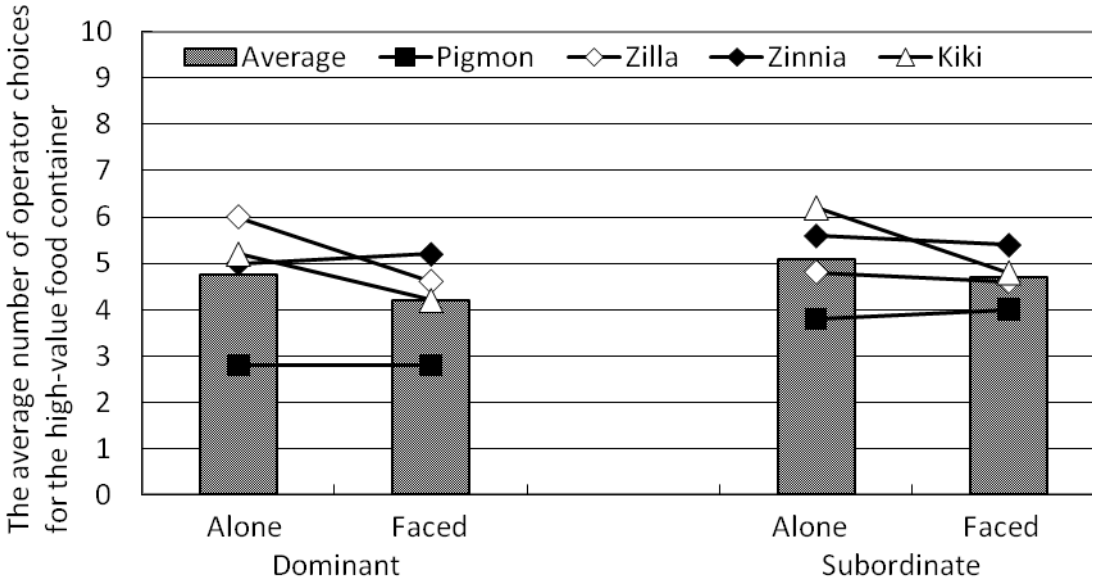
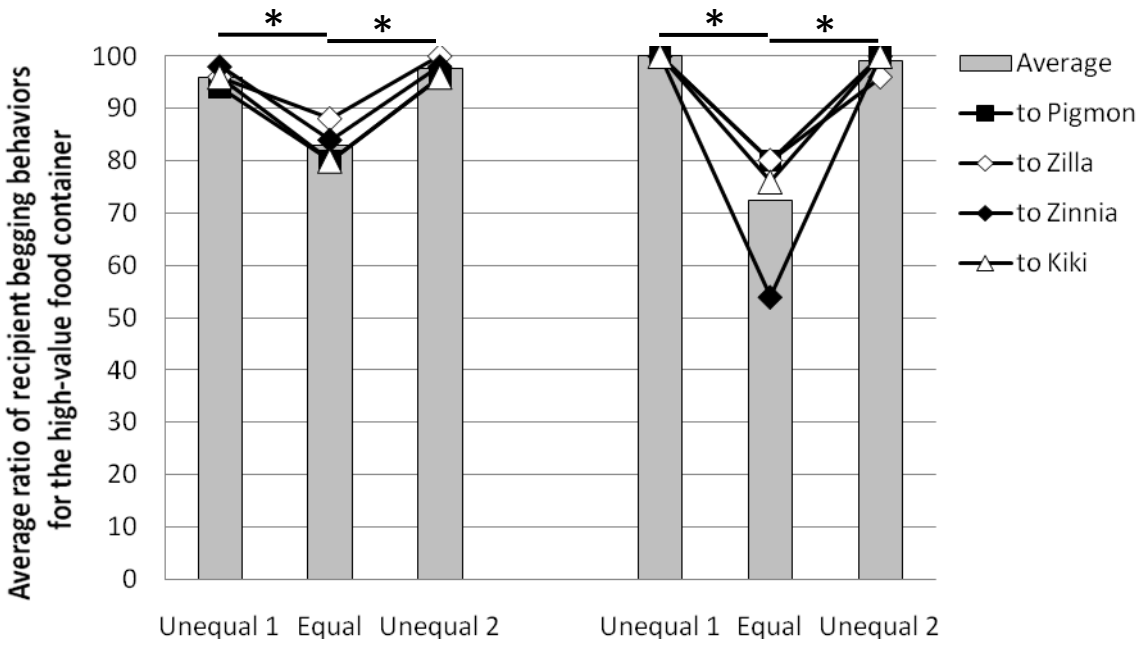

The average number of operator choices for the high-value food container
10
9
8
7
6
5
4
3
2
1
0
Average
Pigmon
Zilla
Zinnia
Kiki
Alone
Faced
Alone
Faced
Dominant
Subordinate

Figure 3c



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888 **Figure 4**

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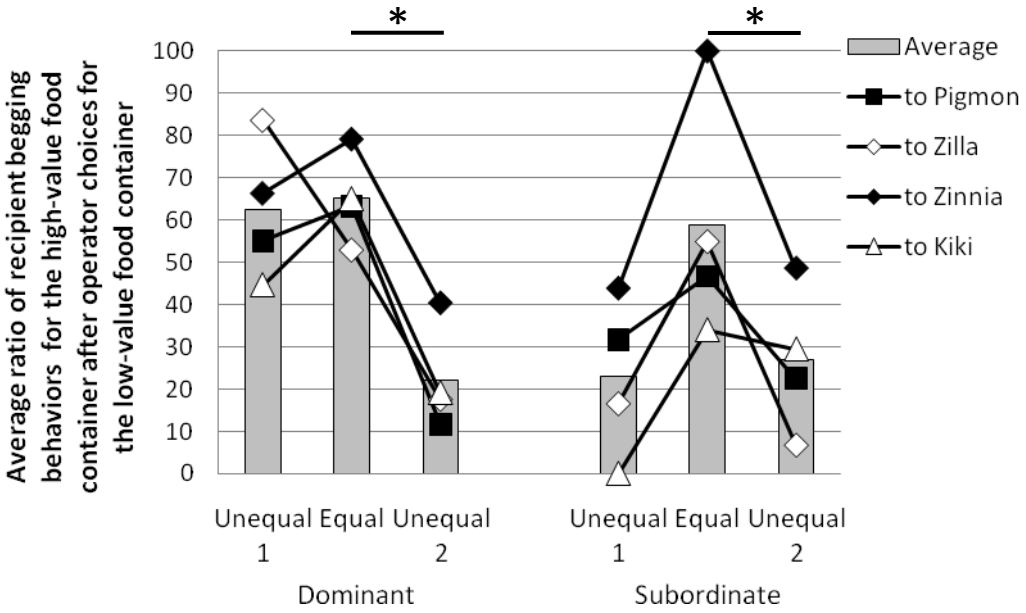
Average ratio of recipient begging behaviors for the high-value food container after operator choices for the low-value food container
100
90
80
70
60
50
40
30
20
10
0
*
*
Average
to Pigmon
to Zilla
to Zinnia
to Kiki
Unequal 1
Equal
Unequal 2
Unequal 1
Equal
Unequal 2
Dominant
Subordinate

Figure 5