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Differences in Between-Reinforcer Value Modulate the Selective-Value Effect in Great Apes (*Pan Troglodyes, P. Paniscus, Gorilla Gorilla, Pongo Abelii*)

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We investigated how apes allocated their choices between 2 food options that varied in terms of their quantity and quality. Experiment 1 tested whether subjects preferred an AB option over an A option, where the A item is preferred to the B item (e.g., apple + carrot vs. apple). Additionally, we tested whether the length of the intertrial interval (ITI) affected subjects' choices. Five orangutans, 4 gorillas, 7 bonobos, and 10 chimpanzees received 3 types of trials: preference (A vs. B), quantity (AA vs. A), and mixed (AB vs. A where A is the preferred food). We used 3 food items that substantially differed in terms of preference (carrots, apples, and pellets). Subjects showed no overall preference for the mixed option (AB) compared with the single option (A), even though they showed clear preferences during both the preference and quantity trials. The intertrial length had no effect on choice behavior. Experiment 2 further explored apes' choices by using 3 highly preferred food items (bananas, grapes, and pellets) in 6 orangutans, 4 gorillas, 8 bonobos, and 18 chimpanzees. Unlike the results of Experiment 1, apes generally chose the mixed option. Our results indicated that apes did not show a general "selective-value" effect but chose depending on the relative value of the food items involved. Subjects were more likely to select the mixed over the single option when (a) the mixed option was composed of items that were closer in value and (b) they were compared against the less valuable item forming the mixed option.

Keywords: decision-making, food preference, quantity discrimination, experimental economics

Faced with a choice between a flat screen TV and the exact same TV set plus a toaster at their local appliance store, most people would show no hesitation in picking the second option. In economic parlance, it is the rational choice, the choice that maximizes gains and minimizes costs. Animals face countless choices in their everyday lives. Which food patch to visit and what travel route to take, or who to groom or support in conflicts are just some examples. Although choices are often rational, several violations of rationally have been documented in human and nonhuman animals in various situations (Brosnan et al., 2007; Camerer & Thaler, 1995; Hsee, 1998; Kanngiesser, Santos, Hood, & Call, 2011; Parrish, Evans, & Beran, 2015; Pattison, Zentall, & Watanabe, 2012; Platt & Huettel, 2008; Romain et al., 2014).

Our study focuses on the one such violation of rationality, the *selective-value* effect (Silberberg, Widholm, Bresler, Fujito, & Anderson, 1998), which consists of a lack of preference for an option composed by a preferred item plus a less preferred item over an option composed by the preferred item alone. A related phenomenon is the so-called less-is-more or less-is-better effect (Hsee, 1998) whereby individuals show a preference for the preferred item over the option including that same preferred item plus a less preferred item. Both effects have been reported in nonhuman primates and other species in the context of the natural choice task. This is analogous to the TV and toaster situation alluded to earlier except that appliances are replaced by food items.

Faced with a choice between a banana piece plus a grape versus only a banana piece, Silberberg et al. (1998) reported in a series of experiments that rhesus macaques (*Macaca mulatta*) and Japanese macaques (*Macaca fuscata*) showed no preference for the mixed option. Prior to the test, the authors had established that macaques showed a clear preference for the banana over the grape. Silber-

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berg et al. (1998) reproduced the same result with chimpanzees (*Pan troglodytes*) using peanuts as the more preferred food and sweet potatoes as the less preferred one. Based on the results, they suggested that macaques and chimpanzees showed a strong selective-value effect by only assigning value to the preferred food.

Beran, Evans, and Ratliff (2009) challenged the conclusions of the Silberberg et al. (1998) study by arguing that their results could be explained by the differences in preference between the food items. Using the same natural choice procedure as Silberberg et al. (1998), they found that two out of four chimpanzees showed a strong preference for the mixed option. In a second experiment, Beran et al. (2009) controlled for chimpanzees' sensitivity in detecting quantitative differences between food items (three out of four subjects were able to detect food differences that exceeded 2 g) and found that chimpanzees showed an unanticipated bias against the mixed option (the so-called less-is-more effect). The authors hypothesized that the less preferred item might have had a negative effect on the choice of the mixed option over the item alone. Furthermore, they reasoned that the less preferred item might have slowed down the pace of the trial and also required more time for consumption. Consequently, in a third experiment, they presented subjects with two kinds of trials. In some trials, the pace was determined by the subjects' speed in retrieving and consuming the food while in other trials the experimenter controlled the pace of trial administration, thus increasing the intertrial intervals (ITIs) to give the chimpanzees plenty of time to retrieve and consume the food items. Beran et al. (2009) found a bias against the mixed option when the chimpanzee controlled the pace of trial administration but the opposite result (preference for the mixed option) when the experimenter controlled the pace. Contrary to Silberberg et al. (1998), Beran et al. (2009) argued that the less preferred food item did have a value, but a negative one. It undermined the value of the preferred food item in the mixed option, guiding the choice toward the other individual item.

Kralik, Xu, Knight, Khan, and Levine (2012) also found a less-is-more effect in rhesus macaques facing a natural choice task both in the laboratory and a field setting. The monkeys consistently preferred the individual choice over the mixed option. This result is consistent with and can be interpreted similarly to some of Beran et al. results (2009). Kralik et al. (2012) postulated that monkeys' responses were governed by an affective heuristic based on the average preference of the items involved in each dish. Because the average value of a preferred plus a less preferred food item would be lower than the average value of the preferred alone, this could explain why subjects reliably selected the option with the single preferred item. Recent studies have also found a tendency to prefer the individual choice instead of the mixed option in pigeons (*Columba livia*; Zentall, Laude, Case, & Daniels, 2014) and dogs (*Canis familiaris*; Pattison & Zentall, 2014), suggesting that a less-is-more effect is at play when animals have to decide between an individual item and a mixture of the same item and another.

Even though only few studies have investigated natural choices in primates, the findings are very mixed. While some experiments have showed a positive bias toward the mixed option (Beran et al., 2009, Experiments 1, 2), others have shown either a negative bias (Beran et al., 2009, Experiments 2, 3; Kralik et al., 2012), or no bias (Beran et al., 2009, Experiment 2; Silberberg et al., 1998). The explanations for these results also vary. Whereas Silberberg and colleagues (1998) suggested that the low preference items had no value when put together with a more preferred item, Beran et al. (2009) postulated a negative value but only when subjects controlled the pace of trial administration. Kralik et al. (2012) postulated also a negative value of the less preferred items that reduced the average attractiveness of the mixed option. However, these studies have always used food items that strongly differed in their value as evidenced by the preference tests in those studies (Beran et al., 2009, Experiment 3 but see Experiment 1; Kralik et al., 2012). In general, the majority of subjects showed a clear preference for some items over others. We think that the difference in value between the different items may have played an important role in explaining these results.

The current study is aimed at reconciling those seemingly contradictory interpretations of the existing results by focusing on the value of the less preferred item in relation to the value of the more preferred item. In other words, our aim was to investigate how the between-item value differences affected subjects' choices. If the relative value of the less preferred item is too low, we predict that subjects will show indifference toward the mixed option, or perhaps even a negative bias against it if they are trying to minimize the time devoted to consume the preferred food item. However, if the relative value of the less preferred item approaches the value of the more preferred item, we predict that subjects will show a preference for the mixed option as the two items will significantly contribute to the overall value of the mixed option.

To test these predictions, we administered a natural choice task to four great ape species in which we varied the relative value of the food items to assess the proportion of choices directed to the mixed option. The inclusion of multiple individuals of multiple great ape species allowed us to assess how widespread the selective-value effect is among great apes. In the first experiment, we investigated the occurrence of the selective-value effect with three food items that differed substantially in relative value. Since the relative value of the less preferred items was low, we expected no preference or a small preference for the mixed option. Moreover, we tested Beran et al. (2009) hypothesis that postulated a trade-off between item procurement and consumption time and mixed option choice by systematically varying the pace of trial administration. We expected a greater proportion of choices directed at the mixed option with longer ITIs.

In the second experiment, we selected highly preferred items that differed slightly but consistently across subjects in the preference between them. Because the relative value of the less preferred item was higher than those items included in Experiment 1 and closer to the highly preferred items, we expected a moderate to high preference for the mixed item option. Because we used the same procedure for preference and mixed trials in both experiments, we combined the two data sets to assess whether the relative preference of the less preferred item in a given combination could predict the preference for selecting the mixed option.

This analysis represents the crucial test of the between-reinforcer value hypothesis investigated here.

Experiment 1

Subjects

We tested seven bonobos (*Pan paniscus*; five females), four gorillas (*Gorilla gorilla*; three females), five orangutans (*Pongo abelii*; four females), and 10 chimpanzees (*Pan troglodytes*; seven females; see Table 1). All species were housed at the Wolfgang Köhler Primate Research Centre (WKPRC) in Leipzig Zoo, Germany. Additionally, a bonobo received the initial food preference session and the first experimental session. After these two sessions, he was removed from the experiment (see Table 1) because he stopped participating.

Table 1
Subjects That Participated in Either One or Both Studies

		Experiment 1		Experiment 2	
Species	Subjects	Preface	Test	Preface	Test
Bonobo	Fimi*	X	X	X	X
Bonobo	Gemena	X	X		
Bonobo	Joey**	X		X	X
Bonobo	Kuno*	X	X	X	X
Bonobo	Lexi*	X	X	X	X
Bonobo	Luisa	X	X	X	X
Bonobo	Yasa	X	X	X	X
Bonobo	Yasongo	X	X	X	X
Bonobo	Loto**			X	
Bonobo	Ulindi			X	X
Chimpanzee	Fraukje	X	X	X	X
Chimpanzee	Lobo	X	X	X	X
Chimpanzee	Lome	X	X	X	X
Chimpanzee	Sandra	X	X	X	X
Chimpanzee	Alex	X	X	X	X
Chimpanzee	Alexandra	X	X		
Chimpanzee	Annett	X	X		
Chimpanzee	Fifi	X	X	X	X
Chimpanzee	Trudy	X	X	X	X
Chimpanzee	Yahaga	X	X	X	X
Chimpanzee	Bangolo**			X	
Chimpanzee	Corrie			X	X
Chimpanzee	Dorien			X	X
Chimpanzee	Frodo			X	X
Chimpanzee	Kara			X	X
Chimpanzee	Kofi			X	X
Chimpanzee	Natascha			X	X
Chimpanzee	Riet			X	X
Chimpanzee	Robert			X	X
Chimpanzee	Swela			X	X
Chimpanzee	Tai			X	X
Chimpanzee	Ulla**			X	
Orangutan	Dokana	X	X	X	X
Orangutan	Padana	X	X	X	X
Orangutan	Pini	X	X	X	X
Orangutan	Raya	X	X	X	X
Orangutan	Bimbo	X	X	X	X
Orangutan	Suaq			X	X
Orangutan	Tana**			X	
Gorilla	Abeeku	X	X	X	X
Gorilla	Kibara*	X	X	X	X
Gorilla	Kumili	X	X	X	X
Gorilla	Viringika	X	X	X	X

* Subjects that received a special set of food items. ** Subjects who did not finish the experimental sessions.

In accordance with the recommendations of the Weatherall (2006) report, groups of apes were housed in seminatural indoor and outdoor enclosures with regular feedings, daily enrichment, and water ad libitum. Subjects voluntarily participated in the study and were never food or water deprived. Research was conducted in the sleeping and/or observation rooms.

No medical, toxicological, or neurobiological research of any kind is conducted at the WKPRC. Research was noninvasive and strictly adhered to the legal requirements of Germany. The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology. Animal husbandry and research comply with the "EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos and Aquaria," the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquariums," and the "Guidelines for the Treatment of Animals in Behavioral Research and Teaching" of the Association for the Study of Animal Behavior.

Materials

We used a rectangular platform (78 × 33 cm) placed on a metal support attached to the front of the subjects' enclosure. The platform could be slid forward against a Plexiglas panel (73 × 64 cm) with two holes (3.2 cm in diameter) in the opposite bottom corners of the panel. We used three types of food: banana flavored pellets (2–3 cm length and 2 cm diameter), carrot slices, and 1/8 pieces of apple. We selected pellets, apples, and carrots because they show a clear decreasing order of preference among apes (pellet > apple > carrot). Food was presented on two white plastic dishes (12 cm in diameter) and covered by a plastic occluder (60 × 30 cm) during baiting. One bonobo displayed a lack of preference for pellets in the first preference session. Therefore we replaced pellets for bananas, and we repeated the baseline session. He showed a marked preference for bananas. Additionally, two bonobos and one gorilla showed a preference for pellets during the baseline session, but they lost this preference in the subsequent sessions. Therefore, we replaced pellets for bananas, and we repeated the baseline session. Kuno, one of the bonobos, showed a marked preference for apples over bananas, so we categorized apples as his most preferred food item, bananas the second, and carrots the third in preference. So in general, all the apes except three bonobos and one gorilla received pellets, apples, and carrots. Two bonobos and one gorilla received bananas, apples, and carrots, and Kuno received apples, bananas, and carrots. Because our focus was on the relative value of each food item and only four subjects responded differently to our initial set of foods, we categorized and treated all the different items as if they were pellets, apples, and carrots in order to simplify the explanation of the results.

Procedure

Subjects were individually tested indoors. The experimenter sat in front of the Plexiglas panel and placed two dishes on the platform, which was in a retracted position from the panel. Before baiting the dishes, the experimenter placed the plastic cover in front of the Plexiglas, thus blocking the subjects' view. After the baiting was completed, the experimenter pushed the

dishes toward the plastic cover, one on the left side of the platform and the other on the right side. Finally, the experimenter removed the plastic cover and let the subject see the platform. With his eyes closed (to prevent apes to potentially follow the eye-gaze or get distracted), the experimenter then pushed the platform toward the Plexiglas panel. The experimenter opened again his or her eyes as soon as the platform hit the Plexiglas panel and let the subject pick one of the dishes. We considered a choice when the subject touched or pointed toward the dish with her hand (through the holes in the panel), although in some cases we also scored a choice when the ape approached the hole with her mouth. Subjects received the food from the dish that they had selected. The next trial began either when the subject picked up the food or after a minute, depending on the session (explained below). In case the subject touched both dishes simultaneously, the experimenter pulled back the dishes and requested the subject both vocally and by gesturing to just pick one, and proceeded to repeat the whole trial as described above.

Design

Each subject received nine sessions. The first session was devoted to evaluating subjects' food preferences (preference trials) by presenting each of the three possible food combinations (pellet-apple, pellet-carrot, and apple-carrot). Here, subjects had to choose between two dishes containing one piece of food, each with different types of food. Subjects received four trials per condition per session for a total of 12 trials per session.

Upon completing the initial food preference session, subjects received the eight test sessions in which they had to choose between two dishes with different types and/or quantities of food depending on the conditions. We manipulated two factors: the food type and its quantity (FTQ) and the ITI. There were three types of FTQ trials depending on the food on the dishes. The preference trials were identical to those administered in the initial food preference session. The other two types of FTQ trials varied depending on whether one of the dishes held two pieces of the same (quantity trials) or two of a different food type (mixed trials). Same food trials assessed whether subjects showed a preference for the dish with the larger food quantity of the same type, and since we used three food types, there were three types of same food trials (2 pellets vs. 1 pellet; 2 apples vs. 1 apple; and 2 carrots vs. 1 carrot). Different mixed trials assessed the effect of replacing one of the food pieces in the dish with the larger quantity for a food piece of a lower quality. This generated the following three types of trials: 1 grape versus 1 grape + 1 apple; 1 grape versus 1 grape + 1 carrot; 1 apple versus 1 apple + 1 carrot. There were two types of ITI trials: long interval with a pause of at least 1 min (subjects sometimes did not approach immediately after 1 min had elapsed) between consecutive trials and short interval with no pause between consecutive trials. Long and short interval trials were administered in blocks of four consecutive sessions with half of the subjects starting with sessions made of long interval trials and the other half with the sessions composed of short interval trials.

Every experimental session consisted of 18 trials: six preference trials, six quantity trials, and six mixed trials presented in the following order: three preference trials followed by 12 quantity and mixed trials and three additional preference trials at the end. The presentation order of the quantity and mixed trials was randomly assigned in every session. The side where each food type appeared was counterbalanced within a session so that food pieces appeared the same number of times in each side. The order in which every condition was presented was randomly assigned in every session. Subjects received one daily session. In cases where subjects did not finish the session, the rest of the session was continued the very next day of tests.

Data Coding and Analyses

All trials were recorded and scored both live on coding sheets and from the videos. We randomly selected 20% of the trials to assess interobserver reliability, which was excellent (Cohen's $\kappa = 0.99$). Our dependent variable was the percentage of trials in which subjects selected one of the two alternatives that they faced. We used nonparametric statistics (Statistical Package for the Social Sciences (SPSS), version 20) to analyze the effect of various variables on the dependent variable. We used the Wilcoxon's test to compare conditions and their deviation from chance (50%). We used the Kruskal-Wallis and Mann–Whitney tests to compare species. We used *R* statistics for constructing the graphs.

Results

Food preference trials. Figure 1 presents the median percentage of trials in which each species selected one type of food over the other for each of the three food combinations during the testing sessions. There were no significant differences in preference between species for any of the three combinations (Kruskal-Wallis test: pellet vs. apple: $\chi^2 = 7.29$, $df = 3$, $p = .06$; pellet vs. carrot: $\chi^2 = 0.000$, $df = 3$, $p = 1$; apple vs. carrot: $\chi^2 = 5.48$, $df = 3$, $p = .14$). Overall, subjects significantly preferred pellet over apple (Wilcoxon's test: $n = 25$, $z = 4.37$, $p < .001$), pellet over carrot (Wilcoxon's test: $n = 26$, $z = 5.10$, $p < .001$), and apple over carrot (Wilcoxon's test: $n = 26$, $z = 4.68$, $p < .001$). These are the same preferences that were observed in the initial food preference session.

Quantity trials. Figure 2 presents the median percentage of trials in which subjects selected the larger quantity for each of the food types. Overall, subjects significantly preferred the dish with the larger quantity for all food types (Wilcoxon's tests: pellet: $n = 26$, $z = 4.49$, $p < .001$; apple: $n = 26$, $z = 4.48$, $p < .001$; carrot: $n = 23$, $z = 4.22$, $p < .001$). There were no significant differences in preference between species for pellet (Kruskal-Wallis test: $\chi^2 = 7.67$, $df = 3$, $p = .053$) or apple trials (Kruskal-Wallis test: $\chi^2 = 3.03$, $df = 3$, $p = .39$). In contrast, interspecific differences emerged in carrot trials (Kruskal-Wallis test: $\chi^2 = 8.17$, $df = 3$, $p = .043$). Pairwise comparisons indicated that bonobos showed a weaker preference than gorillas and orangutans for carrots (Mann–Whitney tests, two-tailed: $U < 5$, $p < .050$ in both cases).

Mixed trials. The ITI had no significant effect on subjects' choices for any of the food combinations (Wilcoxon's test: pellet + apple: $n = 20$, $z = .72$, $p = .47$; pellet + carrot: $n = 23$, $z = 1.46$, $p = .14$; apple + carrot: $n = 20$, $z = .68$, $p = .50$). Therefore, we pooled together short and long ITI trials for each combination in subsequent analyses. Figure 3 presents the median percentage of trials in which subjects selected the mixed option for each of the

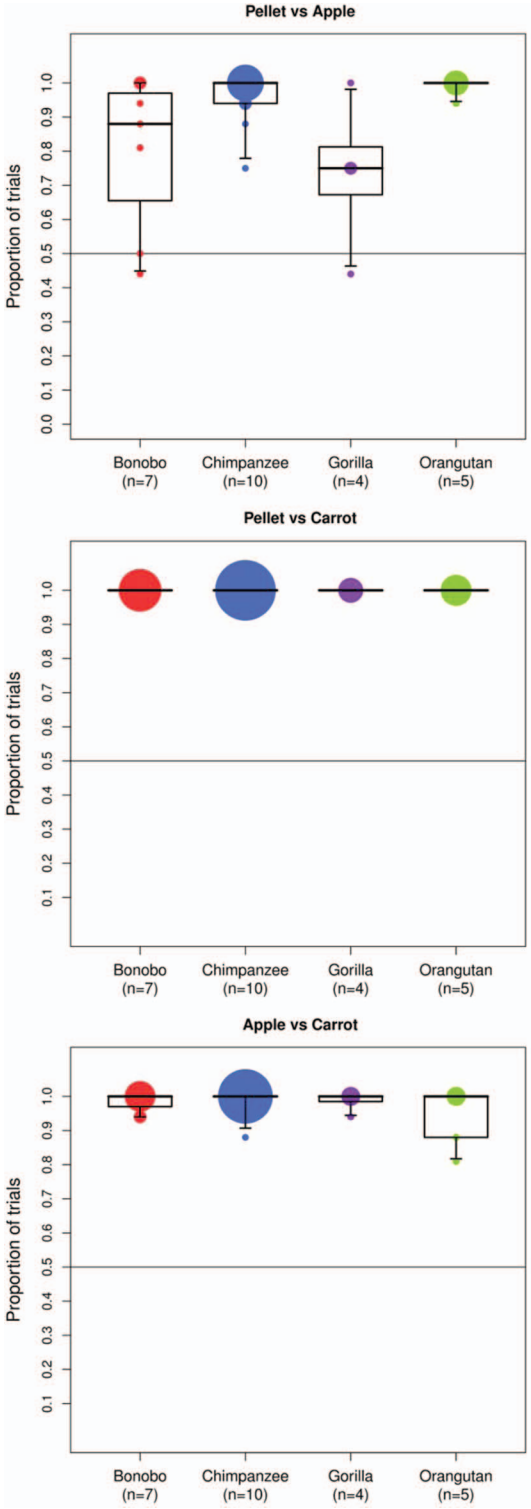

Figure 1. Box plots representing the median percentage of trials in which each species selected pellet over apple, pellet over carrot, and apple over carrot in the preference trials of Experiment 1. Also shown are the IQR (Interquartile range) (boxes) and the frequency of subjects (circles) for the various scores. See the online article for the color version of this figure.

three combinations. Overall, subjects significantly preferred the dish with the mixed option in the pellet + apple trials (Wilcoxon's test: $n = 25$, $z = 4.22$, $p < .001$), but not in the pellet + carrot (Wilcoxon's test: $n = 24$, $z = 1.13$, $p = .26$) or apple + carrot combinations (Wilcoxon's test: $n = 21$, $z = .16$, $p = .87$).

There were no significant differences between species in the pellet + apple (Kruskal-Wallis test: $\chi^2 = 2.19$, $df = 3$, $p = .53$) and pellet + carrot trials (Kruskal-Wallis test: $\chi^2 = 0.79$, $df = 3$, $p = .85$). In contrast, interspecific differences emerged in apple + carrot trials (Kruskal-Wallis test: $\chi^2 = 7.89$, $df = 3$, $p = .048$). Pairwise comparisons indicated that chimpanzees showed a weaker preference for the dish with apple + carrot compared with orangutans (Mann–Whitney test: $U = 5$, $p = .013$).

Comparing those conditions that included the pellet (as the most preferred item) in the mixed option revealed that apes across trials selected pellet + apple option significantly more often than the pellet + carrot option (Wilcoxon's test: $n = 24$, $z = 3.28$, $p = .001$).

Discussion

Apes showed a consistent preference for certain food types (pellet > apple > carrot) and also preferred two food items over one when the comparison involved the same type of food item. In contrast, the preference for the dish with the larger quantity was vastly reduced in mixed trials, especially if carrots, the least preferred food, were involved. In fact, the apes only preferred the mixed option (compared with the single item) in the pellet + apple versus pellet condition, which they chose in a greater percentage of trials compared with those in other combinations. Apes' preferences in the mixed trials were not influenced by the ITI.

Apes chose the mixed option composed of the pellet and the apple over the pellet above chance levels, showing that when both items are highly valuable, they selected the mixed option over the single item. Interestingly, finding a difference in one condition but not the others lends support to the two previous studies whose results appeared contradictory. One possible explanation for our result (and those in previous studies) is that subjects' choices in mixed trials were determined by the value of the items involved. Recall that pellet and apple were apes' two top food choices. Thus, when highly preferred food items, which are closer in value, are involved in the mixture, subjects may be more likely to select the mixture compared with the single item option. In fact, mixed trials formed by items close in value could be perceived as quantity trials, where the apes clearly selected the dish with two items instead of one.

It is unclear, however, whether the observed outcome is only restricted to the pellet + apple combination or could also be observed in other food combinations. Additionally, the current data are insufficient to determine whether subjects' choices were based on the absolute (only take into account the value of the most preferred item) or the relative value of the items involved (each item value relative to the other item present in the mixture). If absolute preference is what determined apes' choices in mixed sets, we predicted that using only highly preferred food items (as opposed to food items that differed vastly in value as in the current experiment) should reduce to chance the preference for the mixed option. In contrast, if relative value of each food item is what

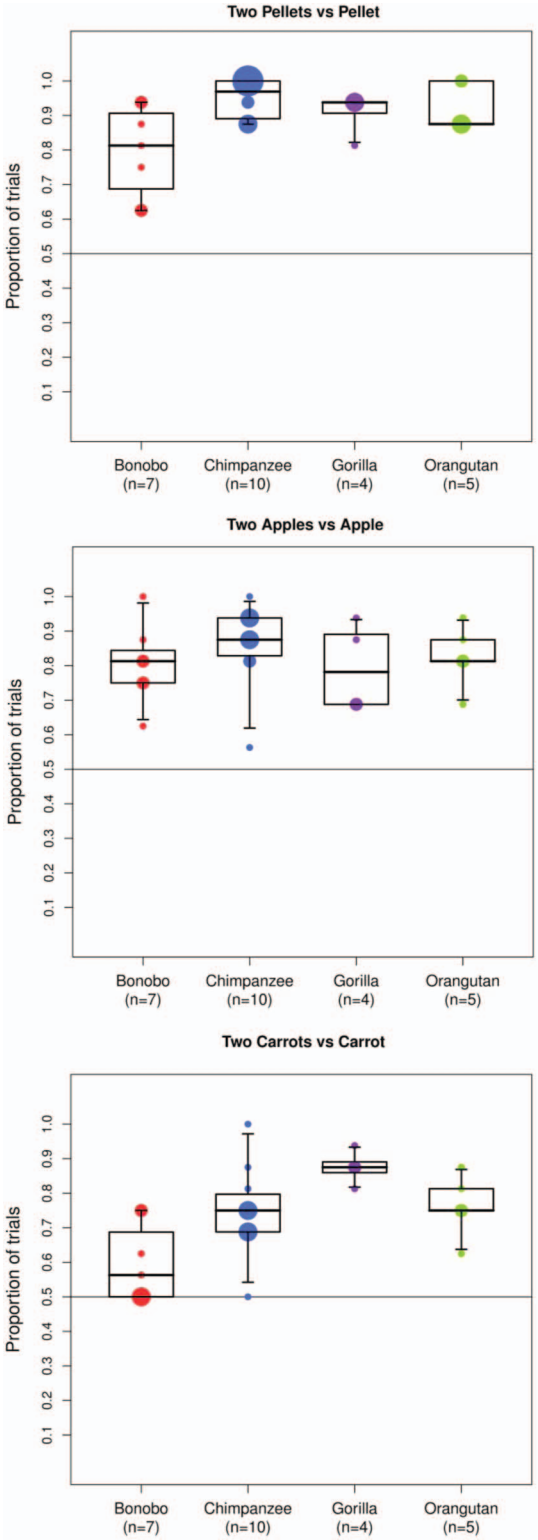

Figure 2. Box plots representing the median percentage of trials in which each species selected the larger quantity for each of the food types in Experiment 1. Also shown are the IQR (boxes) and the frequency of subjects (circles) for the various scores. See the online article for the color version of this figure.

guides apes' decisions in a natural choice task, we predicted that apes would choose a mixed combination that involved two items closer in value more often. We tested these hypotheses in Experiment 2 by using the same procedure as in Experiment 1 except that we presented three highly preferred food items with closer values than those items used in Experiment 1. Therefore, if apes chose based on the relative value of the food items in the mixture rather than the absolute value of the preferred item (or the average value of the mixture), they should choose the mixture more often than the individual item because the total value of the mixture was larger than the value of the individual option.

Experiment 2

Subjects

We tested eight bonobos (*Pan paniscus*; five female), four gorillas (*Gorilla gorilla*; three female), six orangutans (*Pongo abelii*; four female), and 18 chimpanzees (*Pan troglodytes*; 12 females; see Table 1). Additionally, four subjects completed the two preference sessions but were removed from the experiment in subsequent experimental sessions due to their lack of motivation or attention (see Table 1). All apes were housed at the WKPRC in Leipzig Zoo, Germany. They were housed in social groups in enclosures with indoor and outdoor areas. Subjects could choose to stop participating at any time within the sessions. They were never food deprived, and water was available ad libitum.

Materials

The materials were the same as in Experiment 1 except that we replaced apples and carrots with banana slices (1 cm wide on average) and grapes. We used these food items because we knew them to be highly valuable for the apes, and allowed us to test our hypothesis.

Procedure

The procedure of Experiment 2 was the same as that explained above for Experiment 1, with the exception that there was no long ITI between trials. In the first two sessions (preference sessions), the food was placed directly on the sliding platform and not on a dish as in Experiment 1. In the following six sessions (test sessions), we used the same dishes as in Experiment 1. A plastic cover was also used during the six test sessions as in Experiment 1 but not during the two preference sessions.

Design

Each subject received eight sessions. The first two sessions served to evaluate subjects' food preferences (preference trials) by presenting three conditions, one for each of the three possible food combinations (pellet-banana, pellet-grape, and banana-grape). Here subjects had to choose between two dishes, each containing one type of food. Subjects received four trials per condition per session for a total of 12 trials per session. Each food type appeared equally often on each side within a session so that food pieces appeared the same number of times in each side. The order in

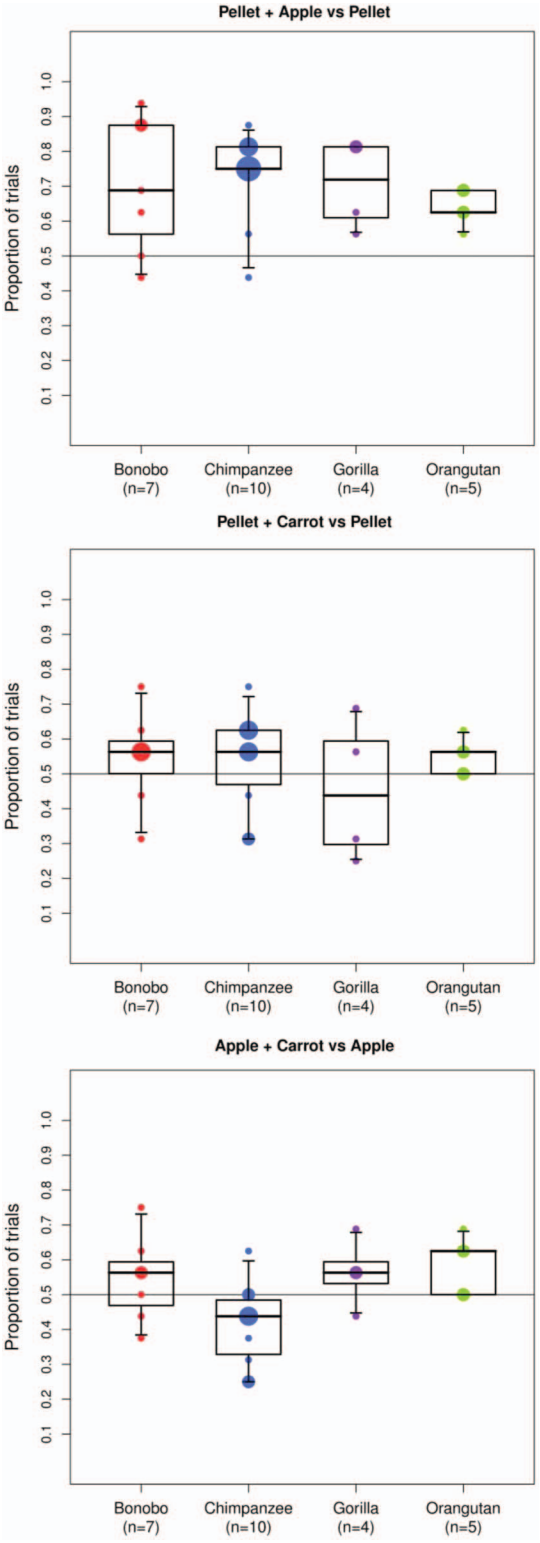

Figure 3. Box plots representing the median percentage of trials in which each species selected the larger quantity (mixed option) for each of the three food combinations in Experiment 1. Also shown are the IQR (boxes) and the frequency of subjects (circles) for the various scores. See the online article for the color version of this figure.

which every condition was presented was randomly assigned in every session. Subjects received one daily session.

After completing the food preference sessions, subjects received the six test sessions in which they had to choose between a dish with one piece of food and another dish with two different food pieces (as mixed trials of Experiment 1). This generated six types of trials (1 banana vs. 1 banana + 1 grape; 1 banana vs. 1 banana + 1 pellet; 1 grape vs. 1 grape + 1 pellet; 1 grape vs. 1 grape + 1 banana; 1 pellet vs. 1 pellet + 1 banana; 1 pellet vs. 1 pellet + 1 grape). The order in which every condition appeared was randomly assigned in every session. The side where each food type appeared was counterbalanced within a session so that food pieces appeared the same number of times in each side for a total of 12 per session.

Data Coding and Analyses

All trials were recorded and scored both live on coding sheets and from the videos. We randomly selected 20% of the trials for both preference and test sessions to assess interobserver reliability that was excellent (Cohen's kappa for preference sessions = 1; Cohen's kappa for test sessions = 1). Our dependent variable was the percentage of trials in which subjects chose one of the two alternatives that they faced. We used nonparametric statistics (SPSS v. 20) to analyze the effect of various variables on the dependent variable. We used the Wilcoxon's test to compare conditions and their deviation from chance (50%). We used Kruskal-Wallis tests to compare species. We analyzed the relationship between food preference and the mixed option preference (over the single item) using Pearson *r*. For each food dyad (e.g., pellet vs. banana), we calculated a food preference score defined as the proportion of times that one item was chosen from the total number of preference trials, A/(A + B), and a mixed item preference score defined as the proportion of trials in which subjects selected the mixed item option in the mixed trials, (A + B)/((A + B)+A). We did this analysis for all species combined and for each species separately. For the sake of completeness, we also included in this analysis the data from Experiment 1. This was possible because conditions across experiments were exactly the same concerning the preference and mixed trials. Moreover, we used proportions to control for the number of trials per food combination in both preference and mixed trials across experiments. We used *R* statistics to construct the graphs.

Results

Food preference trials. Figure 4 presents the median percentage of trials in which each species selected one type of food over the other in each of the three food combinations. Overall, subjects significantly preferred pellet over banana, Wilcoxon's test: $n = 35$, $z = 4.57$, $p < .001$, and pellet over grape, Wilcoxon's test: $n = 33$, $z = 4.96$, $p < .001$, but there was no significant preferences between banana and grape, Wilcoxon's test: $n = 34$, $z = 1.41$, $p = .16$.

Species' preferences did not significantly differ for pellet versus banana, Kruskal-Wallis test: $\chi^2 = 7.1$, $df = 3$, $p = .07$. There were significant differences between species for pellet versus grape, Kruskal-Wallis test: $\chi^2 = 7.84$, $df = 3$, $p = .049$, but pairwise comparisons using the Bonferroni-Holm method revealed no significant differences between species, Mann–Whitney tests, $p > .10$

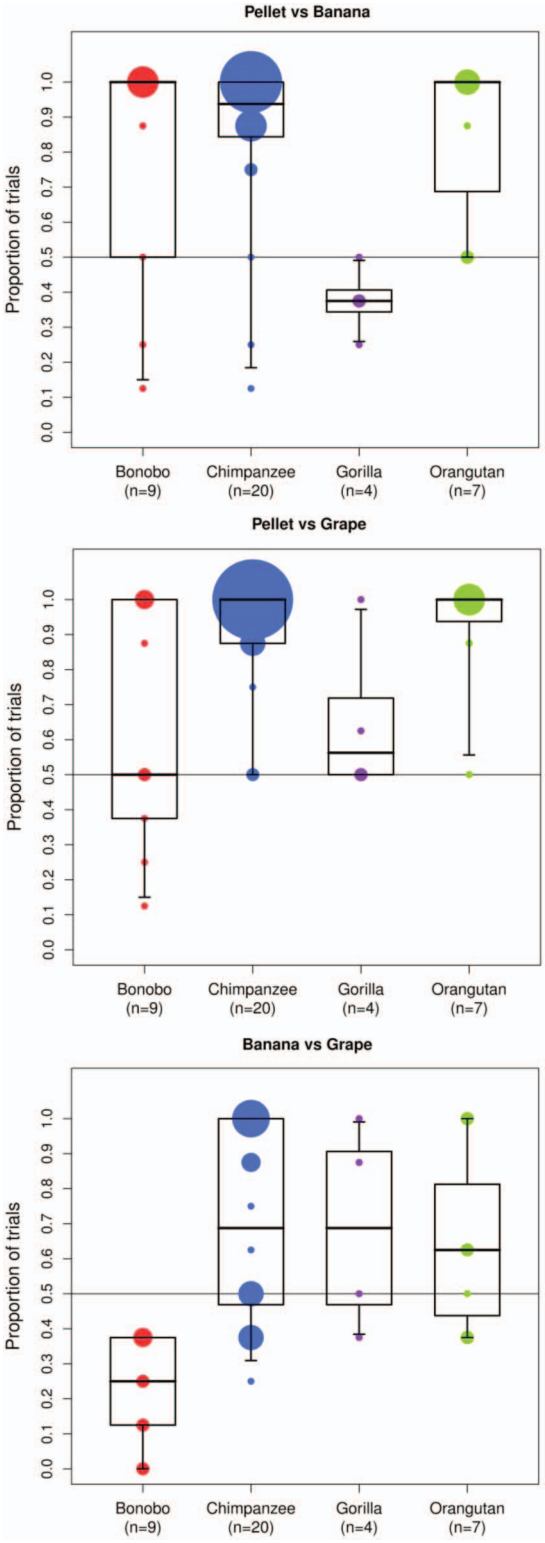

Figure 4. Box plots representing the median percentage of trials in which each species selected pellet over banana, pellet over grape, and banana over grape in the preference trials of Experiment 2. Also shown are the IQR (boxes) and the frequency of subjects (circles) for the various scores. See the online article for the color version of this figure.

in all cases. Species' preference also differed significantly for the banana versus grape, Kruskal-Wallis test: $\chi^2 = 16.96$, $df = 3$, $p = .001$. Pairwise Bonferroni-Holm comparisons revealed that bonobos differed from the three other species in preferring grapes over bananas, Mann–Whitney tests, $p > .05$ in all cases. A reanalysis of the preference test indicated that nonbonobos did significantly prefer bananas over grapes, Wilcoxon's test: $n = 25$, $z = 3.07$, $p = .002$.

Mixed trials. Figure 5 presents the median percentage of trials in which each species selected the mixed option over the single option in each combination. Apes significantly preferred the mixed option over the single option in each of the six combinations, Wilcoxon's test: $p < .001$. The six combinations can be divided into three subgroups with the same mixed option being compared with two different single food items. Overall, apes were more likely to select the pellet + banana combination when the alternative was a single banana compared with a single pellet, Wilcoxon's test: $n = 31$, $z = 3.43$, $p = .001$ (Figure 5a). Similarly, apes were more likely to select the pellet + grape combination when the alternative was a grape compared with a single pellet, Wilcoxon's test: $n = 29$, $z = 4.1$, $p < .001$ (Figure 5b). Additionally, apes were more likely to select the banana + grape combination when the alternative was a single banana compared with a single grape, Wilcoxon's test: $n = 35$, $z = 5.17$, $p < .001$ (Figure 5c).

There were significant differences between species in their likelihood in selecting the pellet + banana over pellet, Kruskal-Wallis test: $\chi^2 = 8.82$, $df = 3$, $p = .032$, and the grape + banana over grape, Kruskal-Wallis test: $\chi^2 = 9.52$, $df = 3$, $p = .023$. Pairwise comparisons indicated that chimpanzees showed a stronger preference for the dish with banana + pellet over pellet compared with bonobos, Mann–Whitney test: $z = 2.74$, $p = .006$. Chimpanzees also showed a stronger preference for the dish with grape + banana over grape when compared with bonobos, Mann–Whitney test: $z = 3.21$, $p = .015$.

Comparing those conditions with the pellet as the single option (pellet + banana vs. pellet; pellet + grape vs. pellet) revealed no significant difference in the likelihood of selecting the pellet + banana option compared with the pellet + grape option, Wilcoxon's test: $n = 29$, $z = 1.43$, $p = .152$. However, recall that bonobos showed the opposite preference for grapes over bananas compared with the other species (see Figure 4). Once bonobos were excluded from the analysis, apes selected the pellet + banana significantly more than the pellet + grape option, Wilcoxon's test: $n = 23$, $z = 2.33$, $p = .02$. In fact, 18 of 23 nonbonobos selected the pellet + banana option more often that the pellet + grape option whereas only one bonobo of five (2 others chose both options equally) did so.

There was an inverse significant relation between food preference (as measured in food preference trials) and the preference for the mixed option, as measured in mixed trials; Pearson $r = -.93$, $p = .001$, $n = 9$. This means that apes' preference for the mixed option increased as the difference in preference between those items decreased. In other words, apes were more likely to choose the mixed option for those pairs composed of items with similar value, regardless of their absolute value. This relation was still apparent in most species when they were analyzed separately (see Figure 6), although chimpanzees, $r = -.87$, $p = .004$, $n = 9$, and orangutans, $r = -.93$, $p < .001$, $n = 9$, showed a stronger relation

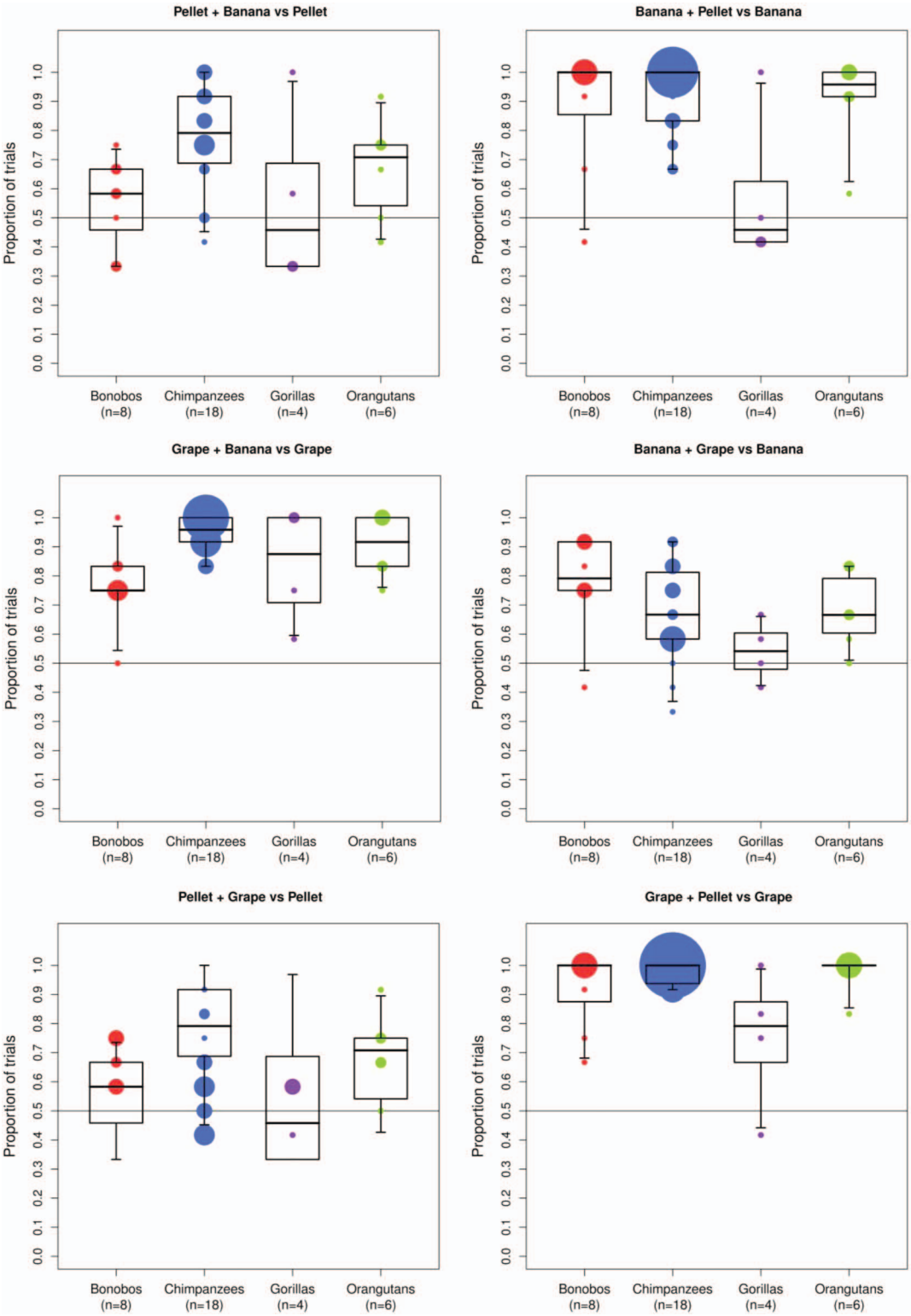

Figure 5. Box plots representing the median percentage of trials in which each species selected (a) pellet + banana, (b) banana + grape, and (c) pellet + grape over each of the individual items present in the combination in Experiment 2. Also shown are the IQR (boxes) and the frequency of subjects (circles) for the various scores. See the online article for the color version of this figure.

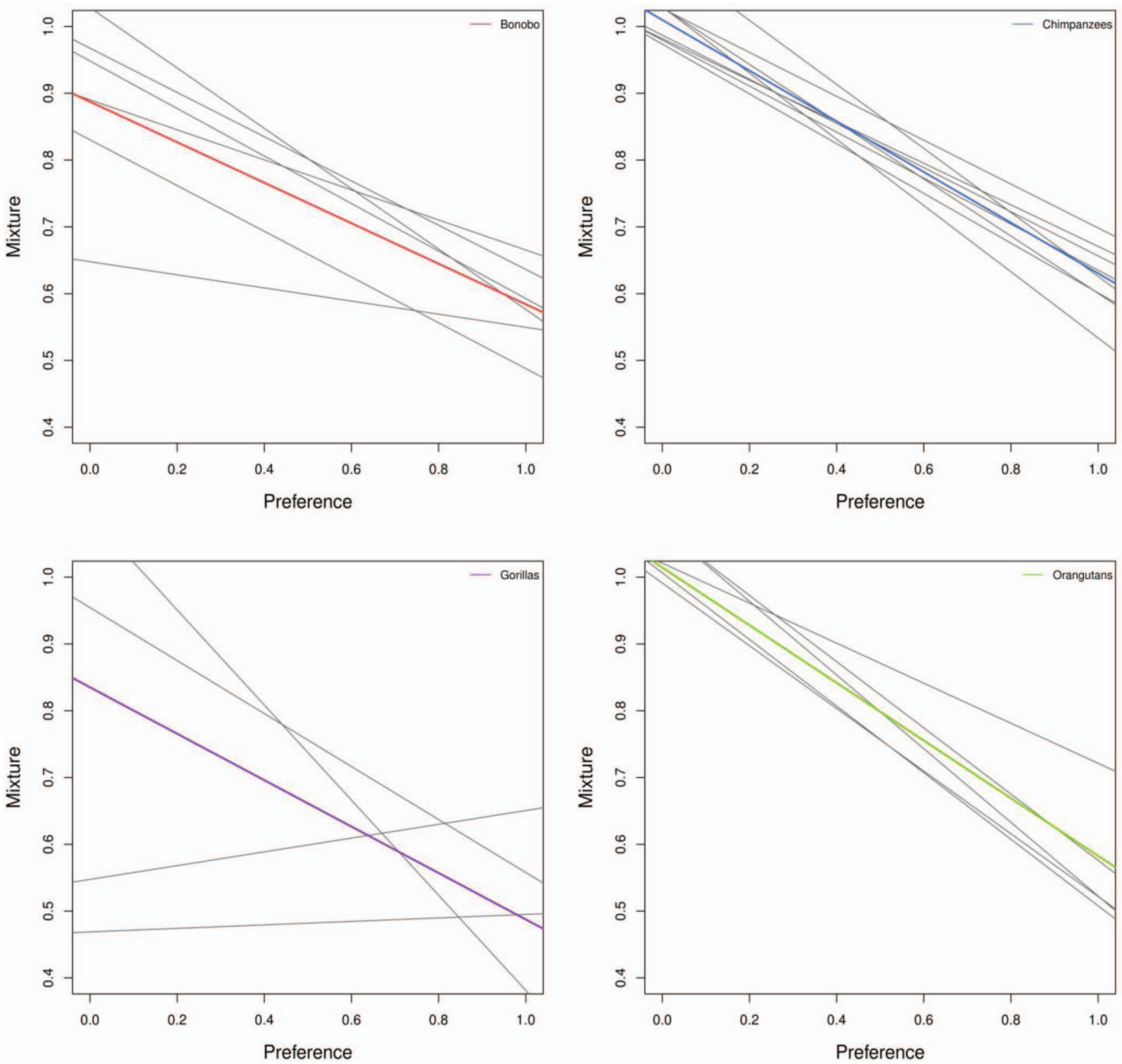

Figure 6. Proportion of trials in which subjects preferred the mixed option over the single item in the mixed trials (*y* axis) as a function of the proportion of trials in which they preferred one item over the other in the preference trials (*x* axis). The *y* axis shows proportion of trials in which the mixed option (A + B) was chosen in mixed trials, (A + B)/((A + B)+A). The *x* axis displays the proportion of trials in which one item was chosen in preference trials, A/(A + B). Correlations are based on the data from both experiments for each of the nine combinations tested (see Figures 3 and 5). Each gray line represents one subject, and colored lines represent the average for each species. See the online article for the color version of this figure.

than bonobos, $r = -.68$, $p = .046$, $n = 9$, and gorillas, $r = -.48$, $p = .20$, $n = 9$.

Discussion

Overall, apes showed a clear preference for the mixed option over the single item in all combinations involving highly preferred food items (which were closer in value than those used in Experiment 1). The strength of the choice for the mixed option varied with the value of the alternative single item in a very consistent manner. The higher the relative value of the single item, the smaller the preference for the mixed option became. However, even when the pellet (the most preferred food item) was the single option, subjects still preferred the mixed option. Furthermore, the smaller the relative value difference

(measured in preference trials) between the items in the mixed option, the higher the preference for the mixed option became. With the possible exception of gorillas, this relation was observed in all the other species. This is consistent with the results of quantity trials in the sense that apes might have conceived mixed trials with items closer in value as quantity trials composed of two identical items.

When the pellet was present in both dishes, subjects showed a weaker preference for the mixed option than when the pellet was only present in the mixed option. This result is consistent with a selective-value effect, that is, the other food item in the mixed option was not really being considered. However, two findings weaken this conclusion. First, the preference for the mixed option was still significantly higher than chance even when the pellet appeared in both dishes. There was an overall preference for the mixed option ranging from 58% to 71%, depending on the species with 10 and 17 individuals scoring 75% or higher (but none below 26%) in the pellet + banana and pellet + grape, respectively (see Figure 5a). Second, the direction of preference does indicate that the items other than pellets in the mixed option were being considered because apes' choices in mixed trials were consistent with their choices in preference trials. In particular, they preferred the pellet + banana option more often that they preferred the pellet + grape option, thus matching the preference for bananas over grapes observed in preference trials. Interestingly, bonobos, unlike the other species, showed a preference for grape over banana instead, and their choices in mixed trials were also reversed, with more subjects choosing the pellet + grape than the pellet + banana option.

Taken together, these results suggest that subjects were not indifferent to the presence of other high quality food (e.g., banana) when paired with a pellet (which they preferred) and compared against another option formed by a single pellet. This represents clear support for the idea that natural choices are based on the relative value of the items that form the combination and not the absolute value (or the average) of the items involved.

General Discussion

We investigated great apes' choices when confronted with two options that differed in the type and/or the quantity of food available in each option. Apes showed clear preferences for certain types of items (after controlling for quantity), and for two items over one (after controlling for type). When confronted with a single preferred item and a mixed option composed of the preferred item and a less preferred one, which substantially differed in value, subjects failed to show a strong preference for the mixed option. These results, which are comparable with those found in earlier studies, have been interpreted as evidence for a selective-value effect (Beran et al., 2009; Silberberg et al., 1998). Note that in those studies, food items also strongly differed in value. In contrast, when the difference in preference between food items was reduced (by using only highly preferred items), apes in general showed a clear preference for the mixed option. The strength for the mixed option was inversely proportional to the magnitude of the difference in preference between the two items. Although all species showed the same pattern of results, the magnitude of the effect varied between species and individuals.

Neither the selective-value nor the less-is-more hypotheses can fully explain the preference for the mixed option for several item combinations that we observed. Of the two hypotheses, the less-is-more hypothesis fared worse than the selective-value hypothesis because, contrary to its prediction, subjects showed no preference for the single option over the mixed one. This means that the preference for one or the other option cannot be based on an "average" of the values of the items included in each option. Furthermore, in general, apes did not change their choices depending on whether they or the experimenter controlled the pace of trial administration, thus undermining the time effect hypothesis, which could have produced a less-is-more effect. Moreover, the strength of subjects' preference for the exact same mixed option (e.g., pellet + grape) changed depending on the identity of the single item option (pellet or grape). This result is difficult to reconcile with the idea that the presence of the less preferred item had detrimental effects on the desirability of the mixed option because the aversive effect hypothesis predicts no difference based on the identity of the single item. Instead, we found that it was the value of the single item (in relation to the mixed option) that determined how desirable the mixed option was. The selective-value hypothesis fared slightly better than the less-is-more hypothesis because it predicted that subjects would show no preference for the mixed over the single option, but it only did so for some combinations in Experiment 1.

Our results support the idea that the relative preference of each item is a major determinant of choice when subjects face a mixed option composed of two food items and a single item that is also present in the mixed option. Furthermore, this "relative value" hypothesis also allows us to reconcile the seemingly contradictory data in the literature. First, note that some of our results coincide with those of Silberberg et al. (1998) in showing that subjects were indifferent to the mixed option under some conditions. More specifically, when the items in the mixed option substantially differed in their relative values, subjects showed no preference for the mixed option. Second, bonobos showed a preference for the single item option in the short ITI, which is consistent with Beran et al. (2009) findings, but this was not observed in the other species. Third, most of our results showed a preference for the mixed option, which Beran et al. (2009) also reported for some of their subjects prior to controlling for subjects' sensitivity in detecting quantitative differences between items. It is conceivable that if Beran et al. (2009) and Kralik et al. (2012) had used items closer in value, they may have obtained results more similar to ours.

The inclusion of multiple combinations of food items can help us infer what calculations might have been underlying apes' choices in the current study. Earlier we had ruled out that apes computed an "average" value for each option. We can also rule out that apes only focused on item quantities because we observed substantial variation in their preference for the mixed (larger) option depending on the type of food involved, but we observed no such variation (but a strong preference for the larger option) in food quantity trials. Thus, the most plausible explanation for these results is that they computed and compared the values of each option prior to making a choice. Next, we discuss how they might have done this.

One possibility is that they identified the common item in each dish and then chose the dish with any additional items (or the dish with the larger number of items). Alternatively, they may have estimated the relative value in each dish and compared those estimates, not the number of items available. The first mechanism is reminiscent of an operation based on logical reduction while the second one is reminiscent of an operation based on aggregation and overall value discrimination.

At first sight, the logical operation may seem the most intuitive one, because it simply requires identifying the common item and selecting the alternative that offers anything extra, regardless of how small. This is the operation that we hypothesize most people would use when deciding between the two offers at their local appliance store. This mechanism, however, does not seem to be what the apes used because it would have predicted no variation in preference for the mixed option depending on the food items involved. In contrast, value discrimination does explain our results. Apes faced a combination of two different items (A and B) and a single item (A or B). In some cases, items A and B massively differed in value (e.g., 96 Times A is chosen vs. 4 Times B when A is presented against B) while in other cases, they were closer in value (e.g., 54 Times A is chosen vs. 46 Times B when A is presented against B). When A and B differed substantially in value, adding them produced an overall value that was only slightly higher than the single option, which meant that the two options were not easy to discriminate. However, when the two items were closer in value, adding them created a value that subjects could discriminate. Moreover, when the single item was the least preferred of the two available in the mixed option, subjects were more likely to distinguish between the two options. This result is especially important because this kind of trial involved the same food items, even the same items in the mixed option and the only thing that changed was the identity of the single item. These results fit the predictions derived from Weber's law, which has been confirmed in countless studies of quantity discrimination (see Beran, in press, for a review).

The preferential focus on quantitative operations compared with logical ones is not a new finding. Recently, Hanus and Call (2014, see also Haun & Call, 2009) found that chimpanzees spontaneously discriminated the probabilities of obtaining food from two sets of cups (that varied in number of cups and food items available). More specifically, chimpanzees preferred options with a higher probability of success but only if the difference between the two options was large enough, as predicted by Weber's law. In some cases, however, the probability of success for one of the options was certain ($p = 1$, e.g., two cups with one food item each), which means that from a logical point of view they should have always chosen this option. Surprisingly, they did not when the probability of success of the other option was also high yet uncertain (e.g., $p = .67$, two cups with one food item each plus an additional empty cup).

In conclusion, our results show that in general apes are able to discriminate between quantities of the same food item (i.e., quantity trials of AA vs. A), but their decisions between a high value item and a low value item against the same value item (i.e., AB vs. A where A is preferred to B) are context-dependent. Their decisions crucially depend on the value of the items involved, showing a significant propensity to choose the AB set over the A set when the differences between A and B in terms of preference are lower. The relative difference in value between food items in natural choice tasks may be the key to understanding both the apes' choices in the current study and the seemingly contradictory results reported in previous studies.

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