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Daniel Brubaker 14 April 2010

Qualitative and Quantitative Value Assessments of Food Rewards
by Brown Capuchin Monkeys
(*Cebus apella*)

by

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An abstract of
A thesis submitted to the Faculty of Emory College of Arts and Sciences
of Emory University in partial fulfillment
of the requirements of the degree of
Bachelor of Sciences with Honors

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Abstract

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The brown capuchin (*Cebus apella*) relies on extractive foraging behaviors to effectively exploit a wide range of ecological substrates for nutritional gain. The Extractive Foraging Hypothesis theorizes that these behaviors developed as a result of the increasing cognitive capabilities that coincide with increases in primate brain size. In turn these behaviors have provided the capuchin with a means of offsetting the energetic costs of evolving and maintaining such a large brain. This link between the complexities of foraging behavior and enhanced cognition is the focus of the present study.

The behavioral flexibility of the brown capuchin in making foraging choices was empirically tested, following a token-exchange paradigm well documented in the literature. A subsequent methodology of direct food choice was then introduced to flesh out the results of the token-exchange tests. Results suggest that brown capuchins fail to simultaneously consider both qualitative and quantitative differences between binary options at significant levels. Failure to exhibit high behavioral flexibility pertaining to relative food value assessment weakens either the foundation of the Extractive Foraging Hypothesis or the argument for co-selection between large brains and cognitive capacities, such as judgment of quality and quantity. Still, further value assessment research on the brown capuchin and other primate species is needed to confirm these findings.

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Introduction:

The foraging and dietary choices of animals correspond to the interaction between the derived benefits of a food source and the associated locating and handling costs. The primary aim then is to optimize nutritional value and net energy gained with respect to time expenditure. Factors including both relative availability and abundance of food sources, caloric content, and digestive capacities tend to influence dietary decisions (Pyke, Pulliam, & Charnov 1977).

Within the primate order, foraging strategies are relatively complex as many species place priority on a nutritionally balanced diet rather than a strict maximization of caloric intake. Wild primate species often consider both the quality and quantity of food sources available and ingested (Felton, Felton, Lindenmayer, & Foley 2009). This tendency toward seeking variety and the extent to which it is rooted in primate evolutionary history has been emphasized by recent findings. Not only does it allow for nutritional balance, but it diversifies the resource pools available thereby lessening dependencies on specific food sources (Addessi, Mancini, Crescimbene, Ariely, & Visalberghi 2010).

Brown Capuchin (*Cebus apella*) Background

The brown capuchin monkey serves as a prime example of a variety-seeking species with access to a diverse range of food resources. For this reason, use of the brown capuchin as a subject species in studies related to value assessment of food choices is logical and well-established within the literature.

The capuchin's diet is the closest of any new-world monkey to omnivory (Jack 2007) and demonstrates incredible diversity depending on time of day and season (Fragaszy, Visalberghi, & Fedigan 2004). Exhibition of such an extensive diet is largely accounted for by skillful extractive foraging techniques; and while the adaptive dental morphology of the capuchin provides them with the thickest tooth enamel of any extant primate, this strategy of food extraction is predominantly a product of behavioral evolution (Janson & Boinski 1992). Foraging techniques that rely on tool use, including nut-cracking behavior (Visalberghi 1987; Ottoni & Mannu 2001), as well as those that involve extraction of insects from tough substrates, provide capuchins with levels of protein that far surpass those of leaves and other plant material. These alternative sources insure that capuchins are not dependent on the availability of an abundance of leaf matter for their protein requirements (Janson & Boinski 1992). According to the Extractive Foraging Hypothesis these behaviors that collectively allow for approximate omnivory are derivatives of a larger brain (Dunbar 1996).

Recent research investigating the link between brain size and cognition proposes the use of absolute neuron number as a measure of cognitive faculty. In this model, there is evidence for a linear correlation between brain size and number of neurons exclusively within the primate order (Herculano-Houzel 2007). In the case of the brown capuchin, the development of extractive foraging behavior has provided them with the perennially high-energy diet required to offset the metabolic costs of a larger brain (Gibson 1986).

The brown capuchin lives in social groups ranging from an average of eighteen individuals in one source (Jack 2007), to a slight eight to fifteen in another (Anderson 2003). Intragroup relations follow linear hierarchies across both sexes, with males individually dominant over females except in the case of an alpha female who ranks below the alpha male (Jack 2007). Juvenile males disperse at sexual maturity (Anderson 2003).

Characterized by a polygynous mating system, reproductive access to females is regulated by and largely reserved for the alpha male (Anderson 2003). Without external swellings signaling ovulation, brown capuchins rely on other courtship signals including head tilting, eyebrow flashing, and grinning as indicators of sexual fertility (Jack 2007). Still other examples of social communication include social grooming, urine washing, and gesturing (Anderson 2003). One capuchin gesture, particularly relevant to the study at hand, involves the extension of an open palm in the direction of a food source, and is aptly classified as a begging gesture (de Waal 1997).

Qualitative Value in Non-human Primates

A significant portion of recent studies investigating primate understandings of qualitative value has used the brown capuchin as the subject species. The studies of Brosnan and de Waal (2003, 2004) have shown that brown capuchins, especially females, have a keen perception of relative equity and value in a social setting (Brosnan & de Waal 2003), recognition likely fostered by their social lifestyles (Brosnan & de Waal 2004). The existence of this sense of fairness stemming from value appropriation has since been disputed by subsequent experimental results (Fontenot, Watson, Roberts, & Miller 2007).

Still, even this subsequent study has substantiated that capuchins do develop food preferences, as the subjects willingly exchanged tokens for “low-quality” oat cereal when “higher-quality” grapes were not visible, but were more reluctant to exchange for cereal when grapes were in view (Fontenot et al. 2007).

Quality discrimination between types of food may seem an obvious and fairly ancient capacity demonstrated by the nutritional choices of many animal species. However, the ability to project established preferences for intrinsically valuable food rewards onto arbitrary tokens of no inherent value reflects a conceptual understanding of extrinsic, qualitative value. Studies have shown that brown capuchins develop preferences for tokens not only associated with variable types of food reward (Brosnan & de Waal 2004) but also with tools of varying utility to the capuchin subjects (Westergaard, Evans, & Howell 2007).

The subjects’ development of token preferences in the Brosnan & de Waal (2004) study has, by the nature of the experimental design, offered evidence for the social transmission of value, in that subjects established preferences for differentially rewarded tokens by observing token exchanges executed by a conspecific model. With every novel pair of tokens introduced, subjects developed preferences for the higher-value token after watching a capuchin model, provided with ten of each token, exchange the tokens for their corresponding values. On the other hand, simply seeing the tokens spatially and temporally associated with their corresponding values, without the presence of a conspecific exchanging them (nonsocial transmission), did not promote learning of token values by the subjects (Brosnan & de Waal 2004).

Capuchins also show a capacity to relate arbitrary tokens with different tools and will display varying preferences for a tool depending upon its circumstantial utility (Westergaard et al. 2007). Since the value of tools is not intrinsic but instead is extrinsically related to its utility, tools themselves can act as symbols of varying value depending upon the situation. In another study with brown capuchins, the experimenters exchanged pieces of food and a syrup-extraction tool directly with the subjects, determining the relative values of each object by noting which objects were readily traded for each other. The experimenters established that, in the presence of an apparatus baited with syrup, the capuchins preferred a grape over a syrup-extraction tool and the tool over a piece of chow. However, when the syrup apparatus was not baited, the value of the tool dropped below that of the piece of chow (Westergaard, Liv, Rocca, Cleveland, & Suomi 2004).

Quantitative Value in Non-human Primates

Studies designed to determine the non-human primate capacity for understanding quantitative value have demonstrated that capuchins can effectively learn ordinal relations (Beran, Harris, Evans, Klein, Chan, Flemming, & Washburn 2008), conserve quantity (Beran 2008), sum quantitative values assigned to arbitrary tokens (Addessi, Crescimbene, & Visalberghi 2007), and discriminate between quantities of large magnitude (Addessi, Crescimbene, & Visalberghi 2008).

Beran's (2005, 2008) quantity discrimination research has provided evidence for multiple features of quantitative understanding, features with broad implications regarding the timing of their development and presence across the primate order. Beran, Beran, Harris, & Washburn (2005) tested the understanding of ordinal relations first in the chimpanzee (*Pan troglodytes*) and rhesus macaque (*Macaca mulatta*), using different colored plastic eggs with varying quantities of a food reward enclosed. Subjects were given choices between two different eggs, or sets of various combinations of eggs; and they demonstrated the ability to select the option of greater value based on the enclosed quantities. The study results also include evidence for approximate cardinal value recognition; subjects picked seven visible rewards over a pink egg, with five non-visible rewards, but two pink eggs over seven visible rewards (Beran et al. 2005). A study conducted by Beran et al. in 2008, produced similar evidence for determination of ordinal relations between symbols in capuchin monkeys (Beran et al. 2008).

Capuchin monkeys also exhibit quantity conservation—recognition that physical rearrangement of an array does not impact array quantity—in choices between arrays of differing quantity. After correctly selecting the larger of two reward groupings, the larger grouping was manipulated without effect on quantity. Subjects disregarded the rearrangements and again chose the larger array (Beran 2008).

The ability of capuchins to discriminate quantity, while stronger in tasks involving choice between sets of directly visible food rewards, is still significant in tasks involving choice between sets of tokens, wherein token numerousness and number of food rewards follow a 1:1 ratio (Addessi et al. 2008). Using tokens, of varying token-to-food reward ratios, to represent extrinsic value, a few capuchin subjects have performed at least approximate summation. Two token types (A representing one food reward, and B representing three) were presented against each other in various quantities. Summation was suggested when subjects chose two B tokens over less than six A tokens (Addessi et al. 2007).

Similar, and perhaps clearer, evidence for summation also exists in squirrel monkeys (*Saimiri sciureus*) and their selection of the larger of two sets comprised of varying combinations of the Arabic numerals 0, 1, 3, 5, 7, and 9 (each numeral representing the number of treats corresponding to its magnitude) (Olthof, Iden, & Roberts 1997).

One of the only exchange studies to simultaneously involve qualitative and quantitative value in its design is that of Drapier, Chauvin, Dufour, Uhlrich, & Thierry (2005). The study investigated maximization of reward in brown capuchins achieved through delayed gratification. Gratification was delayed by executing a sequence of food exchanges with the experimenter, wherein capuchins could trade a small piece of food for a visible, larger piece of the same food or in exchange for a visible food reward of higher qualitative value (determined through preference testing). Exchanges of one food for another of higher quality were more common than exchanges of one food piece for a larger piece of the same food. But even rates of successful quality-based exchanges decreased when the qualitative difference between the two items involved was slight (Drapier et al. 2005). These results suggest that either value differences based on quality are more salient than those based on quantity, or simply that a greater preference exists for higher quality food over a larger quantity of lower quality food. The decline in exchange execution on account of minor qualitative differences may be best explained by the endowment effect—attribution of higher value to a securely possessed reward over a reward of similar or equal value not currently in possession—the existence of which has been demonstrated in brown capuchins (Lakshminarayanan, Chen, & Santos 2008).

One experiment within this Lakshminarayanan et al. study provides additional evidence for quantity discrimination within the token exchange paradigm. After determining that the subjects roughly valued apple and grape rewards equally, the experimenter exchanging apples began offering twice the quantity for the same price—one token. The exchange choices made by the subjects followed this shift in quantitative value and when presented with either a single grape reward or two apple rewards, they more frequently chose the latter (Lakshminarayanan et al. 2008).

Purpose of the Present Study

Due in part to their variable diet and in part to the extractive foraging behaviors—with correlations to brain size and cognition—that allow for such variety, it is hypothesized that brown capuchins will demonstrate behavioral flexibility in their food choices. In short, it is believed that brown capuchins can assess relative value between high and low quality food options when made available in varying quantities.

The present study aimed to simultaneously investigate understanding of qualitative and quantitative value in the brown capuchin. Following the token-exchange paradigm, four differentially colored tokens were assigned a quality (apple or cucumber) and a quantity (one or three), thereby exhausting every possible combination. After establishing subject quality and quantity preferences and ruling out initial, intrinsic preferences for the arbitrary tokens, the associated value for each token was demonstrated to the subjects. Each subject then completed a two-choice preference test for each of the six possible token pairs,[*] in which they repeatedly chose one of the two tokens presented in order to then exchange the selected token for its associated value.

These token pair preference tests were intended to serve as models for foraging contexts requiring the subjects to choose between two quantitatively and/or qualitatively different food options. By first taking the four tokens to be representations of four distinct food options, the quantitative and qualitative values assigned to the tokens[†] can then be taken to symbolize high and low levels of two nutrients, i.e. food high in sugar, food high in protein, food low in sugar, and food low in protein. Likewise, the four tokens may serve as representations of four distinct resource patches and the values assigned to the tokens would then correspond to the quantitative and qualitative values of the food patches, i.e. large patch of apples, large patch of cucumbers, small patch of apples, and small patch of cucumbers.

Stemming from a hypothesis that captive capuchins will concern themselves more with the quality of the food made available to them as opposed to the sufficiency of the quantity provided, one of the predictions was that quality token discrimination will be stronger than quantity token discrimination. It was expected that capuchins would differentiate between two tokens varying only in quality of associated food reward (i.e. 1 apple piece vs. 1 cucumber piece; 3 apple

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[*] 1 apple piece vs. 1 cucumber piece, 3 apple pieces vs. 3 cucumber pieces, 1 apple piece vs. 3 apple pieces, 1 cucumber piece vs. 3 cucumber pieces, 1 apple piece vs. 3 cucumber pieces, and 1 cucumber piece vs. 3 apple pieces

[†] High quality in large quantity, low quality in large quantity, high quality in small quantity, and low quality in small quantity

pieces vs. 3 cucumber pieces) at higher levels than two tokens varying only in quantity of associated food reward (i.e. 1 apple piece vs. 3 apple pieces; 1 cucumber piece vs. 3 cucumber pieces). Still, it was expected that capuchins would develop significant preferences in both cases.

Second, it was hypothesized that brown capuchins will flexibly adjust their preferences for food rewards when two options differ both in terms of qualitative and quantitative value. The prediction followed that, in the pair tests involving composite quantity and quality differences (i.e. 1 apple piece vs. 3 cucumber pieces; 1 cucumber piece vs. 3 apple pieces), the preferences established in the single-variable pair tests would shift appropriately as subjects factored in both variables simultaneously. Therefore, if the subjects show a preference for apple quality and high (three) quantity, then when presented with the 1 apple piece vs. 3 cucumber pieces token pair, these preferences would be in competition. Likewise, when presented with the 3 apple pieces vs. 1 cucumber piece token pair, these preferences would be expected to result in a compounding effect.

Methods:

Background

Subjects were 4, adult female, brown capuchin monkeys (*Cebus apella*) housed at the Yerkes National Primate Research Center in Atlanta, Georgia. Two monkeys from each of two separate living groups were chosen for their extensive experience exchanging tokens with researchers. Nancy [N0] and Winnie [W0] belong to social group one; Bias [B0] and Star [S0] belong to social group two. The separate group enclosures (measuring 3.4 x 8.2 m^2 and 4.1 x 8.2 m^2 for social groups one and two respectively) provide the inhabitants with both indoor and outdoor access. An opaque barrier denies visual and tactile (but not acoustic) contact between the two groups. Water and monkey chow is available *ad libitum*. Additionally, an enrichment meal consisting of a variety of fruits, vegetables, and bread soaked in a protein juice is provided at approximately 17:00 hrs daily. All procedures were approved by the Institutional Animal Care and Use Committee (IACUC) prior to beginning the experiment.

Testing Procedure and Timing

Testing always occurred between 10:00 and 17:00 hrs, before provision of the daily enrichment meal. Subjects were never required to complete multiple test sessions for the present study in one day, but may have participated in testing for concurrent projects as administered by other researchers within the laboratory.

During exchange tests, tokens were presented to the capuchin subject in a relatively large plastic container (23 x 15 x 7.5 cm). After each successful exchange made by the subject, apple or cucumber pieces (approximately 1.5 - 2 g each) were given as rewards. These food rewards were delivered in a smaller plastic container (9 x 6.5 x 5 cm).

Successful exchanges involved subject adherence to timing constraints as well as demonstration of compliant behavior. Subjects were given 30 seconds to obtain a single token and return it to the experimenter's outstretched hand. Instances in which subjects managed to grab multiple tokens were deemed failures, coded as FE (failed exchange), and resulted in a 30-second timeout period. Failure to comply with timing constraints, and throwing or dropping of a token outside of the test chamber was also coded as FE and resulted in the 30-

second timeout. When subjects successfully returned a single token within the 30-second time frame, they were rewarded with apple or cucumber pieces accordingly and given 15 seconds to eat before initiation of the next trial. When presented with 3 pieces of food, subjects typically selected and ate 1 piece at a time. The 15-second eating interval was not started until the subject had emptied the small plastic container of food rewards. In this way, subjects were given an adequate amount of time to ingest either quantity of reward. A digital stopwatch was used to track time.

Testing Materials and Apparatus

A testing chamber (measuring 155 x 61 x 64 cm) was positioned against the wall of one of the enclosures, allowing for the alignment of doors out of the enclosure and into the chamber. The subjects were eager to participate, approaching the test chamber with little prompting from the research team. Upon enclosing each subject within the test chamber an opaque panel was inserted into the chamber bisecting its length and providing the subject with a 77.5 x 61 x 64 cm testing space. The front wall of the testing chamber, a clear panel with multiple circular openings, allowed the subjects to extend an arm outside of the chamber to retrieve visibly desired items. The location of the testing chamber did not restrict vocal contact, but visual and tactile contact with group members was temporarily cut off. Four orange, plastic chain-links were used as tokens after being painted different colors in distinct patterns.

Figure 1: Tokens — black, blue, red, and yellow (5 x 2.5 x 0.5 cm)

The study involved a series of five test formats including controls: two food preference tests (a control test for quality and a control test for quantity), a control test for initial token preference, forced response familiarization sessions, and token pair choice tests. For tests involving options (control tests and token pair choice tests), the researcher avoided looking directly at any given options presented and stood centered behind the options so as not to influence the subjects' choices.

Food Preference Test: Quality Control

The subjects' preferences between apples and cucumbers were evaluated over 30 trials. Single pieces of cucumber and apple were simultaneously presented (one in each hand) to each individual subject. Both hands were held apart in front of the testing chamber allowing the subject to easily select either the piece of cucumber or the piece of apple. The distance between the hands disallowed selection of both simultaneously. Presented with the option, it was assumed that the subject reached first for the piece of fruit that was qualitatively preferred.

The supply of cucumber and apple pieces was kept out of sight so as not to direct their attention to either side of the testing chamber, a factor which may have influenced their proximity to one hand over the other and consequently affected their decisions. To avoid further side bias, the cucumber and apple pieces were randomly alternated between right and left hands. A Chi-square p-value of 0.01 was set as the criterion for this test, in determining a definitive food preference for one reward quality over the other.

Food Preference Test: Quantity Control

This test evaluated the subjects' preferences between two different quantities of a given food reward over 30 trials. Kix ® cereal was used as the reward in order to limit unequal test exposure to cucumbers or apples. A sliding tray apparatus was positioned next to the test chamber allowing the researcher to demonstrate the quantities being presented before giving the subject access to choose. Two clear containers were attached to the sliding tray (approximately 20 cm apart) and simultaneously 1 Kix ® was placed in one container while 3 Kix ® were placed (one at a time) in the second container. After sliding the tray toward the test chamber, the subject was able to reach and obtain food rewards from either of the two containers, but not both.

As in the quality test, the Kix ® supply was kept out of the subjects' sight and the addition of three Kix ® versus one into the containers was randomly alternated from right-to-left between trials. A Chi-square p-value of 0.01 was set as the criterion for this test, in determining a definitive food preference based on quantity.

Initial Token Preference Control Test

Each subject completed a single 20-trial session to determine whether the subjects, on average, demonstrated an inherent preference for one or more of the tokens prior to the establishment of associated value. All 4 tokens were presented simultaneously in the large plastic container. Before every trial, the 4 tokens were shuffled in the plastic container in order to randomize the spatial locations of the 4 tokens relative to each other and within the container. Successful selection and exchange of a single token in each trial was rewarded with 1 Kix ®, a generic reward provided without regard to token exchanged meant simply to reinforce the exchange behavior and reward the subject's effort. Session length was limited to 20 trials because of a tendency observed with these subjects in past token-exchange studies. During initial token preference tests in which the same reward is given for exchange of all tokens, subjects seem to recognize that all tokens provide them with the same reward and they eventually *become* fixated on one token although initially they exhibited no preference between the tokens. If too many trials are carried out with the same reward value assigned to each token, then preferences tend to develop where there were no preferences initially.

Forced Response Familiarization Sessions

Forced response sessions familiarized subjects with the assigned values which were counterbalanced to each of the 4 tokens. The 4 subjects each executed three separate 20 trial sessions. Each session consisted of 5 forced response trials with each token type. The ordering of these trials was randomized. Tokens were deposited one at a time in the test chamber with the subject and then exchanged for the corresponding reward (see Table 1 below) upon the subject's compliancy in returning each token. Before the reward was distributed, the token was visibly juxtaposed with the corresponding food reward, emphasizing the token values through simultaneous temporal and spatial association. Food rewards were then placed in the smaller plastic container and extended toward one of the circular openings in the test chamber. The three, 20 trial sessions were carried out on three separate days, providing the subjects with a total of 15 exposure trials to each token's value.

Table 1: Token Value Assignments

	Black	Blue	Red	Yellow
Bias	One Piece Cuke (1C)	One Piece Apple (1A)	Three Pieces Cuke (3C)	Three Pieces Apple (3A)
Nancy	Three Pieces Apple (3A)	Three Pieces Cuke (3C)	One Piece Apple (1A)	One Piece Cuke (1C)
Star	One Piece Apple (1A)	Three Pieces Apple (3A)	One Piece Cuke (1C)	Three Pieces Cuke (3C)
Winnie	Three Pieces Cuke (3C)	One Piece Cuke (1C)	Three Pieces Apple (3A)	One Piece Apple (1A)

Token Pair Choice Test

Each subject then carried out 6 separate pair choice sessions—in which they were presented with 2 tokens and were required to choose one to exchange—for each of 6 possible token pair combinations (1Avs1C & 3Avs3C, hereafter referred to as the Quality Tests; 1Avs3A & 1Cvs3C, hereafter the Quantity Tests; and 1Avs3C & 1Cvs3A, hereafter the Composite Tests). The sessions consisted of 20 trials. For each trial, the 2 tokens in question were first placed in the relatively large plastic container and shuffled in order to randomize the spatial locations of the tokens, thereby eliminating any side bias demonstrated by the subjects. Once the subject selected the desired token, the container holding the remaining token was removed from sight and the chosen token was requested from the subject using a one-handed, open palm begging gesture. Upon receipt of the chosen token, the token was again held up above the smaller plastic container and juxtaposed with the corresponding food reward before the reward was delivered to the subject. In instances where 3 rewards were required, this demonstration of association was repeated 3 times with each piece of food placed into the small container separately in order to increase the saliency of 3 rewards as opposed to a single reward of greater magnitude. In pair tests that involved 2 tokens of varying quantities, i.e. Quantity and Composite Tests, a 3 second delay was instituted in trials involving exchange of the single quantity token after juxtaposition of the token with the single reward. This delay accounted for the excess time needed to demonstrate the triple quantity reward.

A random sequence of 6 forced response trials (3 of each token in the pair being tested) was executed prior to each 20 trial pair test. These trials intended to refresh the subject's memory of the values associated with the tokens. The order in which each subject completed the 6 pair tests was randomly determined (Table 2 below) in order to eliminate preferences developed for a certain token simply because it was the preferred token in an earlier pair.

Table 2: Pair Choice Test Sequence

	1	2	3	4	5	6
Bias	1Avs1C	1Cvs3A	1Avs3A	1Avs3C	1Cvs3C	3Cvs3A
Nancy	1Cvs3A	3Cvs3A	1Avs3C	1Avs3A	1Cvs3C	1Avs1C
Star	3Cvs3A	1Cvs3C	1Cvs3A	1Avs3A	1Avs1C	1Avs3C
Winnie	1Avs3C	1Avs1C	3Cvs3A	1Avs3A	1Cvs3C	1Cvs3A

Data Analysis

Averages for all 4 subjects were calculated separately for both Quality Tests and then, if these two means were found to be homogeneous (G-test of heterogeneity), collectively analyzed with a replicate G-test of goodness-of-fit. If the G-test of heterogeneity found the means to be heterogeneous, then the two Quality Tests were analyzed separately with Chi-square tests of goodness-of-fit. A similar sequence of analysis followed for the Quantity Tests.

The results from the Composite Tests were analyzed with a 2 x 2 repeated measure ANOVA in order to separate the effects of the quality and quantity variables in these tests. This statistical technique also provided a measure of the interaction effect between the two variables for these bivariate pairs.

Results:

Controls

The results from the food preference control tests (Figure 2) demonstrate that the capuchins strongly favor apple over cucumber and three Kix ® food rewards over one. On average, subjects chose apple rewards over cucumber rewards 90% of the time. A Chi-square statistical test indicated that there is a highly significant difference between the observed data and the expected 50% ($X^2 = 76.800$, $p<0.001$). Preferences for three Kix ® over a single Kix ® were slightly weaker (M = 75.00%) and more variable (SD = 9.860) than their qualitative counterparts, yet still of high statistical significance ($X^2 = 30.000$, $p<0.001$).

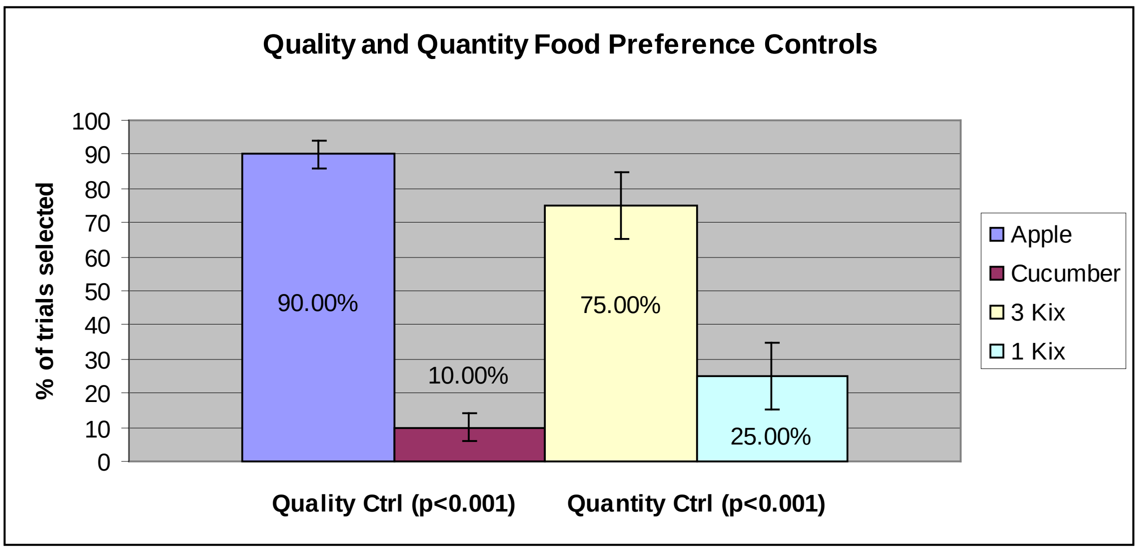

Figure 2: Food Preference Tests—mean percent (±SD=4.082) of quality control trials in which all subjects selected “apple” relative to “cucumber” (left); mean percent (±SD=9.860) of quantity control trials in which all subjects selected “3 Kix ®” compared to “1 Kix ®” (right)

Data from the third control test, for initial token preference, is displayed in Figure 3. The results from the Chi-square test indicate that 53% of the data can be explained by chance ($X^2 = 2.200$, $p = 0.53$). Observation of such a level of chance serves as an implication that, prior to assigned token value familiarization, none of the 4 tokens were intrinsically preferable across subjects. The standard deviations for selection of the four tokens were 1.639, 1.299, 1.090, and 2.487 for the black, blue, red, and yellow tokens respectively.

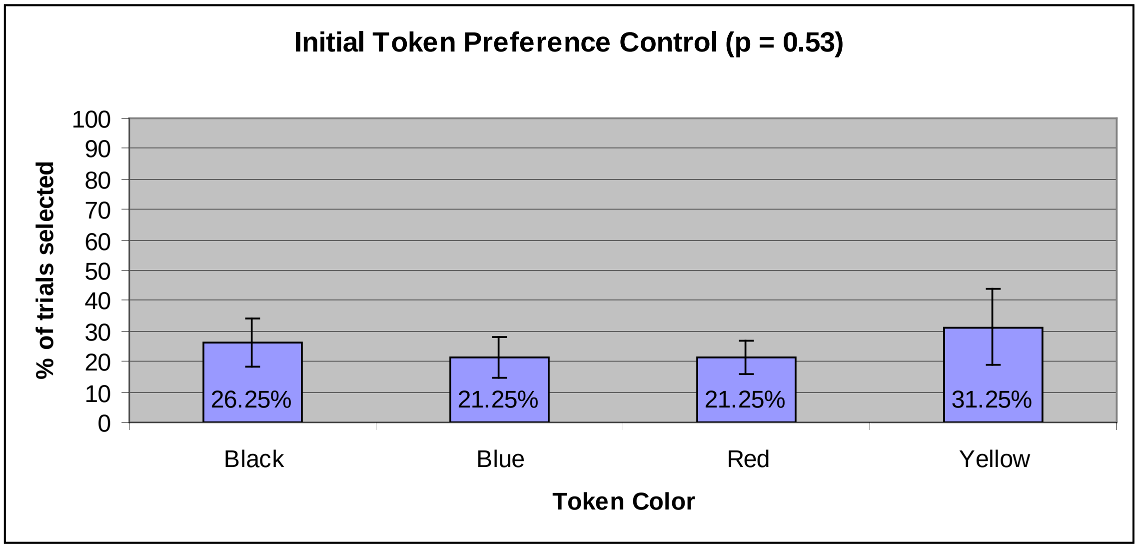

Figure 3: Mean percent (±SD) of trials in which each differentially colored token was chosen over the remaining three tokens

Token Pair Choice Test

Figure 4 displays the mean percent of successful exchanges for apples versus cucumbers, across all subjects, by combining the data from both Quality Tests (1Avs1C and 3Avs3C). A replicate G-test determined that the data from both sets was not heterogeneous ($G_h = 2.174$, $p = 0.14$), and could therefore be pooled. In the Quality Tests, apples were preferred over cucumbers 58.03% of the time. Although close ($G_p = 3.909$, $p = 0.048$), these results are not statistically significant at the decided 0.01 p-level. Compared to the qualitative control test, the data displayed in Figure 4 indicate a less established preference for apples over cucumbers within the framework of the token exchange model.

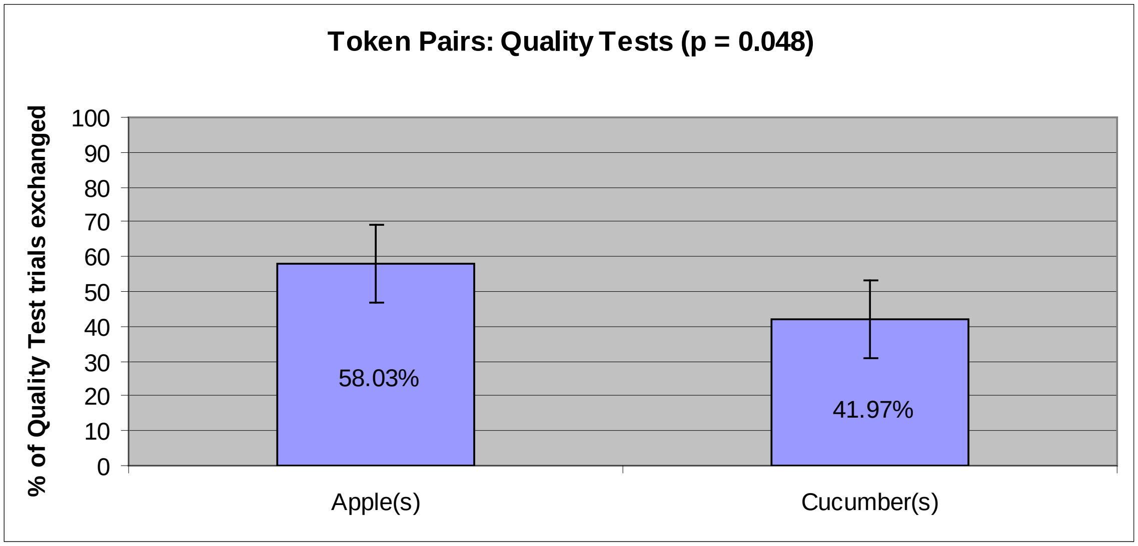

Figure 4: Mean percent (±SD=11.349) of Quality Test trials successfully exchanged for "apple(s)" compared to "cucumber(s)" across all subjects

Data from the two Quantity Tests are presented separately, because the two tests were determined to be significantly heterogeneous by a G-test of heterogeneity at the 0.05 p-level (G_h = 4.045, p = 0.044). As a result, the two tests were analyzed individually by means of Chi-square tests. The mean percent of successful exchanges for 3 apple pieces versus 1 apple piece are displayed in Figure 5. Subjects demonstrated a non significant preference for exchanging the 3A token over the 1A token (X^2 = 5.184, p = 0.16).

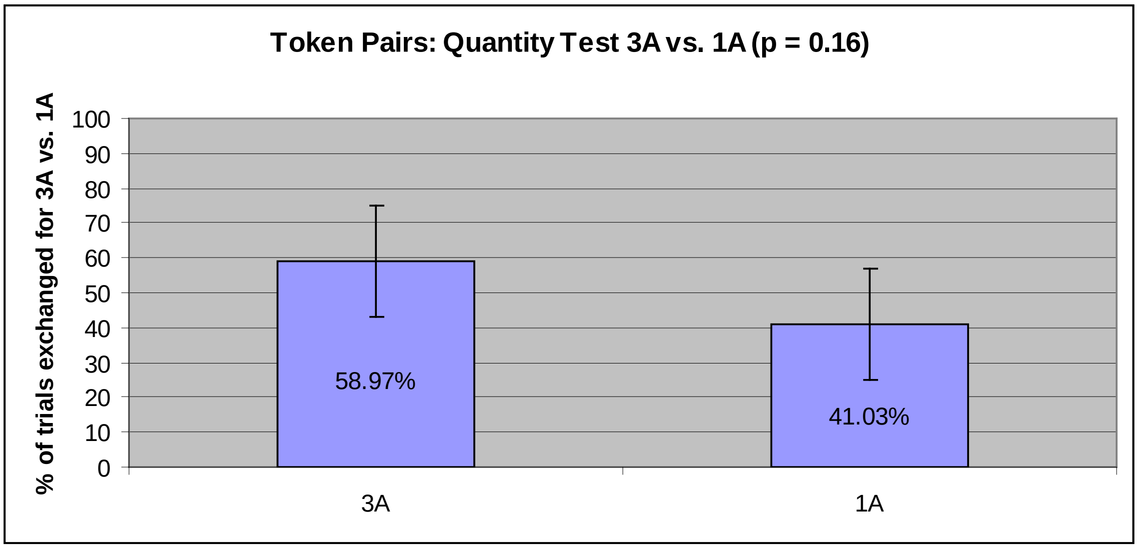

Figure 5: Mean percent (±SD=15.921) of 3A vs. 1A trials successfully exchanged for each reward across all subjects

Figure 6 displays the mean percent of successful exchanges for 3 cucumber pieces versus 1 cucumber piece. In this test, the subjects instead favored the lower quantity 1C token, choosing to exchange with it in 57.14% of the trials. Still, as with the data presented in Figure 5, the preference was non significant (X^2 = 1.237, $p = 0.74$).

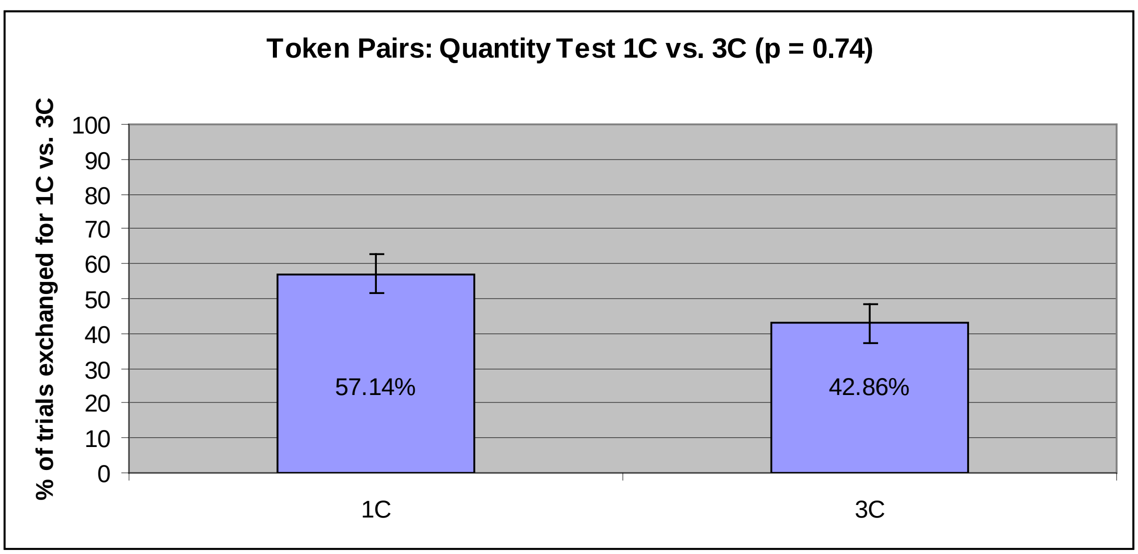

Figure 6: Mean percent (±SD=5.429) of 1C vs. 3C trials successfully exchanged for each reward across all subjects

Figure 7 graphically represents the data for each of the Composite Test pairings (1Avs3C and 1Cvs3A); displayed are the percentages that each token was successfully exchanged over its qualitatively and quantitatively disparate pair. The failure of the subjects to consistently project their preference for greater quantity onto the tokens is again apparent within these tests. In both cases, the percent preference for apples over cucumber approximately mirrors the percentages exhibited in the Quality Tests (58.03% and 41.97% from Figure 4); quantity seems to have no effect. Due to this lack of significant quantity discrimination within the token set, further analysis of the Composite Tests was unwarranted.

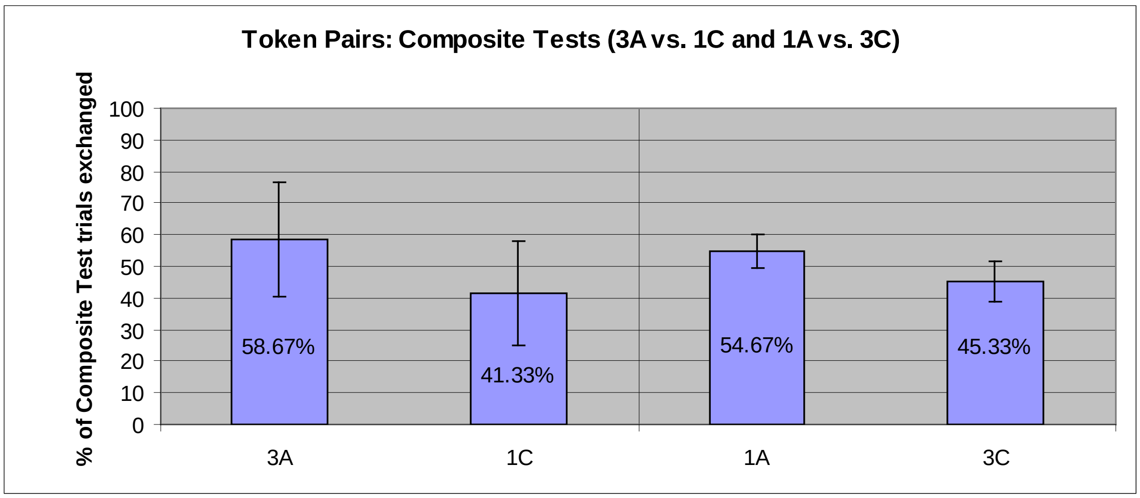

Figure 7: Mean percent of 3A (±SD=18.054) vs. 1C (±SD=16.549) trials (left) and mean percent of 1A (±SD=5.372) vs. 3C (±SD=6.267) trials (right) in which all subjects successfully exchanged the two options in each pairing

Follow-Up Methodology:

Food Pair Choice Tests

Due to the relative inability of the subjects to develop significant qualitative and quantitative preferences between pairs of tokens, the token pair choice methodology was modified. To allow for a more realistic model of capuchin foraging choices in place of the highly symbolic token exchange, tokens were eliminated from the procedure entirely. The subjects were instead presented directly with two food reward options as in the food preference controls. The Food Pair Choice Tests, while requiring less cognitive work by the subjects, is in many ways a purer test of the previously mentioned hypotheses.

The same sliding tray mechanism used for the quantity control test, complete with two attached plastic cups, was used for these tests. With the Quantity and Composite Tests, as was the case with the quantity control, one of each reward option was placed simultaneously in both cups and then two more rewards were added (one at a time) to the higher quantity option. The distribution of singular versus triple rewards between the two cups was randomized between trials, as was the distribution of apples and cucumbers in the Quality and Composite Tests.

Results from Food Pair Choice Tests:

The results for the direct food pair choice tests between apple(s) and cucumber(s) are shown in Figure 8. The data for the Quality Tests (1Avs1C and 3Avs3C) are again combined here (G_h=0.084, p=0.772). The average preference for apple(s) was determined to be 91.88%, a highly significant statistic (G_p=131.627, p<0.001).

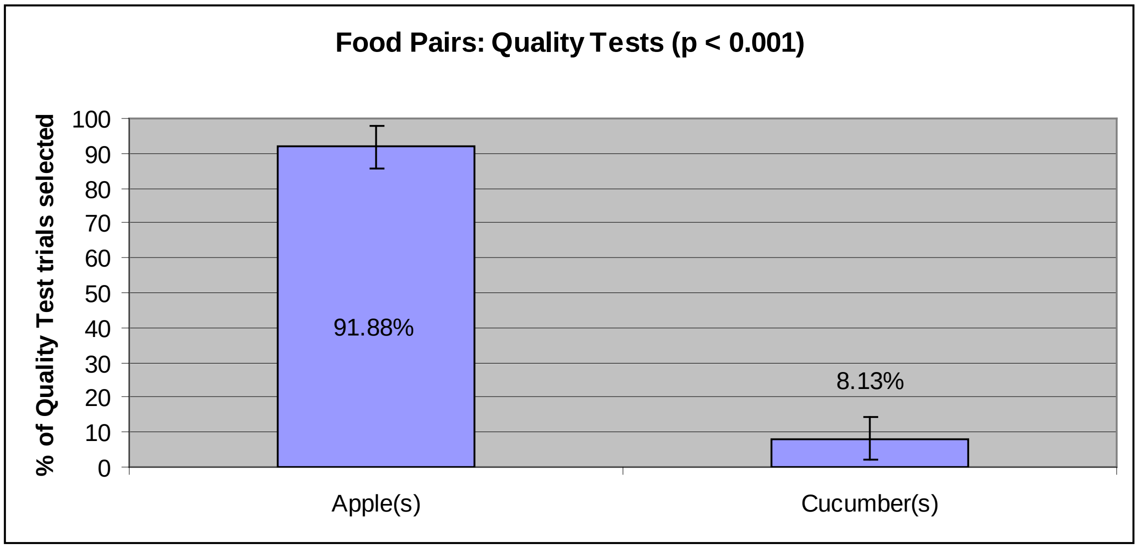

Figure 8: Mean percent (±SD=6.092) of Quality Test trials in which all subjects selected "apple(s)" compared to "cucumber(s)"

In Figure 9 the results from the Quantity Tests (1Avs3A and 1Cvs3C) are displayed together (G_h=0.051, p=0.822). When presented with food pairs, subjects preferred three rewards over one reward 85.63% of the time, exceeding the results obtained from the quantity control test (G_p=90.059, p<0.001).

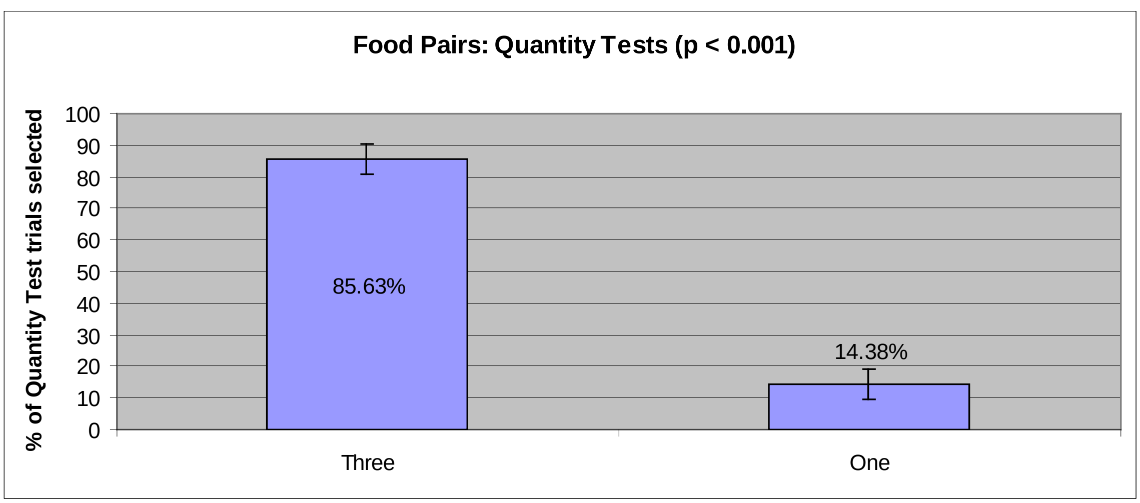

Figure 9: Mean percent (±SD=4.635) of Quantity Test trials in which all subjects selected "three" rewards compared to "one" reward

The results from the Composite Tests (1Avs3C and 1Cvs3A) are graphically represented in Figures 10-12 below. Figure 10 displays the data for both tests in terms of the percentage that each option was selected over its qualitatively and quantitatively disparate pair. The degree to which preference for apple increased (6.87%) with the increase in quantity (3Av1C test) was exceeded by the degree to which preference for cucumber increased (21.87%) with the increase in quantity (3Cv1A test). Likewise, the extent to which preference for three rewards increased (13.12%) with the rise in qualitative value (3Av1C test) was surpassed by the degree to which preference for a single reward increased (55.62%) with the rise in qualitative value (3Cv1A test). These shifts toward both lower quality rewards and single quantities suggest that the capuchins are adjusting their preferences for both variables when they are simultaneously present. The significance of these shifts was calculated using an ANOVA test.

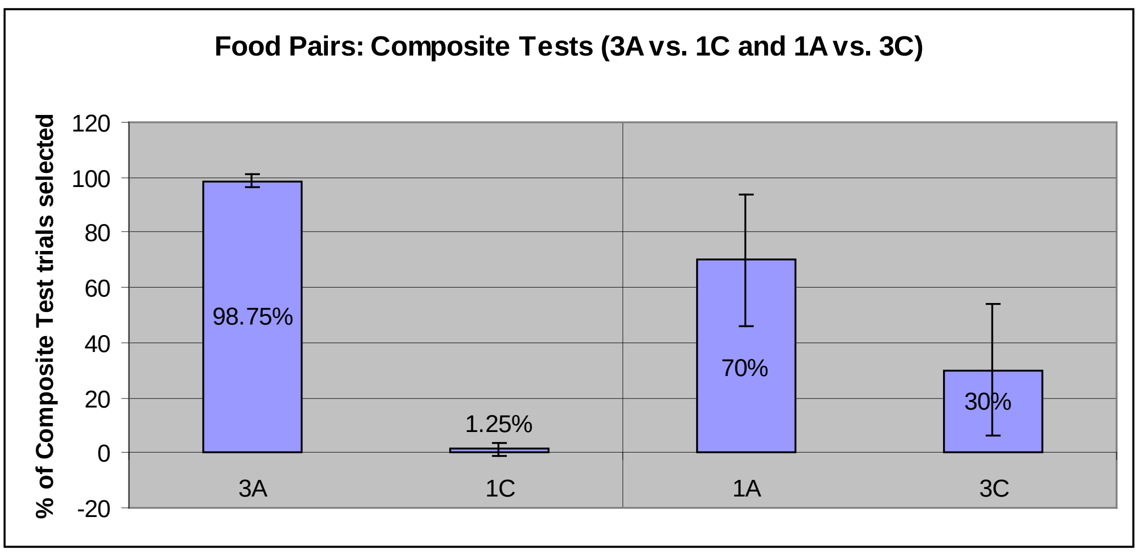

Figure 10: Mean percent (±SD=2.165) of 3A vs. 1C trials (left) and mean percent (±SD=23.717) of 1A vs. 3C trials (right) in which all subjects selected the two options in each pairing

Figure 11 displays the results from a 2x2 repeated measure ANOVA. Of the two main effects, only qualitative value was found to have a significant impact (F=26.77) on capuchin choices within the Composite Tests. The main effect of quantity was not significant (F=4.1) at α=0.01. The parallel relationship between the "cucumber" and "apple" series with respect to quantity indicates that there was not a significant interaction effect between the two variables.

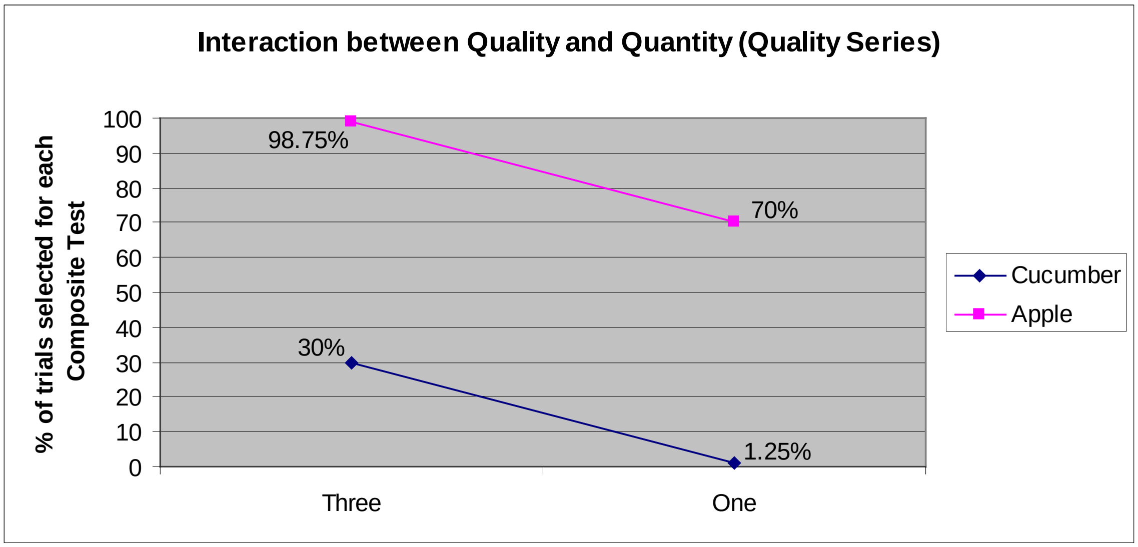

Figure 11: Non significant interaction between the main effects of quality (F=26.77, d.f.N.=1, d.f.D.=12) and quantity (F=4.1, d.f.N.=1, d.f.D.=12) as demonstrated by the Composite Tests (series displayed in terms of quality).

The ANOVA results are displayed again in Figure 12, the only difference being that in this case the quantity series are presented with respect to quality. The steeper slope of the lines in this graph relative to the graph in Figure 11, and the larger gap between the lines in Figure 11 relative to this graph, both serve to indicate the relative strength of the quality variable over quantity.

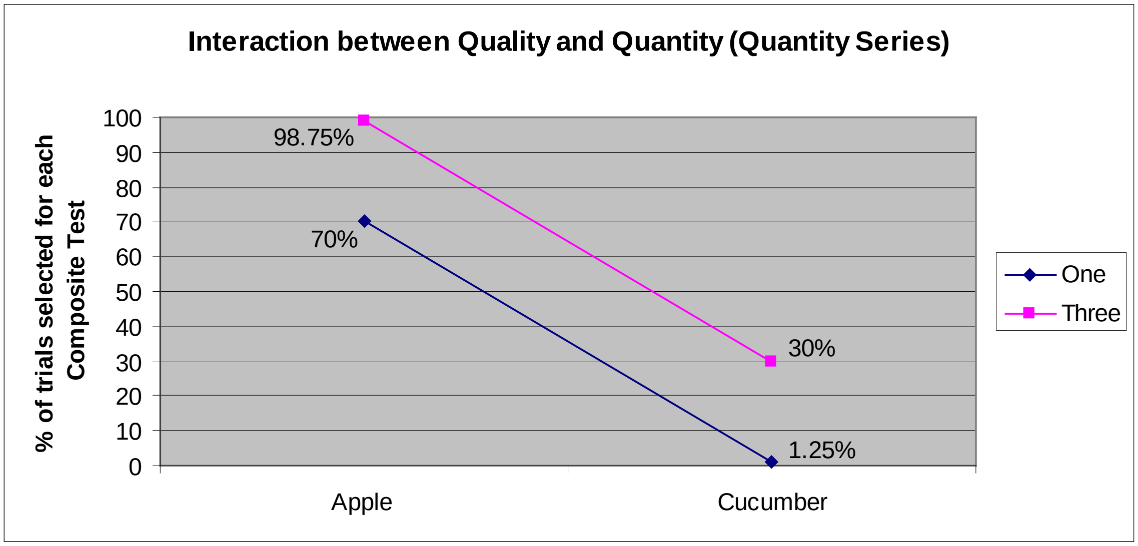

Figure 12: Non significant interaction between the main effects of quality (F=26.77, d.f.N.=1, d.f.D.=12) and quantity (F=4.1, d.f.N.=1, d.f.D.=12) as demonstrated by the Composite Tests (series displayed in terms of quantity).

Discussion:

Token Pair Choice Tests

The study results provide clear evidence that the capuchin subjects hold strong preferences both for apples over cucumbers and for greater quantities over smaller quantities of food rewards. The capabilities of the subjects in extending these preferences onto intrinsically valueless tokens diverged between the variables of quality and quantity. As hypothesized, the subjects projected their qualitative value preferences onto the 4 token set with a stronger correspondence than they managed with their quantitative value preferences. However, the subjects failed to develop statistically significant preferences in either category.

The strong preference among the subjects for apples, exhibited in the quality control test, is reduced to a non significant level (p=0.048) within the framings of token exchange. In previous studies, qualitative preferences have been projected onto tokens at significant levels (Brosnan & de Waal 2004). The slightly large p-value obtained in the present study may be attributed to the scope of the study, particularly to the use of 4 differentially-valued tokens where previous token studies carried out with these subjects have included only 2 differentially-valued tokens. Furthermore, while past studies assigned a single value to each token presented for exchange, the present study essentially assigned two values to each token, a quality and a quantity. The requirement of the subjects to attach two values to each of 4 tokens may have exceeded their capacity for symbolic comprehension. Repetition of these Quality Tests using a similar set of 4, bivariate tokens on a larger subject pool would provide useful data.

The complete inability of the capuchins to project quantitative value preferences consistently across the two Quantity Tests is undoubtedly due in large part to the aforementioned complexities of the token set. It is interesting that while the capuchins favored the higher quantity token in the pairing with the higher quality apple reward, they favored the single quantity token when exchanging for cucumbers. For the subjects, it seems there is more at stake in the former case and perhaps less motivation to discriminate quantity in the latter.

The performance of the subjects on the quantity tasks may have been impaired further by their lack of experience with the quantity variable; their involvement in previous token exchange studies has been centered on qualitative differences. Moreover, quantitative differences may simply not be cues of remarkable salience when compared to differences of quality. This result matches the difference in saliency proposed by Drapier et al. (2005) as an explanation as to why subjects were more willing to exchange a piece of food for a higher quality food reward as opposed to a larger piece of the same food type (Drapier et al. 2005). Without significant results in either the Quality or the Quantity Tests, analysis of the Composite Tests was unjustifiable.

Food Pair Choice Tests

When presented with two food options rather than extrinsically valuable tokens, the subjects demonstrated a significant preference for both apples within the Quality Tests and 3 rewards within the Quantity Tests. As anticipated, subjects discriminated differences in quality at higher levels than differences in quantity.

On the contrary, the results of the Composite Tests did not follow the expectations initially hypothesized for the Token Pair Choice Tests, as the subjects failed to demonstrate a significant interaction between quality and quantity. This finding indicates that the capuchins did not simultaneously factor in both the qualitative and quantitative disparities between the two options. In this case strong preferences for apple quality superseded preferences for 3 rewards over 1. Still, while the interaction effect between the Composite Tests was not significant, in these two tests combined the net preferences for both apples and 3 rewards were diminished relative to their strength in the Quality and Quantity Tests respectively. This decline suggests that both variables were taken into consideration, simply not at significant levels.

Implications for Foraging Behavioral Flexibility

The results of this study offer implications for the evolutionary pressures and preexisting adaptations that simultaneously selected and allowed for the development of complex value systems. One would expect that a multidimensional understanding of value is a prerequisite to an omnivorous feeding strategy. Considering the observable degree of omnivory within the capuchin diet, it stands to reason that capuchins should demonstrate complex value perception. That the subjects did not demonstrate significant consideration of both quality *and* quantity in bivariate scenarios is more likely a result of a minor flaw in the study design rather than an actual inability of capuchins to integrate the value classes. The value difference between 1 and 3 rewards did not match the value difference between apples and cucumbers; it is plausible that if these value differences were consistent then a significant interaction between qualitative and quantitative preferences would exist.

By developing the feeding strategy of omnivory, the cost imparted by conspecific competition over resources is alleviated in social living. With an increased variety of exploitable resources, in the long-term it may prove beneficial for group sizes to expand, and, with such expansion, selection for still larger brains is fostered. A process of circular selection results; a large neocortex allows for flexible behaviors, which, contextually, allows larger social groups, which in turn selects for large neocortices. This logic is an oversimplification resting on an assumption of ceteris paribus; the interaction between these features is dynamic and confounded by a multitude of factors. Still, similar studies of value across the primate order would serve to pinpoint the ecological contexts in which the possession of a large brain allows for the development of complex value perception. Further value research might also allow for an understanding of when, in our evolutionary history, these ecological contexts might have existed.

Directions for Further Research

Continued investigation into the value judgments of capuchins would be greatly beneficial in understanding the degree to which their foraging behavior is flexible. Some obvious directions for future research involve slight modifications to the present study design. Instead of using a single token to represent a single reward *and* multiple rewards, token numerousness could directly match reward numerousness, a format used by Addessi, Crescimbene, and Visalberghi. (Addessi et al. 2008). If the study were to be repeated within the framework of a token exchange, additional tests to verify the comprehension of token value by the subjects would be useful in ruling out the possibility that subjects formed only a tenuous understanding of the tokens' extrinsic values through the familiarization sessions. Such tests might follow an inverse procedure, providing the subject with each possible token pair, alternately presenting the food reward associated with one of the tokens provided, and rewarding the subjects when the correct token was selected for exchange.

Alternatively, inclusion of tokens in the study design may be removed altogether resulting in the format followed in the Food Pair Choice Tests. It seems likely that a threshold exists past which a larger quantity of low quality rewards would be favored over a single reward of high quality. Perhaps the most beneficial follow-up study would investigate the point at which quantitative differences become substantial enough to interact with variable qualitative value at significant levels. Since there is strong evidence of capuchin preference for higher quantities, the value disparity between the two quantity categories should match the value disparity between apples and cucumbers. The higher quantity category should be determined such that the selection for such a quantity over a single reward matches the selection for apples over cucumbers.

Conclusion

Although the capuchins failed to establish preferences amongst the 4, bivariate tokens, they do recognize food reward value both qualitatively and quantitatively. Still, while their preferences shifted in predictable directions when presented with options that differed across both value classes, neither the interaction effect between the two variables nor the main effect of quantity alone was significant. These findings are unusual given the observed feeding flexibility and omnivorous tendencies of the brown capuchin. It was expected that this study would provide support for the Extractive Foraging Hypothesis and parallels between brain size and feeding strategies in general—correlations that, if consistently confirmed, have strong implications for the behavioral ecology of primates. The results instead deny claims for such a correlation, but further research involving more highly disparate quantity categories is necessary in confirming or contradicting the evidence.

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