

RESEARCH ARTICLE

Partner Effects on Food Consumption in Brown Capuchin Monkeys

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It has been claimed that capuchin monkeys (*Cebus apella*) show inequity aversion in relation to food rewards for a simple exchange task. However, other factors may affect the willingness of a monkey to consume foods of high or low value in the presence of a conspecific. In this study, pairs of monkeys were presented with unequally valued foods, but without any task-performance: they simply received the food under four experimental conditions. By looking at the rate of collection and consumption of low-valued cucumber slices we expected to see variation dependent on whether the partner either had 1) cucumber (equity), 2) grape (inequity), 3) inaccessible cucumber or 4) inaccessible grape. Testing 12 adult capuchin monkeys, our findings differed from those of other authors in that the monkeys failed to show negative reactions to inequity, but rather responded with scramble competition (i.e., fast food collection) in the presence of a conspecific without access to food. They also showed facilitated consumption in the presence of a conspecific consuming high-valued food. Possibly, (in)equity plays a different role if food serves as a reward for a task rather than if it is simply made available for consumption. *Am. J. Primatol.* 69:1–9, 2007. © 2006 Wiley-Liss, Inc.

Key words: *Cebus apella*; feeding behavior; foraging; inequity

INTRODUCTION

A recent study by Brosnan & de Waal [2003] suggests that when capuchin monkeys (*Cebus apella*) perform an exchange task, they are more likely to accept low-valued food in the presence of a partner that consumes the same food than in the presence of a partner with access to a more preferred food. If their partner receives a more preferred food for performing the same task, monkeys not only refuse to accept their low-valued food: they sometimes actively reject it. The Brosnan & de Waal [2003] study presented monkeys with a high-valued food,

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a grape, or a low valued food, a piece of cucumber, as rewards for a token exchange task. In some trials, partners would receive the same reward for the same task (equity), while in other trials the value of the food reward differed between partners performing the same task (inequity). The authors' interpretation that monkeys are averse to inequity is only one of several possible explanations of the observed phenomenon [Brosnan & de Waal, 2004, 2006; Henrich, 2004; Roma et al., 2006; Wynne, 2004].

Could it be that monkeys are merely distracted by the presence of more desirable food? Brosnan & de Waal [2004] reject this interpretation based on control tests built into their study, in which subjects without a partner saw high-valued food presented as if a partner were present in the other side of the test chamber. De Waal & Brosnan [2006] argue that inequity aversion relates to expectations surrounding the distribution of payoffs from cooperation. Sustainable cooperation requires that joint endeavors yield joint payoffs, hence that parties ensure that their benefits are commensurate with their efforts. For example, Boesch [1994] provides data suggesting that male chimpanzees who did not contribute to a cooperative hunt were less successful than the hunters themselves in obtaining a share of meat. Given the collective hunting reported for capuchins [Rose, 1997], similar mechanisms of reward division relative to effort may have evolved. If effort is indeed a factor in the evolution of inequity aversion, it is logical to sharply distinguish food as reward for a task from food simply made available for consumption. The present study concerns the latter context.

It has long been known that satiated animals resume feeding in the presence of hungry, feeding ones [James, 1953; Lorenz, 1935; Tolman, 1964]. Social facilitation is essential for survival in cohesive groups: group life requires synchronization of activities and movement [Boinski & Garber, 2000]. A social animal making decisions about hunting and foraging independently from what the rest of its group is doing will soon find itself alone. Spotted hyenas (*Crocuta crocuta*) drank 70% of the time after having witnessed another individual drink [Glickman et al., 1997; Yoerg, 1991]. Similarly, rats successfully conditioned to avoid a particular food nevertheless ate this food in the presence of conspecifics feeding on it [Galef, 1986].

There is a competitive side to the tendency of animals to do what others are doing. If food is subject to "indirect" or "scramble" competition [Janson & van Schaik, 1988], synchronized feeding will be beneficial. Optimal foraging requires exploitation of the same resource as the one others are focusing on before it is depleted. Under these conditions, it is beneficial to consume food faster so as to out-eat the competitor and move on to the remaining food resources faster. Scramble competition is distinguished from "contest" competition, in which individuals actively displace each other from a concentrated food source. The field measures of Janson [1988] show how scramble competition is a major factor for the species under study, because even though capuchin monkeys foraging in large gatherings do not increase the speed of ingestion, they increase foraging effort and travel time. Under this kind of pressure, a monkey simply has to feed when others are feeding while also taking into account its dominance rank relative to the others [Janson, 1990]. Galef [1993] further proposed that one of the advantages of social facilitation of feeding is that feeding when other individuals feed on the same food is a safe way of acquiring information about the palatability of foods.

Capuchin monkeys are cohesive foragers with a flexible diet, and are generally tolerant of nearby group members while eating [Fragaszy et al., 1994]. Experimental research on eating behavior has shown social facilitation of food

consumption in capuchins similar to that in other species (see above). For example, satiated capuchins resume eating when a familiar conspecific is eating nearby [Galloway et al., 2005], and capuchins eat more in the presence of a companion than if alone, especially if their companion is eating at the same time [Addessi & Visalberghi, 2001]. Social facilitation of food consumption has a greater effect with novel foods than familiar ones, however capuchins do not show sensitivity to differences in food when food is merely colored differently [Visalberghi & Addessi, 2001; Visalberghi & Fragaszy, 1995].

In some contexts, capuchin food consumption increases in the presence of a conspecific while in others, as in the Brosnan & de Waal [2003] study, capuchins consume less in the presence of a conspecific. The present study seeks to expand upon these findings by focusing on relative food quality. This study does not aim to replicate the Brosnan & de Waal [2003] study and differs from it in that food did not serve as reward for a task. The food was simply presented all at once for collection at the beginning of the test instead of being handed out item-by-item over the course of multiple trials. The experimenter left the room after presenting the monkeys with the food trays. Therefore, this study truly concerns the effects of eating in the presence of a conspecific without the influences of human experimenters or experimental tasks. Additionally, both monkeys were presented with food at the same time, therefore neither subject is a “demonstrator” for consuming food as in some other studies.

The conditions in which subjects received a relatively low-valued food were 1) equity vs. inequity (i.e., has the partner the same or a higher valued food?) and 2) partner access to food (i.e., can the partner reach the food placed in front of it, hence eat its food, or not?). Our predictions varied with the factor considered most influential under each condition:

- . Equity: If (in)equity would matter most, we predicted that subjects would refuse or eat less of the low-valued food if their partner was eating a high-valued food.
- . Facilitation: If facilitation would matter most, we would predict subjects to eat more in the presence of an eating partner, especially so if the partner was highly motivated, such as when eating high-valued food.
- . Competition: If scramble competition would matter most, we would predict rapid food collection in the presence of a partner who has no access to food herself and is therefore potentially more interested in the subject’s food.

To compare these three hypotheses we measured both food collection and food consumption assuming that the first would be more subject to competitive tendencies, such as those existing in foraging contexts, and the latter more to feeding motivation.

MATERIALS AND METHODS

Subjects

This study included 12 adult female brown capuchin monkeys (aged 4–30 years) housed in two social groups at the Yerkes Primate Center in Atlanta, Georgia. The first group included 15 individuals (two adult males, seven adult females, four juveniles, and one infant). The second group included 16 individuals (two adult males, six adult females, three juveniles, and four infants). Groups had access to both indoor and outdoor enclosures measuring a total of 25m² and 31m² for each group, respectively. Subjects had access to LabDiet high protein monkey chow and water ad libitum. They were also offered food trays in the late

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afternoon, which included oranges, various produce, and vitamins. Subjects were never food- or water-deprived.

Procedure

A total of 12 monkeys were tested under four condition types, each subject in a different randomized order. The subjects were tested under the same four conditions again in another randomized test order for a total of eight tests. Monkeys were tested in pairs, with each individual sometimes acting as the subject and sometimes as the partner, prior to the late afternoon feeding. Test pairs came from the same social group, were chosen based on similar dominance rank in the group, and were tested with the same partner throughout the study. No subject was tested more than once a day. Five subjects had dependent offspring under the age of 1 year during this study. Before testing, the subjects (and their dependent offspring) were transferred to a mobile testing chamber ($144 \times 60 \times 60$ cm) positioned in front of their home area. The chamber was divided by a clear Lexan panel into two equal areas of $72 \times 60 \times 60$ cm, which also separated the test pair. The chamber had a front clear Lexan panel in which a horizontal row of five 2.5-cm-diameter armhole openings allowed subjects to reach through and collect food rewards that were laid out in line with the five openings. Five pieces of food were placed within arm's length of the adult subjects, but out of reach of any accompanying infants. Access to the food was controlled by the experimenter using a clear Lexan panel secured to the test chamber in front of the armholes. Each test commenced when the experimenter lifted the Lexan panel and left the room.

Conditions

Five pieces of food were laid out in front of each individual, and were inaccessible to the other. Under all test conditions, the subject of the pair was presented with accessible cucumber pieces, while her partner's conditions varied (see below). The monkeys could not pick up all pieces at once, as each piece was placed in front of an arm hole; i.e., food collection required five separate reaching movements.

- . Equality (EQ): both the subject and her partner were presented with five small pieces of cucumber.
- . Inequality (IN): the subject was presented with five pieces of cucumber, while her partner was presented with five grapes similar in size to the cucumber pieces.
- . Equality without partner access (EQX): both the subject and her partner were presented with cucumber, but the Lexan was not removed from the partner's side, making the cucumber pieces inaccessible to her.
- . Inequality without partner access (INX): same as the inequality condition, however the Lexan panel was not removed from the partner's side, making the grapes inaccessible to the partner.

The order in which pairs completed a test condition was randomized for each pair to avoid test order effects. Cucumbers and grapes were selected for this study based on food preference tests in a previous study [Brosnan & de Waal, 2003] in which grapes were universally preferred over cucumber. All tests lasted 10 min and began when panels were removed from in front of the armholes (but if partners were prevented from collecting food, their panel remained over the armholes).

Dependent Variables

A Canon mini-DV recorder (Japan) was used to record the tests and all data were coded from these videotapes. The collection of food pieces was noted for each of the five pieces of food by the latency in seconds from the start of the test (i.e., removal of the Lexan panel in front of one or both monkeys).

The rate at which food pieces were consumed was also collected from the videos. The consumption was measured in pieces eaten per minute for each minute during the first 5 min, and the number of pieces consumed during the last 5 min of the test. Minute by minute analysis was not collected for the last 5 min of testing because in most cases the subject consumed all the food that was to be consumed within the first 5 min.

The rapidity of food collection was expressed in the "Collection Speed Index" as 1 divided by the sum of latencies in seconds at which each piece was collected. The smaller the sum of latencies, the larger this index, hence the quicker the five pieces were picked up by the subject. The speed of food consumption, on the other hand, was expressed in an "Eat Speed Index" by multiplying by 5 the number of pieces consumed in the first test minute, by 4 the number consumed in the second minute, by 3 the number consumed in the third minute, by 2 the number consumed in the fourth minute, and by 1 the pieces consumed in the fifth minute. Because the monkeys did not necessarily eat their food piece-by-piece, each minute we judged how much food was consumed on the basis of the food remaining in the test chamber and in front of it. Since there were totally five pieces to be consumed, the maximum Eat Speed Index was 25 if all pieces were eaten in the first minute.

RESULTS

Collection Speed

A repeated measures analysis of variance (ANOVA) of the Collection Speed Index across the four conditions concerned two factors; i.e., equity (equality versus inequality) and accessibility (partner has access to food, or not). This analysis showed a significant effect with regards to accessibility ($F_{1,11} = 4.92$; $P = 0.049$) but not with regard to equity ($F_{1,11} = 0.09$; $P = \text{NS}$). As can be seen in Fig. 1a, subjects collected food faster if their partner lacked access to food, regardless of what kind of food was laid out in front of the partner. Figure 1b shows that this result applies to the large majority of subjects.

Eating Speed

A repeated measures ANOVA of the Eat Speed Index showed that there was no significant effect of either equity or accessibility (Equity: $F_{1,11} = 1.99$, $P = \text{NS}$; Accessibility: $F_{1,11} = 0.21$, $P = \text{NS}$), yet we found a significant interaction between the two ($F_{1,11} = 8.11$; $P = 0.016$). A follow-up paired *t*-test comparison revealed a significant difference between the two accessibility conditions; i.e., the subject's Eat Speed Index increased significantly if her partner was eating grapes compared with if she was eating cucumber ($t = 2.98$; $df = 11$; $P = 0.013$; Fig. 2). There existed no such effect of the partner's food quality between the two inaccessible conditions; i.e., whether her partner had cucumber or grapes in front of her without access ($t = 1.10$, $df = 11$, $P = \text{NS}$; $t = 0.97$, $P = \text{NS}$).

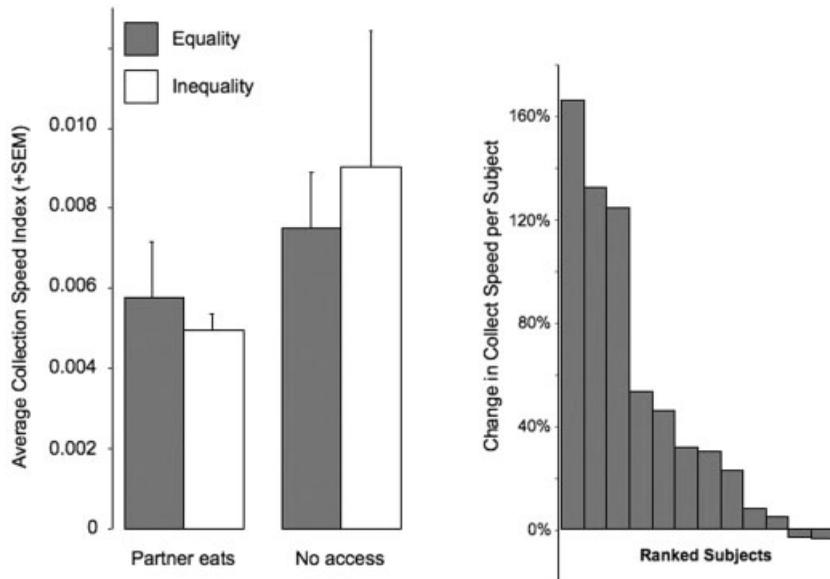


Fig. 1. **a:** Average (+standard error of the mean [SEM]) Collection Speed Index (1/sum of five latencies in seconds) in which food pieces were collected by subjects when partners either did or did not have access to food. Gray bars refer to when the partner has the same low quality food as the subject (equality), white bars to when the food in front of the partner is of higher value than the subject's (inequality). **b:** Bars show the average difference in the Collection Speed Index dependent on the partner's food accessibility. If the eating speed is higher if the partner has access to her food, the difference is positive. If the eating speed is lower, the difference is negative. Each bar represents one subject's data, and subjects are ranked from high to low on this measure, thus illustrating individual variation. The graph shows that 10 out of 12 subjects collected food faster when their partner's food was inaccessible.

DISCUSSION

Capuchin monkeys collected food faster in the presence of a conspecific that could not access her own food. Although a Lexan partition prevented partners from reaching each other's food, subjects were tested in close physical proximity. The effect of this proximity suggests scramble competition, where subjects collected food as quickly as possible before another without food could gain access to her resource.

Whereas scramble competition may account for the measured collection speed, the consumption of food seemed subject to different influences. Subjects ate cucumber faster when their partner ate grapes, but not when their partner could not access her own food. In other words, her partner having better food increased a subject's eating motivation, but only if both were eating. Wynne [2004] suggested that capuchin monkeys in the Brosnan & de Waal [2003] study were not averse to inequity, rather that they were inhibited from eating a low-valued reward while seeing a high-valued reward. When Dubreuil et al. [2006] recently investigated the same issue, they reached a conclusion similar to ours: capuchins consume low-valued food more readily when the partner consumes high-valued food at the same time. Both Dubreuil et al. [2006] and our own study therefore contradict the predictions of Wynne [2004].

One aspect of Brosnan & de Waal [2003] that is supported by our study is that the monkeys pay close attention to what their partner is doing. Instead of being

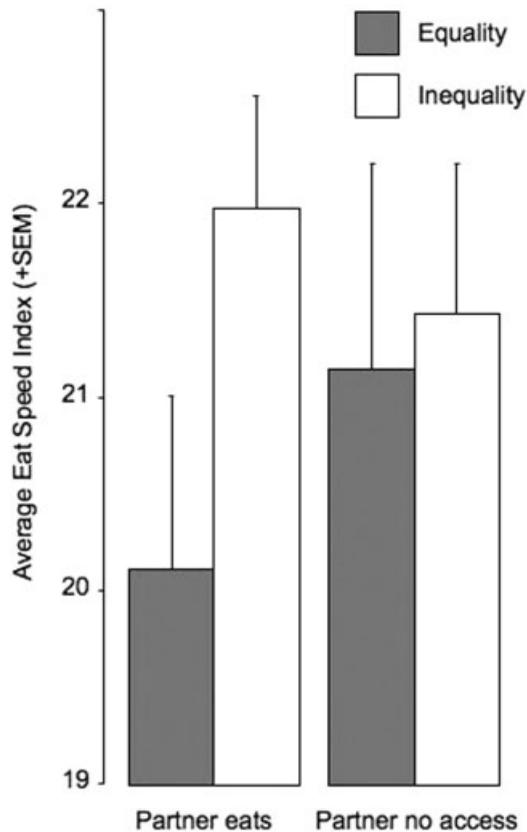


Fig. 2. Average (+standard error of the mean [SEM]) Eat Speed Index for food consumption by subjects when partners had either access to food (i.e., were also eating) or no access (i.e., were not eating). Gray bars refer to condition when the partner has the same low quality food as the subject (equality), white bars to when the food in front of the partner is of higher value than the subject's (inequality).

regulated merely by food availability [Wynne, 2004] or previous experience [Roma et al., 2006], both food collection and food consumption speed depend on the partner's behavior and situation. The increased food consumption found by Dubreuil et al. [2006] and ourselves in the presence of a partner with high-valued food must be due to actual food consumption by the partner, because we found that the increase is absent if the partner is prevented from eating. This fits a social facilitation hypothesis according to which the partner's motivation to eat, which is likely higher in relation to a high-valued food, positively affects the food consumption of a subject with low-valued food.

At first sight, the latter result seems to disagree with Brosnan & de Waal's [2003] finding that monkeys seeing a partner with high-valued food will reject their own low-valued food. However, one should keep in mind that the experiments of Dubreuil et al. [2006], Roma et al. [2006], and the present study merely offer food as food instead of giving food as a reward, as was done by Brosnan & de Waal [2003] and Brosnan et al. [2005]. The present study also lacked a trial-by-trial handing out of food (i.e., the food was given all at once), and had no "demonstrator" since both monkeys received food at the same time. If such major

procedural differences are glossed over, and available food is referred to as “reward,” even though it does not serve as an incentive for behavior, studies of food consumption may be seen as replications of studies of inequity aversion, yet they are not [Brosnan & de Waal, 2006]. In the latter, food is provided contingent on task performance, which means that subjects can compare how they got rewarded for the same performance as their partner. This situation comes much closer to the cooperative, task-oriented context in which inequity aversion presumably evolved (see the Introduction). Future studies should take these distinctions into account. We are in the process of conducting additional studies around the same theme, including more elaborate controls than in the Brosnan & de Waal [2003] study, to find out under which conditions the presence of higher valued food does or does not affect behavior.

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