1 **CAPUCHIN MONKEYS (*SAPAJUS [CEBUS] APELLA*) ARE MORE**
2 **SUSCEPTIBLE TO CONTRAST THAN TO DECOY AND SOCIAL**
3 **CONTEXT EFFECTS**

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16 **Ethics** This study was purely behavioural, non-invasive, and was carried
17 out in accordance with all applicable international, national, and
18 institutional ethical guidelines and legal requirements. All procedures
19 were approved by the Georgia State University Institutional Animal Care
20 and Use Committee (IACUC A19028 and A20018). Georgia State
21 University is fully accredited by the Association for Assessment and
22 Accreditation of Laboratory Animal Care (AALAC).
23

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28

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30 JW collected the data and performed the analyses with input from SFB.
31 Both authors wrote and revised the manuscript.
32

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ABSTRACT

Theories of optimal decision-making typically assume that animals have consistent preferences among options. In reality, economic behaviour in humans and foraging behaviour in some animals is often susceptible to choice-irrelevant factors such as inferior options or conspecifics' outcomes, but the evidence for primate decision-making is mixed. Unlike previous experiments, we assessed the relative magnitude of three context effects. Using a food preference paradigm, we varied the number of cereal pieces to determine how much a piece of food A was "worth" (50% choice) to each of 13 capuchins. We predicted that monkeys would devalue A in the contrast condition (when a higher-quality but unattainable food was present) and overvalue it in the decoy condition (when a smaller version of A was a third option) and social condition (when A, if unchosen, was given to a partner). Capuchins were 4 times less likely to choose A in the contrast condition, but 2 to 3 times more likely to choose it in the decoy and social conditions. When carefully accounting for initial preferences, we found that these primates, like humans, are sensitive to context effects. This suggests that these biases are evolved and impacts how we think about them in humans.

Keywords: decision-making bias, context dependence, decoy effect, contrast effect, capuchin monkey, *Sapajus [Cebus] apella*

INTRODUCTION

Animals from a wide array of taxa change their preference depending on the context, such as what other options or social partners are present, how or in which sequence options are presented, what choices they previously made, or their current energetic state [for example, see 1,2]. Such aspects should be irrelevant if animals form stable preferences and use them to make consistent decisions, but responding to these factors can make more sense when viewed in the context of an individual's environment, which has been hypothesized to shift preferences in consistent ways [3–6]. For example, to be a successful member of the group, social animals *should* consider the effect of their actions on their relationships with others and modify their behaviour accordingly. If an animal is on the brink of starvation, it *should* take on more risk than it usually would. In the real world, making decisions contingent on these factors often makes sense, and indeed, our brains seem wired to do so [7–9]. Further, if an individual has limited cognitive resources, it seems reasonable to follow easier strategies if they work well most of the time,

even if they fail in some situations [10–12]. However, comparative studies of context-dependent choice to date have typically emphasised only whether or not a given effect is present, but not to what extent it is or how its magnitude compares to other context effects. In this study, we quantified the relative importance of two non-social (decoy and contrast) and one social context effect on reward valuation in capuchin monkeys, who have shown human-like decision-making biases in some contexts [2,13–17] though not others [18–23].

The decoy effect – in which one option increases in value when an inferior one is added – has been found in some animal species but not others, but these studies have used vastly different methodologies, making it difficult to compare across studies, much less species. This limits the evolutionary inferences we can draw. For example, bees and grey jays show decoy effects when choosing among artificial flowers and tubes holding raisins, respectively [24]. But in primates, the only study that has found a decoy effect used a perceptual discrimination task [25], but the same monkeys do not show the effect when choosing among tasks that vary in effort required [26]. Further, two studies using food choice tasks, which are arguably most similar to the foraging experiments used with bees and grey jays, found no evidence of this bias [19,27]. One possibility for these results is that the primates' preferences between the initial options were too strong for the decoys to change their behavioural choices, even though they might have changed the perceived value of the options. For example, if you typically prefer a grape 80% of the time over a piece of banana, then the presence of a smaller grape might raise the value of the whole grape, but not enough to actually choose it statistically significantly more often, especially if they easily substitute for each other [28,29]. Here we test the possibility that primates' decoy effects in food choice experiments depends on the strength of their initial preference by assessing preference changes relative to both low and high baseline comparisons. Critically, we established baselines specific to each monkey to better compare shifts in preferences across individuals.

Contrasting the inconsistent evidence surrounding decoy effects, evidence for contrast effects – in which an option decreases in value when a superior one is present, but unattainable – is quite consistent. Indeed, operant conditioning relies on animals' expectations for specific outcomes (such as rewards) after specific actions and changing their behaviour if that outcome changes (i.e., learning) [30,31]. Presenting a reward presumably prompts an expectation to receive it and violating this expectation can result in a negative emotional response. Simply put, the animal may get frustrated [30,32–35]. Such frustration effects have been

proposed to play a role in why animals may respond negatively to inequity, that is, when they receive less than a partner for the same work [15,36].

Here we used an identical paradigm to quantify and compare the extent to which these three context effects change how a food item is valued. We used a food preference paradigm typical for both decoy and contrast effects, although our social condition differs from typical studies on inequity aversion. Typically, the partner receives a food item that is assigned by the experimenter and is independent of what the participant does, whereas in our paradigm, whether the partner received a food item was explicitly linked to the participant's choice. We predicted that the monkeys would devalue a food item (e.g., a piece of apple) if there was a better, though unattainable option present (contrast condition), and overvalue the food if there was a worse option present (decoy condition) or when the food went to a social partner if the participant did not choose it (social condition). For a rational decision-maker, of course, there should be no differences between these conditions, as they should be unaffected by these choice-irrelevant factors.

METHODS

Participants

We tested 13 capuchin monkeys (*Sapajus [Cebus] apella*, 10 female, 3 male, age $M \pm SD = 15.31 \pm 5.57$, range: 7-23 years). These capuchins are socially housed in three mixed-sex groups, each with their own indoor/outdoor enclosures with a variety of climbing structures, visual barriers, and regularly provided enrichment devices. Capuchins routinely separate voluntarily into testing boxes attached to their enclosures for cognitive and behavioural studies. They were never required to come in for testing and could choose not to participate at any time without consequences. Monkeys always had access to water, including during testing, and were never food deprived (except for medical reasons unrelated to research studies). All testing food was given in addition to their daily diet of vegetables, fruit, and primate chow.

Procedure

We administered a series of food preference tests to determine how much a specific food item was valued in units of another food. We considered indifference (50% choice) between two options to indicate equivalence. Each trial began by placing two or three food items

(depending on the condition, see below) on a board out of the monkey's reach. The board was pushed within the monkey's reach and the monkey made a choice by reaching for one of the available options. The experimenter covered the unchosen options with her hands and removed them while the monkey ate the food. The next trial began immediately. Options were counterbalanced so that they appeared in each of the locations on the board in an equal number of trials, but no more than twice in a row in the same location. Each session took place on a different day.

Test conditions

For each monkey separately, we identified food items A and B such that they reliably preferred food A over $\frac{1}{2}$ a cereal piece and a smaller version of itself (decoy food A), but also reliably preferred 5 cereal pieces and contrast food B over food A (see ESM and Table S1).

Monkeys completed 6 sessions with 18 trials for the baseline condition. Monkeys then completed 2 sessions with 18 trials each of the decoy, contrast, and social conditions (Fig. 1) in a randomly assigned order.

Figure 1 Test setup and test conditions. During test conditions, monkeys always chose between food A and $\frac{1}{2}$ to 5 pieces of cereal (baseline). In the decoy condition, a smaller piece of food A was available as a third option. In the contrast condition, a better food item was present, but out of reach. In the social condition, a partner monkey (sitting in an adjacent test box) received food A if the participant monkey did not choose it.

In the *baseline* condition, monkeys chose between food A and X cereal. The number of cereal pieces, X, was the same within a session but varied across sessions. Monkeys completed one session each for X equal to $\frac{1}{2}$, 1, 2, 3, 4, and 5 pieces of cereal in a random order. We then used this preference data to determine two “medium” amounts of cereal for each monkey (Table S1). Amount L (lower bound) was the largest number of

cereal that the monkey chose less than 50% of the time compared to food A. Amount U (upper bound) was the smallest number of cereal pieces that the monkey chose more than 50% of the time compared to food B (Fig. S1).

The *decoy* condition was identical to the baseline condition except that the decoy food A was available as an option in addition to food A and X cereal (Fig. 1). Monkeys completed one session each for X equal to L and U in a random order (e.g., food A vs. 2 cereal and food A vs. 3 cereal).

The *contrast* condition was identical to the baseline condition except that the contrast food B was present in addition to the two food options (food A and X cereal). The contrast food was located in the middle of the board but remained out of the monkey's reach throughout the trial (Fig. 1). Monkeys completed one session each for X equal to L and U in a random order.

The *social* condition was identical to the baseline condition with one exception. If the monkey chose the cereal pieces, then food A was given to the partner monkey in a neighbouring test box (Fig. 1). If the participant monkey chose food A, the partner did not receive any food (see Table S1 for partner assignments). Monkeys completed one session each for X equal to L and U in a random order.

RESULTS

To compare the effect of the different non-social and social contexts on monkeys' valuations of the food at the group level, we fit a mixed effects logistic regression model with choice as the binomial outcome variable. We included individual identity as a random effect to account for individual variability in baseline food preferences. We found a significant interaction effect of condition and number of cheerios on capuchin monkeys' food preferences (Fig. 2), $\chi^2(3) = 26.984$, $p < .001$.

Figure 2. Food preference by condition and number of cheerios. Percentage of trials in which each capuchin monkey chose food A over L cheerios (left panel) or U cheerios (right panel). Horizontal lines indicate estimated marginal means.

Capuchins' choices for food A over L cheerios became 3.9 times less likely in the contrast condition (odds ratio $[OR]=1/3.9$, $SE=0.06$, $p<.001$), but did not change significantly in the decoy and social conditions compared to baseline ($ps>.05$). Conversely, capuchins' choices for food A over U cheerios became twice as likely in the decoy condition¹ ($OR=2.04$, $SE=0.44$, $p=.003$) and 2.8 times more likely in the social condition ($OR=2.76$, $SE=0.60$, $p=.003$), but did not change significantly in the contrast condition compared to baseline ($ps>.05$).

DISCUSSION

Capuchin monkeys showed all three context effects in the predicted direction. They devalued a food item when a higher-quality but unattainable option was present (contrast effect) but overvalued it when an inferior option was available (decoy effect) or when it was given to a partner if the monkey did not choose it (social context effect).

¹ Decoy food A, intended as a non-viable option, was indeed chosen in only 2% of trials.

241 These results held across different food items but depended on
242 monkeys' initial preferences. Only relatively strong preferences for the
243 target food were susceptible to being suppressed by contrast. Conversely,
244 only relatively low preferences were susceptible to being boosted by the
245 decoy or partner outcomes. This dependence on baseline preferences may,
246 in part, explain why previous studies using food preference paradigms
247 with primates [19,27] have found mixed results, because they used the
248 same food items and quantities for each individual. In this study, we
249 carefully calibrated monkeys' initial preferences 1) by changing the food
250 items and sizes and 2) by using a countable food item that does not easily
251 substitute for fruit and vegetable pieces. The latter is important because
252 food preferences may not only reflect differences in value but also the
253 degree of substitutability [28,29], because, for example, one type of nut can
254 replace another but neither can replace water.

255 To our knowledge, this study is also the first to directly compare
256 the magnitude of different context effects using the same paradigm to
257 assess them. The contrast condition had almost twice as big of an effect as
258 the decoy and social conditions, suggesting that devaluing food items in
259 the presence of better ones potentially has a higher impact on fitness.
260 Interestingly, capuchin monkeys' responses to the decoy and social
261 conditions were similar. Note that in the social condition with relatively
262 few cereal pieces (amount L), capuchins did not experience the social
263 outcome (the partner receiving food A) very often because they typically
264 chose food A themselves. However, preferences for food A were also
265 predicted to increase, suggesting a possible ceiling effect. The fact that our
266 paradigm can detect such sensitivity opens up exciting possibilities for
267 future comparative research to systematically assess how differences in
268 species' feeding and social ecologies may shape their relative
269 susceptibility to different biases.

270 In this study, we found that capuchin monkeys, like humans, are
271 susceptible to a range of context effects. These results support the
272 hypothesis that these decision-making biases are evolved and has
273 implications for how we address them in humans. Our paradigm allows
274 researchers to test a wide range of taxa and to directly compare the
275 magnitude, rather than just the presence or absence, of these effects. In
276 particular, studying which aspects of animals' physical and social
277 environments may have shaped the evolution of these biases lets us better
278 understand why we show them and, ultimately, helps us make better
279 decisions.

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ELECTRONIC SUPPLEMENTARY MATERIAL

Capuchin monkeys (*Sapajus [Cebus] apella*) are more susceptible to contrast than to decoy and social context effects

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402 ***Pretest conditions***

403 During *pretest 1* sessions, monkeys completed 9 trials each for two
404 comparisons presented in random order: food A vs. $\frac{1}{2}$ a cereal piece and
405 food A vs. 5 cereal. Monkeys advanced to *pretest 2* when they completed
406 two consecutive sessions in which they chose food A over $\frac{1}{2}$ cereal in 7
407 out of 9 trials and chose 5 cereal over food A in 7 out of 9 trials (i.e., 14 out
408 of 18 total trials per comparison, a statistically significant preference in a
409 binomial test).

410 During *pretest 2* sessions, monkeys completed 9 trials each for two
411 comparisons presented in random order: food A vs. decoy food A and
412 food A vs. contrast food B. Decoy food items were smaller versions of
413 food A. Contrast food items were a qualitatively different food item, but
414 identical in size to food A. For example, if food A was a 1g piece of apple,
415 decoy food A was a 0.5g piece of apple, and contrast food B was a 1g piece
416 of grape. Monkeys advanced to testing when they completed two
417 consecutive sessions in which they chose food A over decoy food A in 7
418 out of 9 trials and chose contrast food B over food A in 7 out of 9 trials.

419 We changed the food items and their sizes to find a suitable
420 combination for each monkey (Table S1).

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Table S1. Partner assignments and test foods. * indicates males. In the pretest conditions, we identified food items for each monkey such that food A was reliably preferred over ½ cereal and a smaller version of itself (decoy food A), but such that 5 cereal and contrast food B were reliably preferred over food A. In the baseline condition, we identified two “medium” cereal amounts that the monkey preferred just less than (amount L) or just more than (amount U) food A (see main text and Fig. S1).

Group	Monkey	Partner	Food A	Decoy Food A	Food B	L	U
1	Logan*	Ingrid	Cucumber 1.5g	Cucumber 0.75g	Apple 1.5g	1	2
1	Ira	Irene	Cucumber 2g	Cucumber 1g	Apple 2g	0.5	1
1	Paddy	Ira	Cucumber 1g	Cucumber 0.5g	Apple 1g	2	3
1	Irene	Ingrid	Cucumber 2.5g	Cucumber 1.25g	Apple 2.5g	2	3
1	Ingrid	Ira	Apple 1g	Apple 0.5g	Grape 1g	1	2
2a	Griffin*	Wren	Apple 1g	Apple 0.5g	Grape 1g	2	3
2a	Lily	Griffin*	Cucumber 1g	Cucumber 0.5g	Apple 1g	0.5	1
2a	Wren	Lily	Cucumber 2g	Cucumber 0.5g	Apple 2g	0.5	1
2a	Widget	Wren	Cucumber 2.5g	Cucumber 1.25g	Apple 2.5g	0.5	1
2b	Nkima*	Gambit	Apple 1g	Apple 0.5g	Grape 1g	1	2
2b	Nala	Nkima*	Apple 1g	Apple 0.5g	Grape 1g	0.5	1
2b	Gambit	Lychee	Apple 1.2g	Apple 0.6g	Grape 1.2g	1	2
2b	Lychee	Nkima*	Apple 2g	Apple 1g	Grape 2g	2	3

Figure S1. Example of a monkey's preference data in the baseline condition. Solid line indicates logistic curve fit. Amounts L and U indicate the lower and upper bound of how many pieces of cereal food A is “worth” (equivalent to).