Published in final edited form as:
Behav Processes. 2015 February ; 111: 118–126. doi:10.1016/j.beproc.2014.11.004.

Defining Value Through Quantity and Quality –Chimpanzees (*Pan troglodytes*) Undervalue Food Quantities When Items are Broken

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Abstract

Decision-making is largely influenced by the relative value of choice options, and the value of such options can be determined by a combination of different factors (e.g., the quantity, size, or quality of a stimulus). In this study, we examined the competing influences of quantity (i.e., the number of food items in a set) and quality (i.e., the original state of a food item) of choice items on chimpanzees' food preferences in a two-option natural choice paradigm. In Experiment 1, chimpanzees chose between sets of food items that were either entirely whole or included items that were broken into pieces before being shown to the chimpanzees. Chimpanzees exhibited a consistent bias for whole food items even when such choice options consisted of a smaller overall quantity of food than the sets containing broken items. In Experiment 2, chimpanzees chose between sets of entirely whole food items and sets of initially whole items that were subsequently broken in view of the chimpanzees just before choice time. Chimpanzees continued to exhibit a bias for sets of whole items. In Experiment 3, chimpanzees chose between sets of new food items that were initially discrete but were subsequently transformed into a larger cohesive unit. Here, chimpanzees were biased to choose the discrete sets that retained their original qualitative state rather than towards the cohesive or clumped sets. These results demonstrate that beyond a food set's quantity (i.e., the value dimension that accounts for maximization in terms of caloric intake), other seemingly non-relevant features (i.e., quality in terms of a sets original state) affect how chimpanzees assign value to their choice options.

Keywords

Chimpanzees; Relative quantity judgment; Conservation; Decision-Making; Value; *Pan troglodytes*

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1. Introduction

Imagine yourself in the cereal aisle of your local supermarket. As you navigate the countless alternatives (e.g., wheat versus corn, sweetened versus healthy, bargain versus premium), you weigh multiple options' relative value in an effort to generate a clear consensus for one choice over the others. Thus, value guides choice behavior, but what determines value? Many factors likely add to the determination of value. However, in some contexts, one can generate relatively simple and easy to understand value relations. For example, using a two-option choice task, a food's relative quantity, size, or quality can dictate value in a combinatorial manner when an individual is choosing among alternatives. Interestingly, because value may be comprised of multiple features, one dimension of an alternative's value (e.g., the nutritional quality of the cereal) may be at odds with a second dimension of that same option's value (e.g., the price of the cereal). And, of course, for humans a number of these factors relate to issues of observational and cultural learning (e.g., what time of day one is supposed to eat certain kinds of food, etc.).

The study of choice behavior and value has been a major topic of inquiry in comparative cognition because, in many ways, one can assume that nonhuman animals make choices largely devoid of the cultural biases or expectations that frequently impact human food choice behavior. Choice behavior by animals often is assessed through food-based discrimination tasks. Food-based discrimination tasks present highly motivating choice options and the stimulus properties are easily manipulated on multiple dimensions. The commonly used relative quantity judgment paradigm requires subjects to choose between two sets of items that differ in the amount or number of items in each set. This paradigm, also known as the natural choice paradigm when food items are used (Silberberg et al., 1998) has many advantages for testing value assignment among animals. Relative quantity judgments of food items require little to no training because they make use of motivating edible rewards. In addition, there is high spatial contiguity between the stimulus, the response loci, and the reward (i.e., the animal immediately receives the chosen set for consumption). Finally, the paradigm produces direct and reliable measurements of food size and quantity preferences (Menzel, 1961). Because food quantity is an extremely salient factor relevant to an animal's survival, it is no surprise that a wide range of species have proven to be successful in these quantity discrimination tasks. The species include but are not limited to salamanders (Krusche et al., 2010; Uller et al., 2003), robins (Garland et al., 2012), dogs (Ward and Smuts, 2007), elephants (Perdue et al., 2012), marine mammals (Abramson et al., 2011), and a variety of nonhuman primates (e.g., Addessi et al., 2008; Beran, 2001, 2004, 2012, Beran and Beran, 2004; Boysen and Bernston, 1995; Call, 2000; Hanus and Call, 2007). Thus, the ability to accurately select the larger of two food quantities appears to have a long evolutionary history in the animal kingdom. These results are unsurprising given the highly adaptive nature of differentiating food quantities toward the end of maximizing intake (Stephens and Krebs, 1987).

Chimpanzees (*Pan troglodytes*) have been of particular interest in research regarding quantitative capacities of nonhuman animals. They demonstrate high proficiency in a wide range of testing conditions, including discriminating between slight differences in food sizes to a degree that rivals and sometimes exceeds the abilities of human adults (e.g., Menzel, 1960, 1961; Menzel and Davenport, 1962). Chimpanzees are successful in discriminating between food sets when the items are presented in different temporal styles (i.e., sequentially or simultaneously) and in different modalities (i.e., visually or auditory). Moreover, they are successful in quantity discriminations after long durations and when only one set is made visible throughout the choice phase (e.g., Beran, 2001, 2004, 2012; Beran and Beran, 2004; Boysen and Berntson, 1995; Dooley and Gill, 1977; Hanus and Call, 2007, Rumbaugh et al., 1987; Sayers and Menzel, 2012).

Despite their aptitude on relative quantity judgment tasks, however, a number of seemingly non-relevant factors sometimes influence chimpanzees' quantity judgments. For example, Parrish and Beran (2014a) demonstrated that chimpanzees were proficient in selecting the larger of two foods when both were plated on the same-sized plates. However, when foods were presented on different-sized plates, chimpanzees erroneously preferred an equal-sized food or a smaller food plated on a small plate relative to a truly larger alternative on a large plate. These same chimpanzees were accurate in differentiating food quantities presented in same-sized containers. However, they often showed a bias towards an equal or smaller amount of food when that amount was presented in a smaller, yet seemingly fuller cup (Parrish and Beran, 2014b). Thus, perceptual illusions appear to affect food choice behavior in chimpanzees in many of the same ways as they do for humans (e.g., Van Ittersum and Wansink, 2012; Wansink, 2006; Wansink et al., 2006).

Moreover, chimpanzee quantity discrimination sometimes is influenced by the properties of the individual elements that comprise a set. For example, two studies reported that chimpanzees were proficient at selecting the larger of two sets of food items but performance suffered if the smaller set contained the overall largest single item of food within it (Beran et al., 2008; Boysen et al., 2001). These studies demonstrated that chimpanzees relied on multiple features of food sets to discriminate quantity. They assigned value to alternative dimensions, including non-relevant stimulus properties or contextual variables. Thus, multiple features of food sets likely play a key role in quantitative decision-making with the end result sometimes being choice of less food over more food. Demonstrating discrimination errors and biases in a nonhuman species like the chimpanzee aids in elucidating the variables that shape our own perception of food value. Furthermore, investigating how value is constructed within the chimpanzee is informative as we can study this phenomenon in a nonhuman animal species that is highly food motivated and extremely adept at quantity discriminations.

In addition to understanding how individuals react to how much food is available in a given choice option, there is also value in understanding what happens when the quantity of a food stimulus is at odds with its quality. Hsee (1998) conflated an option's quantitative value with its qualitative value in a decision-making study. Human participants were given an option between two sets of dinnerware. One contained fewer overall dishes, and none of them were broken. The alternative contained more overall dishes, but some were broken. Notably, the latter set contained at least as many unbroken dishes as the first set. Despite an equal number of unbroken dishes in each set, participants overvalued the first set with fewer overall dishes relative to the latter set that also contained some broken pieces in a sequential evaluation.

This finding was labeled the "less-is-better" effect; the preferred option's qualitative value (cohesiveness) outweighed its quantitative value (numerousness of the intact pieces).

We investigated this "less-is-better" phenomenon in chimpanzees by exploring how value was affected by the relative quality of food items in a set (i.e., the cohesiveness of each set), even if this was inconsistent with the set's relative quantity (i.e., the overall quantity of food in each set). Here, quality was defined as the cohesiveness of the set as this reflects the originally intact state of the food items presented. We manipulated the degree of set cohesiveness by breaking some or all of the items within one set in a relative quantity judgment task. We compared the chimpanzees' performance in these test trials to control trials in which the chimpanzees chose between sets that both were made up of broken or non-broken items. These control trials allowed us to establish baseline performance rates and to ensure that the chimpanzees were capable of choosing the larger quantity when the potential bias towards cohesiveness could not occur.

When the chimpanzees sometimes preferred lesser quantities of whole items, we next assessed whether we could attenuate such biases by providing the chimpanzees with additional information about each set prior to the choice phase. To do this, we broke food items in front of the chimpanzees after they had seen all items in their unbroken state. The motivation for Experiment 2 was based in Piagetian conservation tasks in which quantities are spatially transformed within the subject's view (Piaget, 1965). The question in such conservation tasks is whether the subject can retain the initial choice of a larger quantity despite its newly altered presentation style. The new presentation style may present the quantity in a manner that makes it appear to be a different amount because of the size and shape of the new container that holds it. Several great ape species including chimpanzees are successful in these paradigms, accurately selecting the larger quantity even after its spatial transformation (e.g., Call and Rochat, 1996; Muncer, 1983; Suda and Call, 2004, 2005; Woodruff et al., 1978). In Experiment 2, we adopted this general approach by first presenting the chimpanzees with sets that were completely intact in their original form. Following this stage, the experimenter then broke all items in the larger set in front of the chimpanzees, after which the chimpanzees made their choice between the alternatives. If the chimpanzees conserved the value of each set from its initial, non-broken presentation, they should accurately select the larger set despite its newly broken state. This would help to differentiate a quantitative error (i.e., a misperception of how much food there is when it is broken) from a qualitative bias (i.e., a devaluation of broken food items that were formerly whole, regardless of knowledge regarding quantity).

Finally, we explored the reverse scenario to determine whether the chimpanzees truly were biased against non-cohesive sets, or instead were biased towards food items that retained their original state. For Experiment 3, we presented a set of discrete food items (mini marshmallows) that could be transformed into a larger cohesive unit. If the chimpanzees were biased towards cohesive sets, they should have preferred the set with marshmallows clumped together. But, if the chimpanzees instead were biased towards food items that preserved their original quality or state, they should have preferred the set of discrete marshmallows over the clumped option.

2. Experiment 1

2.1 Methods

2.1.1 Subjects—Four chimpanzees housed at the Language Research Center of Georgia State University participated in this study including two females (Lana – 43 years, Panzee – 28 years) and two males (Sherman – 40 years, Mercury – 27 years). All chimpanzees participated in Phase 1 and three of the four chimpanzees participated in Phase 2 (before completing the experiment, Panzee died from complications related to a long-term illness for which she was receiving regular veterinary care). All chimpanzees were housed together in the same building and spent time together in social groups daily, but they voluntarily separated for test sessions. Chimpanzees participated for preferred food rewards and were otherwise maintained on their normal diet of fruit, vegetables, and primate chow (no food or water deprivation was used). All four chimpanzees had extensive prior experience making choices between different quantities of foods (e.g., Beran 2001, 2004, 2012; Beran and Beran 2004; Beran et al., 2009a, b; Parrish and Beran, 2014a, b; Rumbaugh et al., 1987).

2.1.2 Apparatus—In each trial, we presented individual chimpanzees with choices between two quantities of preferred food items. The food items were either cheese-flavored crackers (37 mm square crackers) or potato chips (42 mm × 65 mm oval chips). The arrangements of these foods occurred in a nearby kitchen in which the foods were placed on two round light blue plastic plates (23 cm diameter). These plates then were carried into the test area and were placed on opposite ends of a sliding shelf mounted on top of a plastic test cart. When the experimenter slid the shelf forward, the chimpanzee indicated its choice of one plate of food or the other by pointing to that plate. The test cart also included an opaque blind that could be lowered completely to prevent the chimpanzee from viewing the food items before the beginning of the trials. During the choice phase, the blind was raised partially so the chimpanzee could only view the plates and the experimenter could only view the chimpanzee’s hands while a response was being made. This prevented the experimenter from providing inadvertent cues to the chimpanzee. These choices by the chimpanzees were unambiguous in terms of direct points to one of the two options that were spatially separated by approximately 20 cm in every trial.

2.1.3 Design and Procedure—We presented chimpanzees with a variety of food presentations, some of which included whole items, some of which included broken items, and some of which included a mix of whole and broken items (see Figure 1). Each set of food items was prepared by Experimenter 1 (E1) in a nearby kitchen (3 to 4 m from the chimpanzee’s test area) and out of view of the chimpanzee. E1 prepared any broken items by snapping them into at least 4 pieces and then placing those pieces on the plate close to one another so that an individual item still retained some degree of its spatial contiguousness despite being broken (for examples, see Figure 1). After preparing the food plates, E1 carried them to the test area and gave them to Experimenter 2 (E2), who placed them on the test cart between the blind and herself. E2 then raised the blind approximately 10 cm and slid the shelf (and food plates) toward the chimpanzee. E2 observed and recorded the chimpanzee’s selection of the left or right food plate. Following the chimpanzee’s selection, E2 immediately delivered the contents of the chosen plate to the chimpanzee. The selected foods were placed into a bowl that was then given to the chimpanzee so that there was a consistent delivery rate no matter the contents of the selected set (whole or broken items). The chimpanzees were prevented from taking the food items off of the plates by the wire mesh separating the animals from the experimenter. The experimenter delivered the food via the bowl by sliding it underneath the mesh following the chimpanzee's selection. This process was repeated for 10 to 20 trials per chimpanzee, per day, depending upon each chimpanzee's motivation to continue working on the task.

2.1.3.1 Testing Phase 1: We presented two trial types in this phase: homogeneous trials and heterogeneous trials. A homogeneous trial consisted of choice options that contained either all whole or all broken food items. There were three homogeneous quantity comparisons: 3 whole items vs. 4 whole items, 4 whole items vs. 4 broken items, and 3 whole items vs. 4 broken items. Heterogeneous trials consisted of one choice option that contained a combination of whole and broken items. There were two heterogeneous quantity comparisons: 4 whole items vs. 3 whole items + 1 broken item, and 3 whole items vs. 3 whole items + 1 broken item.

For all testing sessions, we randomized the side (right or left) on which the larger quantity was placed across trials. Additionally, we randomized trial type within and across sessions for all phases. The chimpanzees each completed 100 test trials, with 20 trials of each trial type in Phase 1.

2.1.3.2 Testing Phase 2: In this phase, we presented four trial types. Three of these were homogenous trial types: 3 broken items vs. 4 broken items; 2 whole items vs. 4 broken items; and 3 whole items vs. 5 broken items. There also was one heterogeneous trial type: 3 whole items vs. 2 whole items + 2 broken items. Because there was no difference in performance across food types in Phase 1 (see Results below), we used only chips in Phase 2. Chimpanzees each completed 48 test trials, with 12 trials per trial type in Phase 2. See Table 1 for the trial types presented in Phase 1 and Phase 2.

2.2 Results

2.2.1 Testing Phase 1—All statistical tests were 2-tailed. We first compared performance in each trial type to determine whether choice behavior differed as a function of the type of food that was presented using a Fisher's exact test. There was not a significant difference across food types (crackers versus chips) in the proportions of choices of either option in any of the conditions: 3 whole vs. 4 whole ($p = 0.49$), 4 whole vs. 4 broken ($p = 1.0$), 3 whole vs. 4 broken ($p = 0.36$), 4 whole vs. 3 whole + 1 broken ($p = 0.11$), and 3 whole vs. 3 whole + 1 broken ($p = 1.0$). Thus, we collapsed across food type for the remaining analyses.

For all trial types, we analyzed whether each chimpanzee exhibited a significant preference for either choice option using individual binomial tests. The results for each chimpanzee for both test phases are shown in Table 1. In the homogenous trial types, all chimpanzees had a significant preference for the larger non-broken quantity (4 whole items) to the smaller non-broken quantity (3 whole items; all chimpanzees, $p < .001$). Additionally, all chimpanzees preferred the equal-quantity presented in the non-broken set (4 whole items) to the equal-quantity broken set (4 broken items; all chimpanzees, $p < .001$). And, all chimpanzees preferred the smaller quantity presented in the non-broken set (3 whole items) to the larger quantity broken set (4 broken items; Sherman $p < .001$, Mercury $p < .001$, Panzee $p < .001$, and Lana $p = .003$).

In the heterogeneous trial types, Sherman, Mercury, and Panzee had a significant preference for the equal-quantity non-broken set (4 whole items) over the partially-broken set (3 whole items + 1 broken item; Sherman $p < .001$, Panzee $p < .001$, and Mercury $p < .001$), but Lana did not ($p = .26$). Sherman, Panzee, and Lana had a significant preference for the larger quantity presented in the partially-broken set (3 whole items + 1 broken item) to the smaller quantity presented in the non-broken set (3 whole items; Sherman $p < .001$, Panzee $p = .04$, and Lana $p < .001$), but Mercury did not ($p = .12$).

We also compared each chimpanzee's performance between select pairs of trial types using individual Fisher's exact tests. First, to determine whether the chimpanzees made more errors (i.e., choices of the smaller quantity) if the larger quantity was *entirely* comprised of broken items, we compared each chimpanzee's performance in the 3 whole vs. 4 whole trials to their performance in the 3 whole vs. 4 broken trials. All chimpanzees performed better in choosing the larger quantity of food when both sets contained all whole items than when the larger quantity of food was comprised of broken items (all $p < .001$).

Also, to determine whether the chimpanzees made more errors if the larger quantity was *partially* comprised of broken items, we compared each chimpanzee's performance in the 3 whole vs. 4 whole trials to their performance in the 3 whole vs. 3 whole + 1 broken trials using a Fisher's exact test. Mercury made more errors in the latter trials (Mercury $p = .02$), but this was not true for the other chimpanzees that showed no difference in performance (Sherman $p = 1.0$, Panzee $p = .18$, and Lana $p = .49$).

2.2.2 Testing Phase 2—As in Phase 1, we analyzed whether each chimpanzee showed a preference for either choice option in each trial type using individual binomial tests (Table 1). When both sets contained all broken items, all chimpanzees had a significant preference for the larger quantity (4 broken items) compared to the smaller quantity (3 broken items; Sherman $p = .04$, Mercury $p = .04$, and Lana $p < .001$). For the 2 whole vs. 4 broken trial type, Sherman had a significant preference for the smaller quantity presented in the non-broken set (2 whole items) to the larger quantity presented in the broken set (4 broken items; $p = .04$), but Mercury and Lana did not (Mercury $p = .77$ and Lana $p = .39$). For the 3 whole vs. 5 broken trial type, Sherman and Mercury had a significant preference for the smaller quantity presented in the non-broken set (3 whole items) to the larger quantity presented in the broken set (5 broken items; Sherman $p < .001$ and Mercury $p = .04$), but Lana did not ($p = .39$). Finally, for the partially broken set, all chimpanzees were indifferent between the smaller quantity presented in the non-broken set (3 whole items) and the larger quantity presented in the partially broken set (2 broken items + 2 broken item; Sherman $p = .39$, Mercury $p = .77$, and Lana $p = .39$).

Next, to determine whether the chimpanzees made more errors (i.e., choices of the smaller quantity) if the larger quantity was partially comprised of broken items, we compared performance in the 3 whole vs. 4 whole trial type from Phase 1 to their performance in the 3 whole vs. 2 whole + 2 broken trial type from Phase 2 using a Fisher's exact test. All chimpanzees made more errors in the latter case (Sherman $p < .001$, Mercury $p < .001$, and Lana $p = .01$).

2.3 Discussion

In Experiment 1, chimpanzees selected the larger quantity of food with all other presentation aspects being equal (i.e., if both sets were broken or both sets were whole). However, comparing sets of whole food items to sets of broken food items disrupted the chimpanzees' preference for larger quantities. If quantities were equal between sets, there was a clear preference for sets of whole items over sets with some or all items that were broken. Additionally, chimpanzees sometimes preferred smaller sets of whole items over larger sets with some or all broken items. In Phase 1 using a 1-item difference, all chimpanzees preferred a smaller set of whole items to a larger set of broken items. This effect diminished for some chimpanzees when we introduced a larger discrepancy (2-item difference) between sets in Phase 2. These were clear errors with regard to maximizing intake, and were consistent with previous studies that have reported failures by chimpanzees to select the larger quantity as a function of presentation style or set composition (e.g., Beran et al., 2008; Boysen et al., 2001; Parrish and Beran, 2014b).

3. Experiment 2

In Experiment 2, we explored whether we could attenuate the choice biases observed in Experiment 1. Here, we first presented the chimpanzees with whole foods that then were broken directly in front of them. This differed from Experiment 1 in which the items were broken out of the chimpanzees' view. In previous studies examining the conservation of quantities, great apes have successfully conserved a food set's quantity across manipulations of the set's presentation style, accurately selecting the larger of two quantities even after the set had been spatially transformed (Call and Rochat, 1996; Muncer, 1983; Suda and Call, 2004, 2005; Woodruff et al., 1978). Thus, perhaps the chimpanzees could overcome their current biases against larger quantities of food that consisted of broken items if those sets were first presented in their original state as whole foods. If the chimpanzees conserved the set's original state, they should prefer the larger sets even after they were broken within view. If the chimpanzees underestimated the broken sets in Experiment 1, the current manipulation of first presenting the participants with whole items that were then broken within their view should increase performance and eliminate the bias against larger or equal sets with broken items as they might conserve the value of the whole set. However, if the chimpanzees undervalued the broken sets because of the nature of brokenness, the bias would persist regardless of the current manipulation. We compared this new trial type to additional trials that presented foods broken out of view as in Experiment 1.

3.1 Methods

The same three chimpanzees (minus Panzee) were tested using the same apparatus (including the plates and sliding shelf) and one food type (chips) as in Phase 2 of Experiment 1.

3.1.2 Design and Procedure—We presented two categories of trials in this phase: homogeneous pre-broken trials and homogeneous whole-to-broken trials. A homogeneous pre-broken trial was identical to homogenous trials from Experiment 1. This trial type consisted of food sets that were either all whole or all broken prior to being presented to the chimpanzee (i.e., the sets of broken items were broken out of view from the chimpanzee). We presented two quantity comparisons within this trial type to the chimpanzees: 3 whole items vs. 4 whole items and 3 whole items vs. 4 broken items.

A homogenous whole-to-broken trial consisted of two sets of initially whole food items, but, prior to the choice phase, the experimenter broke all items in one set in view of the chimpanzee. These trials were presented exactly as in Experiment 1 except for the addition of this breaking event. For this procedure, E2 first raised the blind so that the chimpanzee could clearly view the two whole sets that had been placed behind the blind. E2 then broke all of the chips in one set in front of the chimpanzee. To control for handling time, E2 picked up and manipulated the other whole set as well but did not break any of those items. The location of the sets and the order of handling of each set were randomized across trials. We presented two types of whole-to-broken trials to the chimpanzees: 3 whole items vs. 4 whole-to-broken items and 2 whole items vs. 5 whole-to-broken items.

For all testing sessions, we randomized the side (right or left) on which the larger quantity was placed across trials. Additionally, we randomized trial type within and across sessions for all phases. The chimpanzees each completed 48 test trials, with 12 trials per trial type. See Table 2 for an outline of trial types for Experiment 2.

3.2 Results

As in Experiment 1, we analyzed whether each chimpanzee showed a preference for either choice option in each trial type using individual binomial tests. All chimpanzees showed a significant preference for the larger non-broken quantity (4 whole items) to the smaller non-broken quantity (3 whole items) in the homogeneous condition (Sherman $p < .001$, Mercury $p = .04$, and Lana $p = .006$). Also, in this condition, Sherman and Mercury again showed a significant preference for the smaller quantity of non-broken items (3 whole items) to the larger quantity of pre-broken items (4 broken items; Sherman $p = .006$ and Mercury $p = .04$); however, Lana did not show any significant preference within this comparison (Lana $p = .15$). For the whole-to-broken trials in which we broke the items in the set with the larger overall quantity, all chimpanzees were indifferent between the smaller quantity in the non-broken set (3 whole items) and the larger quantity in the set that involved breaking all items within their view (4 whole-to-broken items; Sherman $p = .15$, Mercury $p = .39$, Lana $p = .39$). In the final trial type, Mercury and Lana showed a significant preference for the larger quantity in the whole-to-broken-set (5 broken items) over the smaller quantity in the whole set (2 items; Mercury $p < .001$ and Lana $p = .006$), but Sherman was indifferent between the two sets ($p = .77$).

Next, we compared each chimpanzee's performance between select pairs of trial types using individual Fisher's exact tests. First, we compared each chimpanzee's performance in the trials involving 3 whole items vs. 4 whole items to their performance in the trials involving 3 whole items vs. 4 pre-broken items. As in Experiment 1, all chimpanzees showed a significantly greater proportion of correct choices when both sets were whole compared to when one set had pre-broken items in it (Sherman $p < .0001$, Mercury $p = .003$, Lana $p = .003$).

To determine whether the chimpanzees made more errors than in baseline when the larger quantity was broken *in front* of the chimpanzees, we compared each chimpanzee's performance in the trials involving 3 whole items vs. 4 whole items to their performance in the trials involving 3 whole items vs. 4 whole-to-broken items using a Fisher's exact test. Again, all chimpanzees showed a significantly greater proportion of correct choices when both sets remained whole compared to when one set had items in it broken within the chimpanzees' view (Sherman $p < .001$, Mercury $p = .04$, Lana $p = .009$).

Critical to our question of conservation in the current experiment, we were interested in whether chimpanzees made more choices of the smaller quantity of whole items when it was compared to a larger quantity that contained pre-broken items versus when it was compared to a larger quantity of items that were all broken within the chimpanzees' view. The chimpanzees' performances did not differ between these two trial types according to Fisher's exact tests (Sherman $p = .59$, Mercury $p = .64$, Lana $p = .99$).

Finally, we measured the consumption times for equal sets of whole and broken chips to determine whether it took the chimpanzees longer to consume one food type over the other. This measure was taken to ensure that the bias towards whole chips was not driven by a quicker consumption rate, which would have led more immediately to the next trial. To assess this, we timed each chimpanzee's consumption duration when given four broken chips or four whole chips (three trials with each trial type). This duration was measured as the time from when the chimpanzees retrieved the food bowl to the time that they stopped chewing. Two of the three chimpanzees actually required more time to consume the whole chips than the broken chips, with all chimpanzees varying widely in consumption times for both food types (Lana: whole items consumption average – 59.2 s, broken items consumption average – 43.2 s; Mercury: whole items consumption average – 26 s, broken items consumption average – 20.7 s; Sherman: whole item consumption average – 36.7 s, broken consumption average – 36.8 s). Additionally, we informally observed no preference for eating whole items over broken items in mixed sets during testing. Thus, processing time does not seem relevant to the issue of choice in this context.

3.3 Discussion

In Experiment 2, we replicated our general findings from Experiment 1. Chimpanzees were proficient in selecting the larger quantity when both sets contained whole items (3 whole vs. 4 whole). As before, Sherman and Mercury preferred a smaller set of all whole items to a larger set of all broken items (3 whole vs. 4 broken). However, Lana was indifferent between these two sets, which was a contrast from the preference she showed for the sets of whole items in Experiment 1. This difference for Lana may have been the result of experience with the task as she may have learned that the broken sets often yielded a higher payoff in terms of total quantity of food. She also was the chimpanzee that least often selected smaller sets of whole items throughout the first experiment.

The introduction of the whole-to-broken sets, in which the experimenter broke the food items in full view of the chimpanzee, mitigated the bias against broken sets, but only to a limited extent. Two chimpanzees (Mercury and Lana) preferred the whole-to-broken set when there was a 3-item discrepancy between sets (i.e., 2 whole vs. 5 whole-to-broken). However, when there was only a 1-item difference, all chimpanzees were indifferent between the smaller quantity of all whole items (3 items) and the larger quantity of whole-to-broken items (4 items).

The manipulation of breaking the food sets in front of these chimpanzees did not mitigate performance in comparison to the original variation of these trials with pre-broken food items. Chimpanzees were equally biased to choose the smaller quantity of all whole items over the larger quantity with broken items in it at choice time, regardless of whether the sets were broken within their view or not. These results suggest that chimpanzees' preference for holistic food sets emerges in response to the food's original state that defined its quality rather than its quantity, with a clear undervaluing of broken items.

4. Experiment 3

In Experiment 3, we further explored the nature of the choice bias towards cohesive sets. Were the chimpanzees biased towards whole foods, or were they instead biased towards the set that retained its original value or state? Thus far we cannot differentiate between the two hypotheses as the food types used were cohesive in their original form. However, in Experiment 3 we presented a discrete food item (mini marshmallows) that we then transformed into a larger cohesive unit, which was the opposite direction from the transformation in Experiment 1 and Experiment 2. If the chimpanzees truly were biased towards cohesive sets, they should have preferred the set with several marshmallows clumped together. Alternatively, if the chimpanzees instead were biased towards food items that preserved their original quality or status, they should have preferred the set with several individual, discrete marshmallows.

4.1 Methods

Sherman, Mercury, and Lana were tested using the same apparatus (including the plates and sliding shelf). We introduced a new food type (mini marshmallows) that was discrete and that could be manipulated in the opposite direction (individual items that could be made to appear more cohesive by clumping them together).

4.1.2 Design and Procedure—We presented two trial types in this experiment: discrete trials and clumped trials. A discrete trial consisted of all individual mini marshmallows in their original state (i.e., separate from each other). We presented one quantity comparison within this trial type: 4 discrete items vs. 3 discrete items. A clumped trial consisted of several mini marshmallows clumped together into one cohesive unit by squeezing them together (see Figure 2). We presented one quantity comparison within this trial type: 3 clumped items vs. 4 discrete items.

For all testing sessions, we randomized the side (right or left) on which the larger quantity was placed across trials. Additionally, we randomized trial type within and across sessions for all phases. The chimpanzees each completed 24 test trials, with 12 trials per trial type.

4.2 Results

We analyzed whether each chimpanzee showed a preference for either choice option in each trial type using individual binomial tests. All chimpanzees showed a significant preference (12/12 trials) for the larger quantity (4 discrete items) over the smaller quantity (3 discrete items) in the discrete trial type (all $p < .001$). Sherman and Mercury also showed a significant preference for the larger discrete set (4 discrete items) to the smaller cohesive set (3 clumped items) in the clumped trial (both 11/12, $p = .006$). Lana showed the same trend in this trial type, selecting the discrete items in 9 of 12 trials, but this did not differ from a chance level of performance, $p = .15$.

4.3 Discussion

The chimpanzees were highly proficient from the outset of this experiment in selecting the larger quantity. In trials with all discrete items, all chimpanzees selected the larger number of marshmallows in 100% of trials. In trials with clumped versus discrete marshmallows, Sherman and Mercury selected the larger number of discrete items significantly more than the smaller number of items that had been clumped together. Lana also showed this general trend, although not to a statistically significant degree. These results suggest that the chimpanzees did not simply select the set that contained the individual largest food item as has been reported in previous chimpanzee quantity studies (Beran et al., 2008; Boysen et al., 2001). In the current set of experiments, the chimpanzees have demonstrated a bias towards sets that present food items in their original state. In Experiment 1 and Experiment 2, this bias manifested as a preference for cohesive or holistic food sets even if it meant choosing the smaller set. In Experiment 3, this bias manifested as a preference for discrete food items rather than largest food items.

5. General Discussion

In the current study, we investigated how food value is constructed by chimpanzees using the natural choice paradigm by pitting one dimension of a food set’s value (quality) against another dimension of that same set (quantity). To establish baseline discrimination performance, we presented sets that only differed in the quantitative dimension. The chimpanzees were highly proficient in selecting the larger of two food sets when presented with two of the same set-types (whole vs. whole or broken vs. broken). These performance levels in the current study are consistent with previous relative quantity judgment tasks among chimpanzees using food items (e.g., Beran, 2001, 2004, 2012; Beran and Beran, 2004; Boysen and Berntson, 1995; Dooley and Gill, 1977; Hanus and Call, 2007, Rumbaugh et al., 1987; Sayers and Menzel, 2012).

Despite this proficiency in baseline trials, the comparison of whole items to broken items disrupted chimpanzees’ quantity discrimination in a way that showed that they were biased against broken foods that were formerly whole. There was a universal preference among the chimpanzees for sets with whole items over sets with all broken items when quantities were equal between the sets. This bias against equal-quantity sets with some broken items persisted for most of the chimpanzees. Even more striking, the chimpanzees sometimes failed to maximize food intake when the larger set was completely or partially comprised of broken items. This error in intake maximization was strongest when there was a 1-item difference between sets with whole items and sets with broken items. However, these erroneous choices of the smaller set persisted for some chimpanzees even when there was a 2- or 3-item difference between sets.

The present results are consistent with a previous study demonstrating that set contiguity affected quantity discriminations among chimpanzees. Beran et al. (2009a) reported a bias against larger food sets that contained spatially separated items. However, the bias documented by Beran et al. (2009) was eliminated when food items were stacked atop one another, which increased the holistic value of the set. The bias also was reduced through the introduction of a higher-preference food type. Moreover, the present results match the human literature reporting a “less-is-better” bias against larger quantity sets partially comprised of broken items (Hsee, 1998). In combination, these studies demonstrate a bias against sets containing items that deviate from their original state. Here, for items that were originally intact, this bias emerged against non-cohesive or broken food items. Alternatively, in our final experiment, this bias emerged against clumped or cohesive sets for items that were originally discrete in their original state. These results provide an additional set feature affecting value determination and subsequent intake maximization in chimpanzees. In addition to set quantity, its quality clearly affects value in a relative quantity judgment task.

In addition to documenting biases such as this one, there is value in understanding how these errors in maximization may be overcome. In an attempt to attenuate the current biases, we presented a novel trial type in the second experiment in which the chimpanzees first viewed each set in its original, unbroken state and then viewed the breaking of one food set. If the chimpanzees were able to conserve the set’s quantitative value following the breaking procedure, they should have always selected the larger of two sets regardless of whether this set was then broken (completely or partially). Despite chimpanzees’ proficiency in classic conservation tasks (Muncer, 1983; Suda and Call, 2004, 2005; Woodruff et al., 1978), their current biases against broken items persisted in Experiment 2. We interpret these results as being indicative of a qualitative bias against broken items that were originally whole rather than a failure to discriminate quantities. The chimpanzees were proficient in discriminating the larger of two sets when both sets contained whole items or both sets contained broken items in baseline trials. Thus, the initial viewing of the unbroken sets should have provided adequate information regarding quantity about the choice options. However, the subsequent breaking of some items de-valued the broken set in a qualitative manner that overrode the set’s quantitative value.

Interestingly, previous attempts to reduce biases against non-relevant set features leading to underestimation among chimpanzees sometimes have proven unsuccessful. Beran et al. (2008) first established that chimpanzees preferred smaller sets that contained the overall largest food item. In a follow-up experiment, the authors used a sequential presentation of food items rather than a simultaneous presentation used in earlier experiments. The sequential presentation did not attenuate the biases. The chimpanzees still relied on the largest individual food item as the dominant cue defining value among the choice options. In the current set of results, the selection of the food set with the largest individual item was not always the choice outcome. Rather, the chimpanzees sometimes selected the larger broken sets in Experiment 1 and Experiment 2. This occurred for larger differences between sets (e.g., 2- or 3-item difference). Also, in Experiment 3 the chimpanzees often chose the set with smaller individual items that remained in their original state instead of selecting a larger item that was the result of clumping individual items into one whole. This showed that it was not always the largest item that attracted a choice. Thus, we argue that both quantity and quality of the food items in terms of a food's original state affected choice behavior for chimpanzees in the current study.

There is the potential that the bias for whole items stems from a higher consummatory impulse towards these cohesive sets that contained the largest individual item. Individual broken items may have taken longer to consume or were more difficult to acquire and eat leading to the current results. As noted, we delivered both broken and whole items via a bowl to reduce the differences between food delivery rates. This consistent delivery mode reduced the likelihood that consumption times differed between the two food types. However, it was possible that these broken items still took longer to consume. To assess this, we measured the average time to consume equal quantities of whole and broken items and found no difference in the consumption rates between the two food types. Previous studies of relative quantity judgments by chimpanzees also have discussed the consummatory value of eating different food item types. Beran et al. (2008) reported that chimpanzees did not consistently eat the largest item first within food sets, despite a clear preference for items with the individual largest item. There still remains the possibility that whole food items have a higher gustatory value in terms of taste or sensation in comparison to broken items. The chimpanzees' bias towards whole sets subsequently might have been reinforced by the gustatory value of consuming these cohesive sets. Because there were trials in which the chimpanzees selected the broken sets, we argue that this cannot solely account for the current findings. Rather, it appears that an earlier perceptual process is likely responsible for the choice patterns seen here and in previous reports.

Value is a multidimensional construct that is determined based on several, sometimes competing, features of a set or a stimulus. Thus, value is not synonymous with overall quantity for edible stimuli, even if quantity is the key feature in caloric maximization. Chimpanzees are largely free from the constraints of cultural and experiential expectations regarding food consumption and value assignment that contribute to some aspects of food choice behavior by humans. Thus, they provide a good model for looking at basic cognitive-perceptual processes that generate the most basic value judgments in natural choice situations. Beyond the current study, we are beginning to explore other ways in which value is affected by multiple dimensions of a set. Future research will assess perceptual-decisional biases that emerge from the availability of choice options and other stimulus features that lead to the undervaluing or underestimation of a set. These manipulations will provide a fuller account of choice behavior and exactly what it is about choices themselves that can affect how they are valued, weighed, compared, and ultimately rank-ordered.

Acknowledgments

Support for this research was provided by a grant from NICHD (HD-060563), a 2CI Primate Social Cognition, Evolution and Behavior Fellowship, and the Duane M. Rumbaugh Fellowship from Georgia State University. We thank the animal care and enrichment staff for maintaining the health and wellbeing of the primates and making this research possible. This study is dedicated to the memory of Panzee.

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Highlights

- Both the quantity and quality of food sets impact food quantity judgments.
- Quality was defined as the cohesiveness or wholeness of items in a set (i.e., their original state).
- Chimpanzees chose the larger food set when both sets contained whole or broken items.
- Chimpanzees chose the smaller set if it was comprised of broken or partially broken items.
- This occurred even when they were first shown the items in their original whole state.

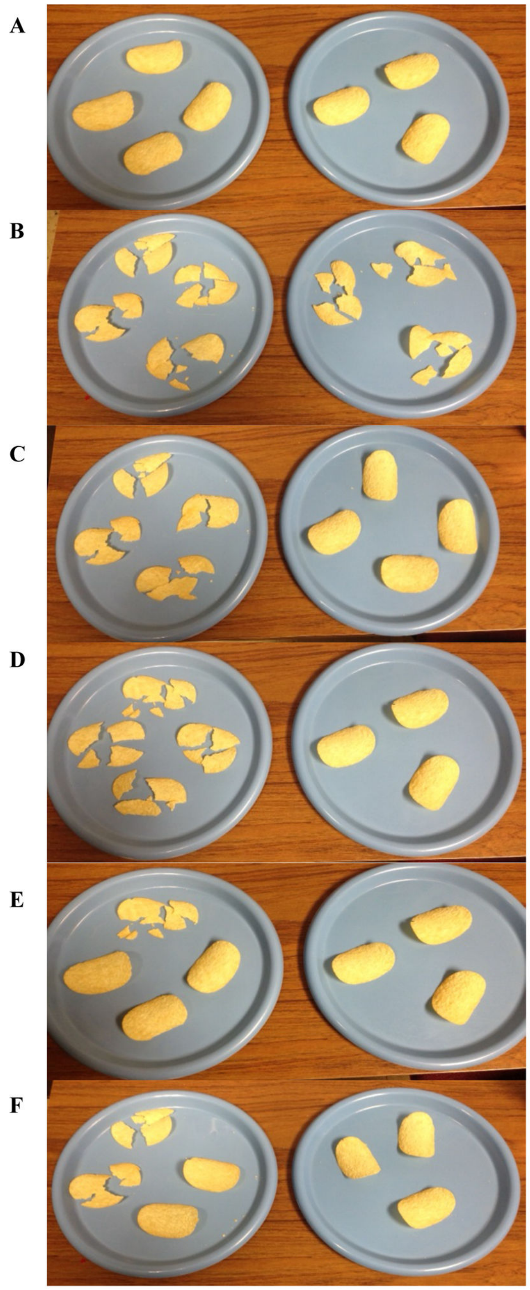

Figure 1.

Trial type images for Experiment 1, including (A) 4 whole items vs. 3 whole items, (B) 4 broken items vs. 3 broken items, (C) 4 broken items vs. 4 whole items, (D) 4 broken items vs. 3 whole items, (E) 3 whole items + 1 broken item vs. 3 whole items, and (F) 2 whole items + 2 broken items vs. 3 whole items.

A

B

Figure 2.
Trial type images for the clumped condition in Experiment 3, including (A) 4 discrete items versus 3 discrete items, and (B) 4 discrete items versus 3 clumped items.

Table 1

Individual binomial test results from Experiment 1: Phase 1 and Phase 2 testing.

Testing Phase			Choice of Whole Food	Choice of Larger Set	*p* Value
Phase 1 Homogeneous	4 whole vs. 3 whole*	Sherman		19/20	< .001*
		Panzee		19/20	< .001*
		Mercury		20/20	< .001*
		Lana		20/20	< .001*
	4 whole vs. 4 pre-broken	Sherman	20/20		< .001*
		Panzee	20/20		< .001*
		Mercury	20/20		< .001*
		Lana	20/20		< .001*
	3 whole vs. 4 pre-broken	Sherman	19/20		< .001*
		Panzee	19/20		< .001*
		Mercury	20/20		< .001*
		Lana	17/20		.003*
Phase 1 Heterogeneous	4 whole vs. 3 whole + 1 pre-broken	Sherman	19/20		< .001*
		Panzee	18/20		< .001*
		Mercury	18/20		< .001*
		Lana	13/20		.26
	3 whole vs. 3 whole + 1 pre-broken	Sherman	1/20		< .001*
		Panzee	5/20		.04*
		Mercury	6/20		.12
		Lana	2/20		< .001*
Phase 2 Homogeneous	4 pre-broken vs. 3 pre-broken*	Sherman		10/12	.04*
		Mercury		10/12	.04*
		Lana		12/12	< .001*
	2 whole vs. 4 pre-broken	Sherman	10/12		.04*
		Mercury	7/12		.77
		Lana	4/12		.39
	3 whole vs. 5 pre-broken	Sherman	12/12		< .001*

Testing Phase			Choice of Whole Food	Choice of Larger Set	*p* Value
		Mercury	10/12		.04*
		Lana	4/12		.39
		Sherman	8/12		.39
Phase 2 Heterogeneous	3 whole vs. 2 whole + 2 pre-broken	Mercury	5/12		.77
		Lana	4/12		.39

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Table 2

Individual binomial test results from Experiment 2 testing.

Testing Phase		Choice of Whole Food	Choice of Larger Set	*P*
	Sherman		12/12	< .001*
4 whole* vs. 3 whole	Mercury		10/12	.04*
	Lana		11/12	.006*
	Sherman	11/12		.006*
3 whole vs. 4 pre-broken	Mercury	10/12		.04*
	Lana	9/12		.15
	Sherman	9/12		.15
3 whole vs. 4 whole-to-broken	Mercury	8/12		.39
	Lana	8/12		.39
	Sherman	5/12		.77
2 whole vs. 5 whole-to-broken	Mercury	0/12		< .001*
	Lana	1/12		.006*