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5 **A concept of value during experimental exchange in brown**
6 **capuchin monkeys, *Cebus apella***

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18 **Key words:** capuchin monkey, *Cebus*, value, barter, sex difference, exchange

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1 Abstract

2 We evaluated the response of brown capuchin monkeys to two differentially-
3 valued tokens in an experimental exchange situation akin to a simple barter. Monkeys
4 were given a series of three tests to evaluate their ability to associate tokens with food,
5 then their responses were examined in a barter situation in which tokens were either
6 limited or unlimited. Capuchins did not perform barter in the typical sense, returning the
7 tokens which were associated with the reward. However females, but not males, showed
8 a different response, preferring the higher-value token. This may indicate that they have
9 learned to prefer one token over the other rather than to associate the tokens with their
10 specific rewards. This sex-difference parallels previous findings of greater reciprocity in
11 female brown capuchins than in males.

12

13

1 Animals almost certainly form preferences for items based upon their intrinsic
2 qualities, but the possibility also exists that preferences are based upon qualities extrinsic
3 to the items themselves. In such a case, the animal essentially forms a concept of the
4 value of that item, which may be used to compare different commodities. For instance,
5 such a concept may be used in biological markets, in which dissimilar goods and services
6 are apparently exchanged in a reciprocal fashion (Noë & Hammerstein, 1994; 1995; de
7 Waal, 1997a; de Waal & Berger, 2000; Stopka & Macdonald, 1999).

8 We consider this ‘concept of value’ to be short-hand for a reward association with
9 some specific item which can be used in comparison with other items having different
10 reward-associations. Thus, the value of item x can be weighted against that of y based
11 upon characteristics extrinsic to both items, rather than upon their intrinsic qualities. One
12 way to experimentally demonstrate such a concept of value is to examine whether
13 animals form preferences for inherently non-valuable items based upon their conditioned
14 association with valued rewards. This ability can be tested in a controlled experimental
15 situation in which animals have been trained to exchange material tokens with a human
16 experimenter for a reward.

17 Non-human primates are excellent subjects for such an exchange task.
18 Chimpanzees exchange items between each other in an experimental setting, both in a
19 contrived situation (Nissen & Crawford, 1936; Savage-Rumbaugh et al., 1978) and
20 spontaneously (Pacquette, 1992). Several great apes exchange freely with humans as
21 well. Hyatt & Hopkins (1998) found that the majority of chimpanzees, without specific
22 training, would give a non-edible token to a human experimenter in exchange for food.
23 Furthermore, solicitation of the token by the experimenter increased the probability that

1 the chimpanzee would return it, which the authors interpreted as evidence for barter.
2 Chalmeau & Peignot (1998) found that gorillas (*Gorilla gorilla*) were not only capable of
3 simple exchange, but that some of them were able to complete complex exchange
4 interactions in which several items had to be exchanged back before the reward was
5 ultimately received.

6 We chose to use capuchin monkeys because these primates are known to share
7 material items and food with each other in experimental settings (Thierry et al., 1989; de
8 Waal et al., 1993; de Waal, 1997b; 2000; Westergaard, 1997; 1998a; Brosnan & de Waal,
9 2002) and are apparently relatively good at exchange (Westergaard, 1998b; Westergaard
10 et al. 2004). Capuchins are also known to participate in reciprocal interactions in which
11 donation and receipt of food and/or services are temporally separated, making them likely
12 candidates to possess a concept of value as defined above. Capuchins participate in
13 cooperative interactions in which they must work together to pull in a tray which will
14 reward only one (Mendres & de Waal, 2000; de Waal & Berger, 2000). Upon receipt of
15 the food, the capuchins share with the individual who helped them obtain it, indicating
16 attitudinal reciprocity (de Waal & Berger, 2000).

17 Using the same capuchin monkeys as in our cooperation and food sharing studies,
18 we did a series of three studies to evaluate their ability to acquire exchange behavior, then
19 use this behavior in a conditioned association task. We first trained the capuchins on a
20 basic material exchange task, as no other study has documented the acquisition of
21 exchange behavior in this primate. Following this, their response to two inherently non-
22 valuable but differentially conditioned tokens was evaluated in a situation in which
23 subjects were given access to two different tokens and had to return the correct token to

1 the experimenter in order to receive the food reward. We refer to this as the barter task,
2 given that success in the task appears to meet Chapman's (1980) requirements for "pure
3 barter".

4 We predicted that capuchins would develop a preference for the higher value
5 token over the lower value token due to the tokens' associations with differentially
6 valued food items. We further predicted that, after learning to associate the food rewards
7 with the different tokens, the capuchins would be able to successfully obtain food
8 rewards in the barter situation.

9

10 **General Methods**

11 *Subjects*

12 The subjects included 14 adult and subadult brown capuchin monkeys housed in
13 two social groups at the Yerkes National Primate Research Center, in Atlanta, Georgia,
14 USA. Only 10 monkeys exchanged consistently enough to participate in testing, 3 adult
15 males, 2 subadult males, and 5 adult females. All but one of the adult females were
16 pregnant and/or carrying a dependent offspring at some point during testing.

17 The groups in which the subjects lived were housed in two large, indoor/outdoor
18 enclosures. Each enclosure contained ample three-dimensional climbing space as well as
19 trapezes, perches, and enrichment items. Purina small primate chow was provided twice a
20 day, at approximately 9:30 hours and 17:30 hours. A tray consisting of fruit, vegetables,
21 and bread with a protein solution was provided to each group every day at approximately
22 17:30 hours. Running water was available *ad libitum*. This feeding schedule was

1 followed regardless of the day's testing, and subjects were never food or water deprived.
2 For more details about the testing facility, see de Waal, 1997a.

3 The subjects had previously been trained to enter transport cages, which allowed
4 us to place individual animals into a test chamber with their cooperation. Individuals
5 were comfortable with this procedure and were well habituated to the test chamber. The
6 test chamber was divided by a mesh partition into two equal sized (36 X 60 X 60 cm)
7 compartments, and all testing was carried out in only one of these compartments. The test
8 chamber was backed by an opaque panel, so in the test chamber the subjects had vocal,
9 but no visual or tactile, access to their group. This allowed us to interact with subjects in
10 a controlled manner with minimal distractions from the group. Dependent offspring were
11 always allowed into the test chamber with their mothers.

12 All but 2 of these individuals had previously been used in food sharing and
13 cooperation studies in our lab. Although this previous experience doubtless made them
14 more sensitive to the possibility of being rewarded for certain tasks, none of their
15 previous experience involved tokens, nor had they been involved in a task in which
16 different items yielded different rewards. As a result, this was their first exposure to
17 experimental value testing and token exchange.

18

19 *Exchange Paradigm*

20 For this study, exchange was operationally defined as the subject returning an
21 inedible token to the experimenter, for which the subject received a food reward,
22 following Hyatt & Hopkins (1998). Unless otherwise noted, exchange consisted of the
23 experimenter placing the token(s) into the test chamber, then standing in front of the test

1 chamber with left hand outstretched, palm up, as a begging gesture, and holding the
2 reward above the left hand with the right hand. Subjects received the reward upon the
3 placement of the token into the exchanger's left hand. Attempted exchanges in which
4 tokens were thrown out of the test chamber or were not placed into the experimenter's
5 hand were not rewarded. All sessions were videotaped, along with time in hundredths of
6 a second, on either a Super-VHS or digital video recorder and data were later collected
7 from the videotapes by S.F.B. A second observer collected some latency data during
8 testing.

9 Subjects underwent a number of different experiments, each consisting of some
10 procedure repeated multiple times. Throughout, "test" refers to an experimental type,
11 "trial" to the procedure that is repeated multiple times per test, and "session" will refer to
12 the set of trials for a particular test (i.e. most tests consist of multiple-trial sessions
13 occurring on different days).

14

15 *Statistics*

16 All statistical tests reported are on a total sample size of 10 individuals, 5 male
17 and 5 female. Analysis of dichotomous preferences for one item over another were
18 conducted using two-tailed binomial tests on data pooled for each subject. In some cases,
19 we also conducted comparisons between two independent groups using the Mann-
20 Whitney U test or between two dependent groups using the Wilcoxon Sign-Rank Sum
21 test. Since the sample size was below 15, only exact tests were used (Mundry & Fischer,
22 1998). All statistics are two-tailed.

23

1 **EXPERIMENT 1**

2 This experiment was designed to ascertain the ability of capuchins to exchange,
3 and, after determining their food preferences, to determine whether they could associate
4 tokens with specific rewards.

5

6 *Exchange Training and Acquisition*

7 Fourteen adults and subadults were initially tested for their ability to exchange.
8 One individual, the alpha male of his group, had had exposure to exchange with humans
9 in his previous laboratory (D. Fragaszy, personal communication) but all other subjects
10 were believed or known to be naïve to the specifics of our procedure. The token initially
11 consisted of a small granite rock (approx. 4 cm in diameter) and the reward was a
12 Kellogg's Apple Jack (a sweet, apple-flavored breakfast cereal approx. 1 cm in diameter).
13 Each session consisted of 20 one-minute trials.

14 Initial training assessed whether monkeys would return the rock spontaneously to
15 an experimenter holding out her hand. For the subjects who did not spontaneously
16 exchange after 5 sessions (i.e. 100 trials), shaping commenced, in which the subject was
17 initially rewarded for throwing the rock out of the test chamber or even for merely
18 touching the rock. Gradually, the stringency of the criteria increased until the subject
19 exchanged correctly.

20 After task acquisition, five baseline test sessions (BL) were run to establish the
21 standard latency to exchange, which was defined as the number of seconds it took the
22 subject to return the token to the experimenter's hand after the token had been placed in
23 the chamber. The session in which the subject first successfully exchanged in 90% of the

1 trials was counted as the first BL session. For each BL trial, the latency to exchange and
2 the errors made (*e.g.* throwing the item out of the test chamber) were recorded, as well as
3 *ad libitum* data on social behaviors aimed at the human exchanger. At least two
4 experimenters played this exchanger role in different BL sessions to assure that the
5 subjects generalized exchange across multiple persons (although all testing was
6 completed by S.F.B.). If a subject failed more than 10% of trials during any single BL
7 session, training recommenced.

8

9 *Conditioning Procedure (CP)*

10 This task was designed to teach the capuchins the value of two different,
11 inherently non-valuable tokens. The procedure was intended to condition subjects that
12 two different tokens were worth two different food items (one of which was more
13 valuable than the other). The tokens used in the conditioning procedure were a small
14 poly-vinyl chloride (PVC) pipe and a large metal washer. The capuchins did not show an
15 initial preference for either of these tokens, nor for either of 4 other pairs of tokens tested
16 (Brosnan & de Waal, unpublished data). Since there was no initial preference for either
17 token, and we planned to use these value associations in future testing, for all subjects the
18 PVC pipe (pipe) was associated with a piece of fresh bell pepper and the metal washer
19 (washer) was associated with a Froot Loop. These food items had previously been
20 established as the lowest (bell pepper) and highest (Froot Loop) value food items for all
21 10 capuchin subjects (see Food Preference Test below).

22 Prior to the first conditioning test, the subjects were exposed to 5 of each token
23 for 30 minutes to reduce their novelty. For each trial, 5 of each of the two tokens were

1 placed on the floor of the test chamber (for a total of 10 items) simultaneously. The
2 subjects could exchange the tokens back in any order they chose. Each returned token
3 was rewarded appropriately by the experimenter. The food reward was handed to the
4 subject immediately upon return of a token and, typically, an exchange took about 5
5 seconds from the subject picking up a token to receiving the food reward. Each subject
6 received two sessions with five trials per session, for a total of 50 exchanges with each
7 token.

8

9 *Food Preference Test (FPT)*

10 This test established food preferences for each individual in the manner of de
11 Waal (1997b). The subject had to make a choice between two simultaneously offered
12 food items, of which it could obtain only one. The experimenter held the foods in
13 different hands in front of the subject, separated by approximately 10 centimeters. The
14 subject was allowed to reach through the mesh of the test chamber and take only one of
15 the food items. Ten choices were offered between each possible pair of foods, split
16 between 2 different sessions. Reward position was alternated randomly, but with an equal
17 number on each side. It was noted from which side the item was obtained to ensure that
18 no subject simply preferred the item from one side to that from the other. The trials were
19 run in quick succession, with each new pair of foods being offered when the previous
20 choice was consumed.

21 Each individual's preferences were established across five different foods, a
22 Kellogg's Froot Loop (a sugary, fruit-flavored breakfast cereal), a 500 mg Noyes
23 precision food pellet (Sucrose pellets), a green bell pepper piece, an apple piece, and a

1 cucumber piece. All fruit or vegetable pieces were approximately 2 cm in diameter. A
2 reward was considered to be preferred if the subject chose it at least 80% of the time over
3 the alternative.

4

5 *Token Preference Test*

6 The purpose of this test was to see if the subjects would recognize the value of
7 inherently non-valuable tokens based on previous conditioning. The procedure was the
8 same as the Food Preference Test, except the choice was made between two tokens,
9 instead of two items of food. Ten choices were offered per session, at the end of which
10 the subjects received a single peanut to maintain their motivation to cooperate. Each
11 subject received 5 test sessions, hence 50 trials. These data were used to ascertain that a
12 preference had been established during the conditioning procedure. All subjects were
13 used in subsequent tests, regardless of whether they demonstrated a preference for one
14 token over another, as we had no way of knowing whether they failed to demonstrate a
15 preference because they lacked a concept of value or because they lacked motivation to
16 participate in the preference test. Specifically, it seemed possible that due to motivational
17 or some other environmental differences, a subject might fail to demonstrate a preference
18 in this test but do so in subsequent experiments. Only one male failed to show a
19 preference in the token preference test (see Results).

20

21 **Results**

22 *Acquisition*

1 Twelve of the initial 14 individuals successfully learned the exchange task (two
2 adult females did not learn to exchange in 25 sessions). Of these, 10 learned to exchange
3 with no shaping (that is, within 5 sessions) and 2 adult females required extensive
4 shaping (15 or more sessions). Of the 10 that learned with no shaping initially, 2 subadult
5 males ceased exchanging consistently for unknown reasons (most likely social stress) and
6 were not included in subsequent tests. This left only 10 subjects, 5 adult males and 5
7 adult females, for all following tests. As there were no differences in behavior between
8 the 8 subjects who required no shaping and the 2 subjects who did require shaping, their
9 results are lumped for all subsequent analysis.

10

11 *Food Preferences*

12 All ten subjects preferred Froot Loops over bell pepper (mean \pm SEM preference
13 for FL of 95.00 ± 2.69 %, binomial test: $p < 0.001$). There was no sex difference in
14 preference for the Froot Loop (mean \pm SEM preference for females of 98.00 ± 2.00 % as
15 compared to preference for males of 92.00 ± 4.90 %; Mann-Whitney: $U = 9$, $n = 10$, $p =$
16 1.00).

17

18 *Token Preference Test*

19 Nine out of 10 subjects chose the more valuable washer more often than they
20 chose the pipe, and the exceptional subject chose each token equally often (mean \pm SEM
21 preference for washer of 78.40 ± 4.93 %; binomial test: $p < 0.001$). To see whether
22 preference for the higher-value reward differed in strength from preference for its
23 corresponding token, the percentage of washers chosen (over pipe) for each individual

1 was compared with the percentage of Froot Loops chosen (over bell pepper). The
2 preference for the token was weaker than for the reward (Figure 1: Wilcoxon: $T = 45$, $n =$
3 9 , $p < 0.001$). There was no difference between males and females in their preference for
4 the washer (Mann-Whitney: $U = 6$, $n = 10$, $p = 0.222$).

5

6

7

INSERT FIGURE 1 APPROXIMATELY HERE

8

9

10 **Discussion**

11 Capuchin monkeys can be taught to exchange material items with a human
12 experimenter, thus this behavior can be used to investigate the monkeys' perception of
13 value. Material exchange is not necessarily a spontaneous behavior in capuchin monkeys,
14 but it is rapidly acquired by a majority of individuals and can be learned by most of the
15 rest. There is no difference in responses to later tests for individuals who exchanged
16 spontaneously versus those who required extensive shaping. Capuchins seem less
17 inclined to material exchange than great apes, as captive chimpanzees require even less
18 experience to acquire the task (S. Brosnan, personal observation).

19 As predicted, capuchins form preferences for inherently non-valuable tokens
20 based on the association of these tokens with different rewards. The subjects learned to
21 prefer the washer, the high-value token worth a Froot Loop, to the pipe, the low-value
22 token worth a bell pepper piece, apparently based on their preference for the Froot Loop.
23 The strength of the preference for the food reward itself was greater than the strength of

1 preference for the corresponding token, which might be expected, given that the food
2 reward has intrinsic value and the token only associated value.

3

4 **EXPERIMENT 2**

5 As the previous experiment indicated that capuchin monkeys are easily able to
6 associate food rewards with inherently non-valuable tokens, we next examined whether
7 they would be able to return the correct token to receive a proffered reward in a task akin
8 to a simple barter situation. This and the following experiment were designed to ascertain
9 how the conditioned value affected the subjects' exchange behavior.

10

11 *Value Association Test, Unlimited Tokens*

12 The subject had to return the token that was associated with a proffered reward in
13 order to receive the reward. The experimenter began by holding the reward in front of the
14 subject, to make the subject aware of it. Following this, the two different tokens were
15 placed on a table in front of the subject, approximately 4 cm from the test chamber and
16 16 cm apart. The experimenter placed her open left hand (receiving hand) directly between
17 the tokens (each was ~2 cm from her hand), then held the reward in her right hand,
18 directly over her outstretched left hand. The subject could choose and return either of the
19 tokens.

20 Once again, the tokens were a washer and a PVC pipe. The washer was the
21 higher-value of the tokens, worth a Froot Loop, and the PVC pipe was the lower value,
22 worth a piece of bell pepper. The subjects only received the reward if the correct token
23 (e.g. the one that was associated with the proffered reward) was returned. The position of

1 the tokens was alternated each trial and the order of presentation of rewards was random,
2 but with an equal number of both rewards each session. If the subject failed to return
3 either item after 25 sec, the tokens were removed and the next trial commenced. In
4 situations in which the subject maintained possession of a token at the end of the trial,
5 one of each token was still made available for the next trial, to assure the subject knew
6 they had access to at least one of each token. Each session consisted of 25 trials and each
7 subject received 4 sessions.

8

9 **Results**

10 The number of correct returns was calculated for each individual as those
11 responses in which the token returned was associated with the proffered reward. For this
12 test, the subject had access to one of each token for each trial (exchange). Since for each
13 exchange the subjects always had access to one of each token, in each trial the subjects
14 had a 50% chance of returning the correct token. Subjects did not return the tokens
15 correctly (Figure 2: mean \pm SEM of 47.8 ± 0.75 % for correct token; binomial test: $p =$
16 0.851), and there was no sex-difference (female mean \pm SEM of 50.9 ± 1.09 %; male
17 mean \pm SEM of 53.8 ± 1.68 % for correct returns; Mann-Whitney: $U = 6$, $n = 10$, $p =$
18 0.222)

19 However, the capuchins as a whole did show a preference for the higher-value
20 token (mean \pm SEM of 62.42 ± 7.07 %; binomial test: $p < 0.001$). Upon further analysis
21 we realized this was due to a sex-difference (Mann-Whitney: $U = 1$, $n = 10$, $p = 0.016$),
22 with female capuchins being more likely to return the high-value token than the lower-
23 value token (female mean \pm SEM of 79.9 ± 7.15 %, binomial test: $p < 0.001$), while

1 males were, if anything, more likely to return the lower-value token (male mean \pm SEM
2 of 44.9 ± 4.54 %, binomial test: $p = 0.031$) The females did not return the higher-value
3 washer significantly more often when the Froot Loop was offered than when the bell
4 pepper was (FL offered mean \pm SEM of 40.4 ± 3.27 ; BP offered mean \pm SEM of $36.6 \pm$
5 4.13 ; Wilcoxon: $T = 10$, $n = 4$, $p = 0.125$).

6

7

8

INSERT FIGURES 2 and 3 APPROXIMATELY HERE

9

10 **Discussion**

11 As opposed to our initial predictions, capuchins did not return the tokens that
12 were associated with the proffered rewards. However, the females showed a strong
13 preference for returning tokens worth the higher-value food regardless of what reward
14 was being offered. This presented two challenges: first, to describe the strategy the
15 females were apparently following, and second, to understand the sex difference in
16 responses. The sex difference is addressed later in the General Discussion.

17 We realized that the capuchins could follow two different strategies to obtain the
18 rewards. First, subjects may return the ‘correct’ token, or the token which is associated
19 with the proffered reward, attempting to maximize the overall number of rewards earned,
20 which we dubbed the Matching strategy. This was the strategy we initially predicted, but
21 it was not followed in this situation. This strategy seems cognitively quite demanding,
22 requiring the subject to know that the tokens have different values, to remember these

1 values, and to associate the tokens with the proffered reward (which also must be
2 recognized).

3 Second, subjects may return only the highest value tokens, which we call the High
4 Value strategy. While this strategy is inferior in terms of achieving rewards, it may be
5 superior in that it allows for the maximum receipt of high-value rewards with minimum
6 effort. The subjects need not pay attention to the proffered reward or remember the
7 values of the tokens, but must only recognize which token will acquire their preferred
8 food. This is similar to the females' behavior in this test.

9 There were several possible explanations for this preference for the higher-value
10 token. First, it is possible that the capuchins do not understand the task, and the
11 statistically significant preference for the higher-value token by the females was a fluke.
12 Further testing will shed light on this possibility. Second, perhaps the capuchin females
13 do show a robust preference for returning the higher-value token, following the High
14 Value strategy. However, while this may require the least attention for the best rewards, it
15 seems unlikely that the capuchins cannot make the conditional association required for
16 the Matching strategy. This leads to the third possibility, that the capuchins can perform
17 the conditional association, but are not in a situation in which it is beneficial. In this
18 experimental situation, in which tokens are unlimited, the capuchins could receive all of
19 the higher-value rewards by following this High Value strategy. As none of our animals
20 are food deprived, the lower value foods may not have been sufficiently motivating. The
21 third experiment was developed as a way to encourage the capuchins to maximize their
22 performance without food deprivation.

23

1 **EXPERIMENT 3**

2 This task was designed to determine if capuchins will spontaneously make
3 conditional associations, using tokens whose associated values are already familiar, if
4 they are in a situation in which they must pay attention to maximize receipt of higher-
5 value rewards. To this end, we designed a limited token situation to minimize the gains of
6 indiscriminately returning the higher-value token. In the prior experiment, subjects had
7 access to one of each token prior to every exchange. In this “limited” task, a set number
8 of tokens is given to the subjects prior to a series of exchanges, while allowing the
9 subjects to see the order in which rewards will be offered. Thus, subjects who know
10 which token is associated with which reward should attempt to maximize high value
11 rewards by returning the correct token, while those who only know that one token is
12 superior to the other should continue to show a preference for the higher value token.
13 This test was completed on all 10 subjects to see if the males responded in another
14 manner to this different situation.

15

16 *Value Association Test, Unlimited Tokens*

17 The procedure for this test was similar to that of the unlimited test, except that the
18 tokens were now a limited resource. Five of each token were placed with the monkey in
19 its test chamber at the commencement of the session, rather than giving the subject
20 guaranteed access to one of each token per trial. This meant that subjects depleted their
21 supply of tokens as they exchanged, and these tokens were not replaced. As a result,
22 subjects could run out of either of the token types before all of the associated rewards had

1 been offered. Sessions consisted of 10 trials (5 of each reward type placed with the
2 monkey) and each subject received 5 sessions for a total of 50 trials.

3

4 **Results**

5 The number of correct returns was calculated per subject in the same manner as
6 above. Subjects did not return the correct token (the one that was associated with the
7 reward) more than the incorrect one (Figure 2: mean \pm SEM of 50.54 ± 2.97 % for
8 correct token; binomial test: $p = 0.099$), and there was no sex difference in whether or not
9 the correct token was returned (female mean \pm SEM of 48.08 ± 4.18 %; male mean \pm
10 SEM of 53.00 ± 4.37 %; Mann-Whitney: $U = 8$, $n = 10$, $p = 0.421$).

11 For this test, measurement of the subject's preference for a token was more
12 complex. Since the subject was given 5 of each token prior to the commencement of the
13 session and these tokens were not replenished during the session, there was no guarantee
14 that one of each token would be available for each trial, and the probability of returning
15 any one token was different for each trial dependent upon previous returns. Thus, we
16 calculated which tokens they chose to return first in the trials as a proxy for the preferred
17 token. To do this, we calculated the frequency of high-value tokens returned in the first
18 half of exchanges, that is how many high-value tokens they chose to return in the first 5
19 exchanges in each series of 10 exchanges. In this case, subjects showed a preference for
20 returning first the higher value token, the washer (mean \pm SEM of 3.1 ± 0.22 , binomial
21 test: $p < 0.001$), however, once again this result is due to a sex difference (Mann-
22 Whitney: $U = 3.5$, $n = 10$, $p = 0.056$), with females showing a strong preference for
23 higher value-tokens (female mean \pm SEM of 3.5 ± 0.26 washers returned in the first half,

1 binomial test: $p < 0.001$) and males showing no preference (males: mean \pm SEM of 2.72
2 ± 0.27 washers returned in the first half, binomial test: $p = 1.00$).

3

4 **Discussion**

5 Once again, there is no evidence that the capuchins are following the Matching
6 strategy, in which they return the token associated with the proffered reward. However,
7 again the females, but not the males, preferred to return the higher-value token. In this
8 limited situation, the females are more likely to return the higher-value tokens first,
9 indicating a preference for them. Thus, this test provides more support for the conclusion
10 that capuchin females are following the High Value strategy.

11

12 **GENERAL DISCUSSION**

13 Overall, capuchins failed to return the correct token regardless of whether their
14 access to tokens was unlimited or limited. So, capuchin exchange behavior does not
15 support the Matching strategy, in which subjects maximize the overall number of rewards
16 received. If our assumptions of what the capuchins must know are correct, evidently the
17 capuchins did not have the cognitive capacity to retain these two value assessments and
18 relate them to the offered reward.

19 It is, to us, somewhat surprising that the capuchins cannot do this conditional
20 association task. There are several possibilities for why this may be. First, even in the
21 limited task the capuchins may not be in a situation which drives them to use all of their
22 abilities to obtain food. These are captive individuals who have *ad libitum* access to food
23 and water, and receive fruits and vegetables daily. Thus, food may not be in sufficiently

1 short supply to be motivating. These results might be different in the case of more
2 deprived individuals (e.g. those living in the wild). Second, it may be that the capuchins
3 could learn this task if subjected to a longer period of training and conditioning, but that
4 their natural first response is not to match the tokens and rewards. Finally, it may be that
5 the capuchins do not possess the cognitive sophistication which will allow them to
6 perform such a task.

7 However, among the females, a preference for returning the higher-value token is
8 consistent across two sets of tests separated in time, indicating the High Value strategy.
9 Apparently, the capuchin females have not learned two value associations (e.g. washer =
10 Froot Loop and pipe = bell pepper) but instead have learned a single value association
11 (washer > pipe) and use this to complete the task. If our assumptions about what the
12 capuchins must know or understand in order to follow the High Value strategy are
13 correct, these females probably do not consider the explicit worth of each token but
14 instead, learn only to prefer the washer to the pipe. Thus, they return the washer more
15 frequently.

16 There are several alternative explanations for the females' behavior that we
17 cannot completely rule out. First, it may be that the capuchins are confusing this task with
18 the earlier token preference tests, and hence are simply demonstrating their preference for
19 the higher-value token. However, the capuchins have been subjected to food preference
20 tests for years with no confusion, the token preference tests and the value association
21 tasks were separated in time by several days, and the tasks were set up in a different
22 fashion. Moreover, the fact that this "confusion" occurs among the females, but not the
23 males, seems unlikely.

1 Another possibility is that the capuchin females may be “asking” for the higher-
2 value food, that is returning the token that matches the food they *desire* rather than the
3 food that is being offered. Finally, they may understand the action as barter, but they are
4 uninterested in the lower-value rewards to the point of ignoring them. Such behavior
5 would create a similar response. This last possibility could best be distinguished by using
6 food deprived individuals.

7

8 *Capuchin sex difference*

9 In this test, both males and females showed an equal preference for the higher-
10 value token in the Token Preference Test, but only females showed non-random
11 responses to the barter situation. Thus, the sex difference is in the utilization of
12 preferences, rather than the ability to form preferences *per se*. This sex difference is
13 somewhat surprising, but in line with some previous research. While, obviously,
14 comments on the basis of such a small sample size are speculative, the consistency with
15 which we found these results merits further attention.

16 One possibility is that there was some mechanical difference between the males
17 and the females that rendered the sex difference likely (e.g. perhaps the males were less
18 inclined to pick up washers from a flat surface). While this is always possible, the
19 relatively small degree of sexual dimorphism in this species leads us to believe it is
20 unlikely. We believe this result may be related to sex differences in reciprocal behavior
21 found previously in brown capuchins.

22 Several independent lines of evidence indicate that female brown capuchin
23 monkeys have been found to be more reciprocal than males in both food sharing (de

1 Waal, 1997a) and allogrooming (di Bitetti, 1997). In field situations, females allogroom
2 more reciprocally than males (di Bitetti, 1997). In experimental situations, capuchin
3 males share indiscriminately with almost all partners, regardless of return benefits,
4 whereas capuchin females share on a reciprocal basis, meaning that there is a contingency
5 between give and take (de Waal, 1997a). It has been hypothesized that this different
6 attitude to sharing and exchange may have evolved owing to different reproductive
7 strategies and societal pressures on males and females. Adult male capuchins residing
8 within a social group may increase their fitness by sharing indiscriminately with females
9 and juveniles in the group, as they are potentially the fathers of current and future
10 juveniles. On the other hand, females are reproductively vested only in themselves and
11 their offspring and can most increase their fitness by restricting sharing to their own
12 offspring and close female allies with whom they have a reciprocal relationship (de Waal,
13 1997a).

14 If a similar principle is involved in this material exchange task, this difference
15 between a paternal investment strategy by males and reciprocity by females may make
16 females more attuned than males to value in reciprocal interactions. For males, this
17 tendency to interact outside of reciprocal relationships may lead to them paying less
18 attention in our exchange task. Although they are as likely as females to prefer the higher
19 value token to the lower value one, they do not show a barter strategy which reflects
20 these preferences. Among females, their tendency to maintain reciprocal relationships
21 may make them more likely to follow some strategy during our material exchange task.
22 Although they fail to follow the strategy to maximize their receipt of rewards, they do

1 show a strong preference for high value tokens, returning them regardless of the reward
2 offered.

3

4 **Acknowledgments**

5 This research was made possible by a grant IBN-0077706 from the National
6 Science Foundation to the senior author, an NSF Graduate Research Fellowship to the
7 first author, and the NIH basegrant (RR-00165) to the Yerkes National Primate Research
8 Center. We are grateful to Laura Mullen, Lisa Bradley, and Jason Davis for assistance
9 with testing and data collection. We also thank the animal care and veterinary staff for
10 maintaining the health of our study subjects. Finally, we thank Kate Baker, Julian Bragg,
11 Bill Hopkins, and Harold Gouzoules for helpful discussion and several anonymous
12 reviewers for helpful comments on an earlier draft of the manuscript. The Yerkes Primate
13 Center is fully accredited by the American Association for Accreditation of Laboratory
14 Animal Care.

1 **Figure Captions**

2

3 *Figure 1:* The capuchin's preferences for the higher value food (Froot Loop) as compared
4 to their preference for the higher value token (washer), which was the token associated
5 with the Froot Loop. The capuchins preferred the higher value over the lower value for
6 both food and tokens, although the token preference was less strong than the food
7 preference. There was no sex-difference in preference for either the food or the token.
8 The line at 50% represents preferences expected by chance.

9

10 *Figure 2:* The percentage of tokens returned correctly (that is, tokens returned that were
11 associated with the proffered reward) in the unlimited barter situation, in which one of
12 each token was available for each exchange, and the limited barter situation, in which the
13 number of tokens was set at the commencement of the trial. The line at 50% represents
14 the percentage of correctly returned tokens expected by chance alone. The subjects did
15 not return the tokens that were associated with the proffered reward.

16

17 *Figure 3:* The percentage of washers returned in the unlimited barter situation, in which
18 one of each token was available for each exchange, and the limited barter situation, in
19 which the number of tokens was set at the commencement of the trial. For the limited
20 situation, the percentages on the Y-axis indicate the percentage of washers returned in the
21 first five (that is, the first half) of exchange sessions. The line at 50% represents the
22 percentage of returned washers expected by chance alone for both the unlimited and
23 limited token scenarios. There is a strong sex difference, with males returning washers at

- 1 chance levels only and females returning washers at higher than chance levels (indicated
- 2 by asterisk), supporting the Value Maximization hypothesis.

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