

23 Abstract

24 Capuchins, like other primates, use feedback from sensory cues and digestion to make decisions
25 about which foods to consume and which to avoid. However, little is known about how capuchins
26 make consumption decisions when simultaneously presented with novel and familiar foods, or
27 how food familiarity and macronutrient concentration together influence food choice, topics with
28 potential implications for developmental and health research. In this study, we evaluated the role
29 of familiarity, as well as fat and sugar concentration, in the food selections of captive tufted
30 capuchins (*Sapajus apella*). In the first experiment, over ten sessions, subjects were assigned to
31 either a group that chose between one familiar and one novel food item both high in fat or sugar
32 (high condition), or to a group that chose between one familiar and one novel food item both low
33 in fat or sugar (low condition). In the second experiment, subjects were divided into three groups,
34 familiarized with a food over five feeding sessions, and then offered the familiarized food and a
35 novel food that varied in fat or sugar for 10 sessions. When offered foods high in fat, capuchins
36 showed no clear signs of neophobia, forming an initial preference for the novel food, rejecting
37 foods less frequently, and selecting foods faster than when offered foods low in fat. These trends
38 were generally not observed in response to foods with sugar. When presented with options that
39 varied in macronutrient concentration, subjects showed an initial interest in the novel food
40 irrespective of whether it was high in fat or sugar, yet formed a final preference for the higher-
41 concentration item. Findings suggest that the concentration of fat or sugar in novel foods may be
42 an important mediator of exploratory behavior, and that capuchins rely on immediate feedback
43 from taste and other sensory cues to make consumption decisions.

44 **Key words:** Neophobia, neophilia, food preferences, capuchins

45

46 **Introduction**

47 The food preferences of capuchin monkeys (*Sapajus apella*) are shaped by both innate
48 tendencies and individual experience. Capuchins, like some other species of non-human
49 primates—including rhesus macaques (*Macaca mulatta*: Johnson, 2000) and chimpanzees (*Pan*
50 *troglydtes*: Visalberghi, 2002)—are in part innately neophobic, showing caution in their
51 exploration and consumption of novel foods (Addessi et al., 2004). Neophobia is thought to be
52 evolutionarily advantageous to primates, acting as a protective mechanism from the potentially
53 adverse consequences of toxins in unknown plants (Hladik & Simmen, 1996; Glander & Milton,
54 1982). Some previous studies have shown that wild capuchins react more slowly to and eat smaller
55 quantities of novel foods than familiar foods (Sabbatini et al., 2007), and that adults are more
56 neophobic than infants and juveniles (Fragaszy et al., 1997; Visalberghi et al., 2003a). However,
57 capuchins are a generalist species with a diet in the wild ranging from fruit to arthropods
58 (Visalberghi et al., 2003a) and face the “omnivore’s dilemma,” balancing the potential risks of
59 unknown foods with the possible benefits of an adaptable diet capable of meeting their nutritional
60 needs (Rozin, 1976). Novel foods are therefore not avoided unconditionally, but rather gradually
61 explored (Glander & Milton, 1982). Furthermore, novel foods do not remain novel for an extended
62 period of time, and capuchins can develop an enduring response to a novel food even after a
63 relatively short number of exposures (Addessi et al., 2004).

64 The specific factors that may affect the exploration of novel foods—including perceived
65 risk of predation, social facilitation (Visalberghi et al., 1998), age, and rank (Visalberghi et al.,
66 2003a; Addessi et al., 2004)—are numerous and the subject of considerable investigation. One
67 particularly salient set of factors concerns the palatability and macronutrient concentration of
68 foods. Capuchins rely on feedback from food—in the form of taste, texture, and digestive

69 consequences—to determine what is and is not safe to eat (Provenza et al., 1996). Flavor cues are
70 an important driver of this selection behavior and preference formation. Visalberghi & Addessi
71 (2000) found that when capuchins were presented with a familiar food that they knew to be
72 palatable but had been made unpalatable with the addition of pepper, subjects adapted quickly by
73 decreasing their consumption. When the food was subsequently made palatable again,
74 consumption increased. These findings highlight the flexibility and adaptability of capuchins as
75 well as their ability to learn from flavor signals. Capuchins and other primates also demonstrate a
76 positive hedonic response to sweet tastes, responding in a favorable manner to sweet chemical
77 compounds (Johnson, 2007; Nofre et al., 1996). This may be adaptive, as toxicity and sweetness
78 are rarely correlated in plants encountered in the wild (Addessi et al., 2004).

79 While sweet taste may be an indication of a lack of food toxicity in the wild, optimal
80 foraging theory suggests that primates would choose high energy foods. In one experiment,
81 Visalberghi et al. (2003b) offered capuchins all pairwise combinations of seven novel foods,
82 finding that food preference rank was correlated with the glucose and fructose concentration of
83 foods. However, Visalberghi et al. (1998) found that preference for novel foods was not associated
84 with sugar concentration, but rather with total caloric value. Another study observed no association
85 between food composition or caloric value and consumption (Sabbatini et al., 2007). Similar mixed
86 findings have been seen among other primate species. Squirrel (*Saimiri sciureus*) and spider
87 monkeys (*Ateles geoffroyi*) preferred foods based on total calorie value, regardless of carbohydrate
88 or protein composition, while pigtail macaques (*Macaca nemestrina*) favored foods based on
89 carbohydrate and fructose concentration, irrespective of total calorie value (Laska et al., 2000,
90 2001). More recent work in nutritional ecology has used novel analytical frameworks like
91 nutritional geometry to challenge the theory of energy maximization and highlight the importance

92 of nutritional balancing in the dietary strategies of some primate species (Felton et al., 2009;
93 Righini, 2017).

94 The dichotomous choice paradigm—in which subjects are simultaneously presented two
95 items and select one—is a useful technique to determine preference rank among a collection of
96 foods that differ along salient dimensions. Dichotomous choice experiments have been used to
97 examine how calorie and macronutrient concentration are associated with food preferences among
98 a variety of both familiar foods (Laska et al., 2000, 2001) and novel foods (Visalberghi et al.,
99 2003). However, we are unaware of any studies that have used this technique to observe the
100 behavior of primates in response to the simultaneous presentation of a novel food and familiar
101 food. Such an approach could provide some indication of how primates learn to incorporate novel
102 foods into a familiar diet. In addition, it is still not well established how familiarity interacts with
103 food properties—specifically macronutrient type (e.g., fat and sugar) and concentration—to
104 influence food choice. In the current study, we systematically observed the behavioral responses
105 of capuchins to foods that varied in fat or sugar concentration and explored how food familiarity
106 and novelty affect choice. We conducted two experiments, described in sequential order below,
107 using variations of the dichotomous choice paradigm.

108 *Experiment 1*

109 In experiment 1, we set out to answer two questions. First, how do capuchins choose
110 between novel foods and familiar foods that are matched by fat or sugar concentration? Second,
111 does behavior toward novel and familiar foods depend on fat or sugar concentration? We
112 simultaneously presented subjects with a familiar high (or low) fat food item and a novel food item
113 with equally high (or low) fat concentration. This experiment was then repeated with high and low
114 sugar foods. We predicted that capuchins would initially choose and consume the familiar food

115 item more frequently than the novel food item. We also predicted that over time, as subjects
116 sampled the novel food, the two foods would be consumed with similar frequency because of their
117 comparable macronutrient and caloric profiles. In addition, we hypothesized that exploration and
118 consumption of the novel food item would happen faster in the high fat and sugar conditions than
119 the low fat and sugar conditions.

120 *Experiment 2*

121 In experiment 2, we investigated the propensity of subjects to select and consume a novel
122 food, as opposed to a familiar food, when the two foods vary in fat or sugar concentration. In other
123 words, is neophobia or macronutrient concentration a stronger driver of consumption behavior,
124 and how does this change over time? We familiarized subjects to a novel food item of either high
125 or low macronutrient (fat or sugar) concentration through a series of five “exposure” sessions. In
126 10 subsequent “choice” sessions, we presented subjects with the familiarized food from the
127 exposure sessions and a novel food item of either higher, lower, or equal macronutrient
128 concentration. We predicted that capuchins would initially prefer the familiar over the novel food
129 regardless of their relative fat or sugar concentration, but that ultimately, as subjects sampled the
130 novel food, the food with higher fat or sugar concentration would be favored.

131

132 **Methods:**

133 *Subjects and housing*

134 Subjects were 18 tufted capuchin monkeys (*Sapajus apella*) studied from 2015-2016. All
135 subjects were captive-born and housed at the Laboratory of Comparative Ethology at the NIH
136 Animal Center in Poolesville, MD. All subjects were maternally reared and ranged in age from 3

137 to 34 years (mean age \pm SE: 11.44 ± 1.82 ; see Table 1). Eight subjects (seven males, one female)
138 were pair-housed in sets of quad cages (163 x 163 x 71 cm) furnished with perches and various
139 enrichment. The remaining ten subjects were part of a social group that consisted of one adult
140 male, four adult females, and five juveniles (<7 years old), and resided in two indoor runs (6.9 x
141 4.2 x 2.1 m) furnished with wood shavings, perches, and swings. Capuchins had *ad libitum* access
142 to water and were provided enough biscuits twice per day such that they always had some leftover
143 to consume at any time (Purina Monkey Chow #5045, St. Louis, MO). Fresh fruit (apples, oranges,
144 bananas, or grapes) and scattered foraging enrichment (sunflower seeds, popcorn, peanuts, wheat,
145 granola, or trail mix) were additionally provided once per day in the afternoon when testing had
146 been completed. Subjects were relocated following the completion of experiment 1 and before the
147 start of experiment 2 for unrelated management procedures. The social group was relocated to two
148 outdoor runs (2.68 x 2.77 x 2.43 m each) with two inside quad cages (163 x 163 x 71 cm) used for
149 testing. The social group was given approximately two months to acclimate to the new
150 environment before experiment 2 testing began. The caged subjects were also relocated before
151 experiment 2, but the housing conditions remain unchanged (Table 1).

152 All procedures adhered to the Guide for the Care and Use of Laboratory Animals, were
153 approved by the National Institute of Child Health and Human Development Animal Care and Use
154 Committee (IACUC approval number 15-064), and followed the American Society of
155 Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

156 [TABLE 1 HERE]

157

158

159 *Separation procedure*

160 We separated all subjects for testing. The pair-housed capuchins were tested in a steel and
161 Plexiglass testing cage (45 x 40 x 48 cm) attached to one quadrant of the cage. Subjects in the
162 social group were tested in a cubicle (86 x 76 x 79 cm) within one-half of their run. Separation
163 procedures were identical for experiments 1 and 2.

164 *Experiment 1 design*

165 We randomly divided subjects into two testing groups (Table 1) that varied in the
166 concentration (i.e., high or low) of macronutrients (fat or sugar) with age and sex balanced across
167 groups.¹ The experimental paradigm was a dichotomous choice task: subjects in the “high”
168 condition group were offered foods high in either fat (>45g fat/100g food) or sugar (>65g
169 sugar/100g food), whereas subjects in the “low” condition group were offered foods low in either
170 fat (< 5g fat/100g food) or sugar (< 5g sugar/100g food). Novel foods were unknown to the
171 subjects, whereas familiar foods were part of their regular diets or regular enrichment. Novel foods
172 were selected on the basis of how well they matched the general macronutrient profiles and caloric
173 value of the familiar foods in their respective experimental condition. Familiar foods used in the
174 experiment were selected from the limited number of food items that subjects had regular
175 experience with and exposure to. When selecting among these familiar foods, we tried to ensure
176 they had similar calorie content yet also fit within the sugar and fat requirements of our design.
177 Each subject received 15 trials per day for 10 sessions. Experiment 1a consisted of foods that

¹ Due to time and resource constraints, we chose to employ a between-subjects, rather than within-subjects experimental design.

178 varied in fat concentration and experiment 1b consisted of foods that varied in sugar concentration
179 (Table 2).

180 [TABLE 2 HERE]

181 *Experiment 1 procedure*

182 Subjects were tested separately. During each trial, an experimenter, who was separated
183 from the subject by an opaque screen, placed an equal amount (each food item cut to approximately
184 equivalent sizes of around 1 x 1 x 2 cm) of two foods onto a white testing board (30.48 x 20.32
185 cm). In experiment 1a, a familiar food item high or low in fat (low familiar: LF or high familiar:
186 HF) and a novel food item high or low in fat (low novel: LN or high novel: HN) were presented.
187 In experiment 1b, the food items presented varied in the amount of sugar they contained. The
188 experimenter placed foods in one of the two locations (separated by 20.32 cm) with locations (left
189 or right) randomized for each trial. Once the opaque screen was removed, a second experimenter
190 used a stopwatch to measure latency to retrieve a single food item. Once a selection was made, the
191 experimenter retrieved the other food to limit each trial to only one selection and prepared for the
192 next trial. During the trial, experimenters looked toward the middle of the board to avoid cueing
193 the subject. The inter-trial interval (ITI) was 10 seconds, during which time the capuchin could
194 either reject (throw or drop) or consume (eat or lick) the food item. The experimenter recorded the
195 behavioral response of the capuchin during the ITI. If the subject made no choice within 30
196 seconds, a new trial began after the 10-second ITI. “Null” responses were thus trials in which
197 subjects made no choice, and “rejection” responses were those in which the subjects made a
198 selection (retrieved the food item) but did not consume it. Each trial lasted until a selection had
199 been made up to a maximum of 30 seconds, with 15 trials per day for 10 consecutive days
200 (sessions).

201 *Experiment 1 data analysis*

202 We removed capuchin M1 from analysis because of unusual, erratic behavior and refusal
203 to approach the food board. We conducted all statistical analyses by aggregating responses in the
204 first three sessions (sessions 1-3, hereafter referred to as the “initial phase” – IP) and those in the
205 last three sessions (sessions 8-10, referred to as the “final phase” – FP). This aggregation provided
206 us with a larger sample of observations and allowed us to parsimoniously observe if any behavioral
207 change or learning occurred over time.

208 In order to assess if subjects demonstrated phase-specific neophobic behavior and were
209 disproportionately more likely to consume the familiar item or the novel item, we calculated the
210 proportion of total consumptions that were of novel foods (as opposed to familiar foods) for each
211 subject during the initial and final phases. To do this, we divided the number of novel
212 consumptions by sum of novel and familiar consumptions across 45 trials (i.e., the number of trials
213 in a phase). Null and rejection responses were dropped from this analysis in order to only consider
214 trials in which a food item was consumed. We then used a one-sample Wilcoxon signed-rank test
215 to determine if each group’s novel food selection rate in each phase was significantly different
216 from chance (i.e., 50%).

217 To assess if behavior differed based on the macronutrient concentration (i.e., high or low)
218 condition, we used a Mann-Whitney U test to compare the frequency of consumption behavior of
219 the high condition group to that of the low condition group. Finally, to determine whether subjects
220 made food selections more quickly in the high condition than low condition, we used a Mann-
221 Whitney U test to compare latency across conditions.²

² The data that support the findings of this study are available from the corresponding author upon request.

222 *Experiment 2 design*

223 We divided the 18 subjects into three testing groups of six subjects each that varied in
224 degree of fat or sugar concentration. Age and sex were balanced across groups. The experiment
225 consisted first of five “exposure” sessions during which a single novel food was offered in each
226 session in order to induce familiarity. This was done for two reasons: there were an insufficient
227 number of foods already familiar to the subjects that met the macronutrient requirements of the
228 experiment, and because—while outside the scope of this paper—we sought to observe the
229 familiarization process itself. Subjects in group 1 received a low fat (or sugar) food (L1), subjects
230 in group 2 received a high fat (or sugar) food (H1), and subjects in group 3 received a high fat (or
231 sugar) food (H2). In the subsequent 10 “choice” sessions, the experiment consisted of dichotomous
232 choice tasks. Group 1 was offered the choice between the familiarized low fat (or sugar) food (L1)
233 and a novel high fat (or sugar) food (H2); group 2 was offered the familiarized high fat (or sugar)
234 food (H1) and a novel high fat (or sugar) food (H2); and group 3 was offered the familiarized high
235 fat (or sugar) food (H2) and a novel low fat (or sugar) food (L2). See Table 3 and Table 4 for
236 further details.

237 [TABLE 3 HERE]

238 *Experiment 2 procedure: exposure sessions*

239 Procedures were similar to experiment 1. We tested capuchins separately. During each trial,
240 one experimenter, who was separated from the subject by an opaque screen, placed a novel food
241 in the middle of a testing board while another experimenter measured latency to retrieve the food
242 item. Once retrieved, we recorded whether the food was rejected (thrown or dropped) or consumed
243 (eaten or licked). If a food item was not selected within 30 seconds, a new trial began after the 10-

244 second ITI. Each monkey received 10 trials per day for five consecutive days (sessions). Based on
245 previous work, we concluded that the number and length of exposure sessions would likely be
246 sufficient for novel food familiarization (Visalberghi et al., 2003b).

247 *Experiment 2 procedure: choice sessions*

248 Following the five exposure sessions, we conducted one choice session (of 15 trials per
249 session) per day for 10 consecutive days (Table 4). Behind an opaque screen, an experimenter
250 placed two foods onto the testing board: the food the subject had been offered during the exposure
251 sessions (hereafter referred to as the familiarized food item), and a novel food item. As in the
252 exposure sessions, another experimenter recorded latency to selection and the subject's behavioral
253 response. If the subject made no choice within 30 seconds, a new trial began after the 10-second
254 ITI.

255 [TABLE 4 HERE]

256 *Experiment 2 data analysis*

257 All analyses were done independently for the fat experiment (2a) and sugar experiment
258 (2b). As in experiment 1, we performed statistical analyses on the initial and final phases of the 10
259 choice sessions, where the initial phase was an aggregation of the first three choice sessions (6-8),
260 and the final phase was an aggregation of the last three sessions (13-15).

261 To assess differences in consumption rates of novel and familiarized food items, we
262 determined the proportion of each subject's total consumptions that were of the novel food in each
263 phase (choice sessions only). For each subject, we divided the number of novel consumptions
264 across 45 trials (15 trials per session and 3 sessions per phase) by the number of trials in which a
265 food was consumed. We only considered trials in which a food item was consumed and so the

266 outcome variable was strictly dichotomous. Using a one-sample Wilcoxon signed-rank test, we
267 determined if each group's novel food consumption rate in each phase differed from chance. We
268 also evaluated the frequency of rejection and null responses, as well as latency to select novel and
269 familiarized foods.

270

271 **Results:**

272 *Experiment 1: consumption of novel foods*

273 In experiment 1a (fat), subjects in the high condition were more likely than chance to
274 consume novel items in both the initial and final phase (initial phase: median = 1.00, $W_+ = 36$, $z = 2.51$, $p < 0.05$; final phase: median = 1.00, $W_+ = 36$, $z = 2.56$, $p < .01$). Subjects in the low
275 condition did not consume novel foods at a rate different than chance in either phase (initial phase:
276 median = 0.46, $W_+ = 15$, $z = -0.83$, NS; final phase: median = 0.40, $W_+ = 11$, $z = -1.30$, NS).

278 In experiment 1b (sugar), subjects in the high condition were less likely to consume the
279 novel food, but only in the initial phase (initial phase: median = 0.11, $W_+ = 3$, $z = -2.03$, $p < 0.05$;
280 final phase: median = 0.46, $W_+ = 14$, $Z = -0.49$, NS). Novel selection rate among subjects in the
281 low condition did not differ significantly from chance (initial phase: median = 0.33, $W_+ = 8$, $z = -$
282 1.66 , $p = .097$); final phase: median = 0.12, $W_+ = 9$, $z = -1.55$, NS).

283 *Experiment 1: consumption by macronutrient condition*

284 Capuchins in the high fat group were more likely to consume the novel food than capuchins
285 in the low fat group in both the initial phase ($U = 0$, $N_1 = 8$, $N_2 = 9$, $p < 0.01$) and final phase ($U =$
286 2 , $N_1 = 8$, $N_2 = 9$, $p < 0.01$) (Figure 1). They were also less likely to consume the familiar food

287 than the low condition group in both the initial phase ($U = 5.5$, $N_1 = 8$, $N_2 = 9$, $p < 0.01$) and final
288 phase ($U = 0$, $N_1 = 8$, $N_2 = 9$, $p < 0.01$).

289 There were no significant differences in frequency of novel food consumptions between
290 the high sugar group and low sugar group in either the initial phase ($U = 31.5$, $N_1 = 8$, $N_2 = 9$, NS)
291 or final phase ($U = 24.5$, $N_1 = 8$, $N_2 = 9$, NS). In the initial phase of experiment 1b, familiar foods
292 were consumed at a higher median frequency by capuchins in the high sugar group than capuchins
293 in the low sugar group ($U = 16.5$, $N_1 = 8$, $N_2 = 9$, $p = 0.06$). However, there were no differences in
294 familiar food consumption in the final phase ($U = 31.5$, $N_1 = 8$, $N_2 = 9$, NS).

295 **Figure 1:** Consumption frequency of novel and familiar food items among high ($N = 8$) and low
296 ($N = 9$) macronutrient groups across experiment 1a (fat) and experiment 1b (sugar). Initial phase
297 (IP) refers to sessions 1-3; final phase (FP) refers to sessions 8-10. X: median number of trials
298 food consumed; boxes: 25-75 percentile; whiskers: lower and upper adjacent values defined as
299 $[Q1 - 1.5 \times IQR]$ and $[Q3 + 1.5 \times IQR]$; Group 1 (high condition).

300 [FIGURE 1 HERE]

301 *Experiment 1: rejections and null responses*

302 In each the initial phase and final phase of the high fat condition, just two of eight subjects
303 had a null response in more than 2% of trials, and only two rejected items more than 2% of the
304 time. Frequency of null and rejection responses were similar in the high sugar condition; just two
305 subjects had more than 4% of trials end in null or reject responses in each phase.

306 Although generally infrequent, rejections were more common in the low value conditions,
307 and novel items were rejected more than familiar items. Across all sessions in experiment 1a (fat),
308 2.5% of all trials in the high condition were rejections (of which 86.7% were rejections of the novel

309 item), compared to 29.4% of all trials in the low condition (of which 60.9% of rejections of the
310 novel item). Similarly, in experiment 1b (sugar), 5.2% of trials in the high condition were
311 rejections (of which 46.8% were rejections of the novel item), compared to 19% of trials in the
312 low condition (of which 93.8% were rejections of the novel item).

313 *Experiment 1: latency to retrieve food items*

314 We measured the latency to retrieve food items regardless of whether they were consumed.
315 In experiment 1a (fat), median (IQR) latency to retrieve food items in the high condition was 3.52
316 (2.94) seconds in the initial phase and 1.59 (2.51) seconds in the final phase. In the low condition,
317 latency was 6.83 (2.84) seconds in the initial phase and 7.11 (3.73) seconds in the final phase.
318 Subjects in the high condition group were quicker to initiate contact with a potential food item
319 than subjects in the low condition group (initial phase: $U = 16$, $N_1 = 8$, $N_2 = 9$, $p = 0.05$; final
320 phase: $U = 7.0$, $N_1 = 8$, $N_2 = 9$, $p < 0.01$).

321 Median (IQR) selection latency of the high condition group in experiment 1b (sugar) was
322 2.69 (2.27) seconds in the initial phase and 2.06 (2.22) seconds in the final phase. In the low
323 condition, latency was 4.45 (2.29) seconds in the initial phase and 2.32 (1.9) seconds in the final
324 phase. Difference in latency between conditions was not statistically significant.

325 *Experiment 2: consumption of novel foods*

326 For all three groups across both experiment 2a and 2b, the median number of trials in which
327 the novel food was consumed was higher in the initial phase than the final phase, while the number
328 in which the familiarized food was consumed was lower (Table 5).

329 For group 1 in the fat condition (L1 exposure; L1/H2 choice), the proportion of consumed
330 foods that were novel was greater than chance in the initial phase, but not the final phase (initial

331 phase: median = 0.80, $W_+ = 21$, $z = 2.10$ $p < 0.05$; final phase: median = 0.69, $W_+ = 17$, $z = 1.26$,
332 NS). This same pattern was observed in the sugar condition (initial phase: median = 0.92, $W_+ =$
333 21, $z = 2.10$, $p < 0.05$; final phase: median = 0.69, $W_+ = 16.5$, $z = 1.16$, NS).

334 Among group 2 (H1 exposure; H1/H2 choice), novel food consumption was not significant
335 in the initial phase and final phase—in both the fat condition (initial phase: median = 0.72, $W_+ =$
336 13, $z = 1.35$, NS; final phase: median = 0.48, $W_+ = 12$, $z = 0.21$, NS) and the sugar condition
337 (initial phase: median = 0.84, $W_+ = 18$, $z = 1.47$, NS; final phase: median = 0.64, $W_+ = 15$, $z =$
338 0.84, NS).

339 Group 3 (H2 exposure; H2/L1 choice) novel food consumption was not different than
340 chance in the initial or final phase in either the fat condition (initial phase: median = 0.47, $W_+ =$
341 8, $z = -0.42$, NS; median = 0.38, $W_+ = 2$, $z = -1.68$, $p = 0.09$) or sugar condition (initial phase:
342 median = 0.28, $W_+ = 5$, $z = -1.05$, NS; final phase: median = 0.21, $W_+ = 3.5$, $z = -1.37$, NS).

343 Group 1 and 3 both chose between a high value food and a low value food. In the initial
344 phase of both experiment 2a and 2b choice sessions, Group 1, for whom the high value food was
345 novel, chose this food at a higher rate than Group 3, to whom the same food had been familiarized
346 in the exposure sessions (fat condition: $U = 5$, $N_1 = N_2 = 6$, $p < 0.05$; sugar condition: $U = 3$, $N_1 =$
347 $N_2 = 6$, $p < 0.05$). This same trend was observed in the final phase (fat condition: $U = 4$, $N_1 = N_2$
348 $= 6$, $p < 0.05$; sugar condition: $U = 5.5$, $N_1 = N_2 = 6$, $p < 0.05$). See Table 5 for more details.

349 [TABLE 5 HERE]

350

351 *Experiment 2: rejections and null responses*

352 For subjects in Group 1 and 2 in the fat condition, who received a novel high fat item in
353 the choice session, rejections accounted for 2% and 7.5% of all trials, respectively, of which 38%
354 and 29% were rejections of the novel item. Group 3 rejected 4.5% of all trials on average, of which
355 23% were rejections of the novel item. In the sugar condition, subjects in Group 1 and 2 rejected
356 foods in 5% and 7% of trials, respectively; 38% and 28.5% of Group 1 and 2 rejections were on
357 the novel item. Null responses accounted for less than 2% of all trials regardless of group in the
358 high fat condition. In the high sugar condition, null responses accounted for 7.5% of responses for
359 Group 1 and 2 and 3% of responses for Group 3.

360 *Experiment 2: selection latency*

361 Selection latency was not significantly different between novel and familiarized items. In
362 both experiment 2a and 2b—with the exception of Group 3 novel item latency—median latency
363 across all choice sessions ranged from 0.95 seconds to 1.5 seconds. Group 3, which was
364 simultaneously offered a low value novel food and high value familiarized food in the choice
365 sessions, had a median latency of 2.02 seconds for novel items and 1.27 seconds for familiarized
366 items in experiment 2b, and a median latency of 2.11 seconds for novel items and 1.20 seconds for
367 familiarized items in the experiment 2a. There were no significant differences between overall
368 latency in the initial and final phases in either experiment 2a or 2b.

369

370 **Discussion:**

371 In two experiments, we used a dichotomous food choice paradigm to observe associations
372 between food properties—familiarity and fat or sugar concentration—and the tendency of captive
373 capuchins to select and consume food items. Overall, our findings did not support the hypothesis

374 that capuchins are neophobic when presented with a familiar and novel food, although there were
375 notable differences between the fat and sugar conditions. When two foods with similarly high
376 macronutrient concentration were presented to subjects in experiment 1, the novel food was
377 initially consumed at a higher rate than the familiar food in the fat condition, whereas the opposite
378 was observed in the sugar condition. Both of these initial preferences disappeared over time. Even
379 though subjects in the high sugar condition consumed the novel food at a lower rate than chance
380 in the initial phase, they did show some level of initial exploration of the novel food: most
381 consumed the novel food at least once over the first few exposures of the first session and
382 continued to do so in about 10% to 20% of trials across all sessions, while also rejecting novel
383 foods infrequently. A pattern of early exploration and interest in the novel food was supported by
384 the results from experiment 2, which showed that when capuchins were familiarized with a food
385 high in fat or sugar and then offered a choice between this familiarized food and a novel food of a
386 similar macronutrient profile, they initially selected the two items at similar rates.

387 Wild primates are cautious in their approach toward and consumption of novel foods
388 (Visalberghi et al., 2003a; Sabbatini et al., 2007; Visalberghi et al., 2002). Although some research
389 has found that captive primates show signs of food neophobia as well (Visalberghi and Fragaszy,
390 1995), our observations are generally consistent with Englerova et al. (2019), Forss et al. (2015),
391 and others that document limited or no neophobia and even signs of neophilia among those in
392 captivity. Social facilitation may account for some of the observed neophilic behavior in the high
393 value conditions of experiment 1 and across all three groups in experiment 2. Previous studies
394 have found that capuchins are more likely to approach and consume a novel food presented in a
395 social setting than a solitary setting (Visalberghi et al., 1998; Visalberghi & Addessi, 2000). Local
396 group food norms have also been shown to be a strong predictor of foraging behavior in some wild

397 primates (van de Waal et al., 2013). In our experiments, all subjects were visible to others during
398 testing, and they had direct physical contact when they were returned to their pair mate or group.
399 This setup may have allowed subjects to ascertain the safety of novel foods through observation
400 and olfactory cues, thereby diminishing any preexisting caution and encouraging exploratory
401 behavior. Future analysis could explore whether subjects tested first are more neophobic than those
402 tested later.

403 Importantly, our findings suggest that reactions to novel foods may be dependent on
404 macronutrient concentration. We found that capuchins showed some behaviors consistent with
405 neophobia—including longer selection latency, more food rejections, and less frequent
406 consumption of novel foods—only when offered a choice between two food items that were both
407 low in fat or sugar. Similarly, Johnson (2007) observed that rhesus monkeys demonstrated
408 neophobic behavior in response to a novel no-sugar food but not toward a novel high-sugar food.
409 Primates may use specific sensory cues (e.g., olfactory, visual, tactile) to infer food palatability,
410 toxicity, and macronutrient concentration, which may explain their willingness to consume foods.
411 In the wild, for example, ethanol concentrations in ripening fruits can be detected by primates via
412 olfactory receptors and often correlate positively with soluble sugar concentration, while some
413 toxic plants contain distinct odors that discourage consumption (Dominy et al., 2001; Dominy,
414 2004; Nevo and Valenta, 2018). Indeed, effectively utilizing available cues is an evolutionarily
415 advantageous strategy, reducing the risk of consuming potentially poisonous substances
416 encountered in the wild while also promoting safe consumption (Johnson et al., 1975).

417 Some previous literature has found that primates choose foods that maximize their caloric
418 intake, whether captive (Laska et al. 2000; Visalberghi et al., 2003b) or wild (Emerson and Brown,
419 2012). We found that controlling for calories, on average capuchins will choose and consume

420 foods that are highest in sugar concentration. High fat foods were also preferred to low fat foods
421 but were also somewhat higher in calories because it is difficult to find low fat foods that have the
422 same calorie content as high fat foods. Preferential consumption of foods high in fat and sugar was
423 observed within the first few exposure sessions of experiment 2, which may suggest preference
424 formation is largely immediate rather than a more gradual reinforcement learning process. Simple
425 sugars, including fructose and sucrose, are found in fruits like those in this study and provide clear
426 and direct sensory reward in the form of sweetness. It is less well-understood how and if fats,
427 typically characterized by a more neutral taste profile, provide similar immediate, positive sensory
428 feedback. In addition to the potential taste mechanisms of fats, primates may respond positively to
429 their odorant and tactile cues (Hladik and Simmen, 1996). Despite favoring the food higher in fat
430 or sugar concentration, capuchins in group 1 and 3 in experiment 2 still consumed a non-trivial
431 amount of the lower-value foods when they were simultaneously presented. This finding suggests
432 that capuchins seek to maintain variety in their consumption even while maintaining a clear
433 preference for one food. Indeed, Addessi (2008) found that capuchins were faster to consume foods
434 and ate more when presented with a varied selection of multiple food items than a monotonous
435 selection of just a single food type.

436 Our study is not without limitations, including our relatively small sample size ($n=18$) and
437 lack of controls for food characteristics that could potentially affect behavior, including smell,
438 color, and texture. Although we sought to minimize the calorie difference, high fat foods were
439 somewhat higher in calories than low fat foods due to the limited selection of foods that vary in
440 fat concentration but have similar calories. Capuchins may also have been conditioned or more
441 willing to accept foods from handlers because of their comfort and familiarity with these
442 individuals, whose presence could implicitly indicate foods are safe for exploration (Forss et al.,

443 2015). Future research should examine how responses toward novel and familiar foods vary by
444 age, such as a comparison of the behavior of juveniles and adults, which we were unfortunately
445 unable to do due the small sample size. To better understand relative preferences, a continuous
446 measure of consumption (e.g., measuring the amount of food consumed in each trial) would also
447 be beneficial. Our setup was also limited to the simultaneous presentation of only two food items.
448 Additional work should explore how and if behavior changes as a function of the number of options
449 available.

450 Our results suggest that fat and sugar concentration in food is an important moderator of
451 neophilia and neophobia in captive capuchins. The ability of capuchins to quickly discriminate
452 between foods based on macronutrient concentration, engage in exploratory behavior when cues
453 suggest it is safe to do so, and maintain dietary variety are all behaviors consistent with optimal
454 foraging theory. Further examination into the specific sensory cues that drive these behaviors may
455 help disentangle the mechanisms that shape food choice in primates.

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587 **Table 1:** Age, sex, housing, and experimental condition. In Experiment 1, the “High” (“Low”) condition
 588 group was offered foods high (low) in either fat or sugar concentration as shown in Table 2. For the
 589 feeding schedule of Groups 1-3 in Experiment 2, refer to Table 4.

| Subject | Age (years) | Sex | Housing | Experiment 1 Condition | Experiment 2 Condition |
|----------------|------------------------|------------|----------------|-----------------------------------|-----------------------------------|
| M1 | 4 | M | Social group | High | Group 3 |
| M2 | 9 | M | Social group | High | Group 2 |
| M3 | 4 | F | Social group | High | Group 1 |
| M4 | 13 | F | Social group | High | Group 3 |
| M5 | 17 | F | Social group | High | Group 3 |
| M6 | 8 | M | Pair | High | Group 3 |
| M7 | 11 | M | Pair | High | Group 3 |
| M8 | 5 | F | Social group | High | Group 1 |
| M9 | 12 | M | Pair | High | Group 2 |
| M10 | 3 | M | Social group | Low | Group 1 |
| M11 | 11 | F | Social group | Low | Group 1 |
| M12 | 23 | M | Social group | Low | Group 1 |
| M13 | 13 | M | Social group | Low | Group 1 |
| M14 | 3 | F | Social group | Low | Group 2 |

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|-----|----|---|--------------|-----|---------|
| M15 | 34 | F | Social group | Low | Group 2 |
| M16 | 9 | M | Pair | Low | Group 2 |
| M17 | 11 | M | Pair | Low | Group 3 |
| M18 | 16 | F | Pair | Low | Group 2 |

590 **Table 2:** Macronutrient concentration of foods used in experiment 1³ (HF = high fat/sugar familiar food;

591 HN = high fat/sugar novel food; LF = low fat/sugar familiar food; LN = low fat/sugar novel food).

| Experiment 1a (Fat manipulation) | | | | | Experiment 1b (Sugar manipulation) | | | | |
|----------------------------------|------|----------------|----------------|--------------|------------------------------------|------|----------------|----------------|--------------|
| Food | Type | Kcals /100g | Sugar /100g | Fat /100g | Food | Type | Kcals /100g | Sugar /100g | Fat /100g |
| Sunflower seed | HF | 584 | 2.6 | 51.4 | Raisin | HF | 310 | 69 | 0 |
| Almond | HN | 607 | 3.6 | 53.6 | Dried mango | HN | 314 | 75 | 0.78 |
| Popcorn | LF | 337 | 1.1 | 4.2 | Wheat | LF | 339 | 0 | 2.5 |
| Sourdough pretzel | LN | 393 | <3.6 | 3.6 | All bran | LN | 380 | 2.76 | 2.63 |

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³ Nutrition information can be obtained at: <https://www.myfooddiary.com/foods/>

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598 **Table 3:** *Fat and sugar concentration of foods used in experiment 2.*

| Experiment 2a (fat manipulation) | | | | | Experiment 2b (sugar manipulation) | | | | |
|---|-------------|-----------------------|------------------------|----------------------|---|-------------|-----------------------|------------------------|----------------------|
| Food | Type | Kcal /100g | Sugar /100g | Fat /100g | Food | Type | Kcal /100g | Sugar /100g | Fat /100g |
| Toasted rice | L1 | 370 | 7.4 | 0 | Rice cake | L1 | 400 | 0 | 0 |
| Roasted pistachio | H1 | 533 | 6.7 | 46.7 | Pitted date | H1 | 325 | 70 | 0 |
| Roasted cashew | H2 | 607.1 | 10.7 | 50 | Dried cranberry | H2 | 325 | 67.5 | 0 |

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608 **Table 4:** Design layout for experiment 2. L1 = low value fat or sugar item (toasted rice and rice cake,

609 respectively); H1 = high value fat or sugar item (roasted pistachio or pitted date, respectively); H2 = high

610 value fat or sugar item (roasted cashew or dried cranberry, respectively).

| | Exposure Sessions (1-5) | | | | | Choice sessions (6-15) | | | |
|----------------|-------------------------|--------------|--------------|--------------|--------------|------------------------|--------------|-----------------|---------------|
| | Session 1 | Session 2 | Session 3 | Session 4 | Session 5 | Session 6 | Session 7 | Session 8... | Session 15 |
| Group 1 | L1 | L1 | L1 | L1 | L1 | L1, H2 | L1, H2 | L1, H2 | L1, H2 |
| Group 2 | H1 | H1 | H1 | H1 | H1 | H1, H2 | H1, H2 | H1, H2 | H1, H2 |
| Group 3 | H2 | H2 | H2 | H2 | H2 | H2, L1 | H2, L1 | H2, L1 | H2, L1 |

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622 **Table 5:** Median (IQR) number of trials (out of 45) per phase in which a novel or familiar food was
 623 consumed, by group. (IP = initial phase; FP = final phase. L = low macronutrient value food; H1 = high
 624 macronutrient value food 1; H2 = high macronutrient value food 2. Exp = exposure sessions; Ch = choice
 625 sessions. N = 6 for each group.)

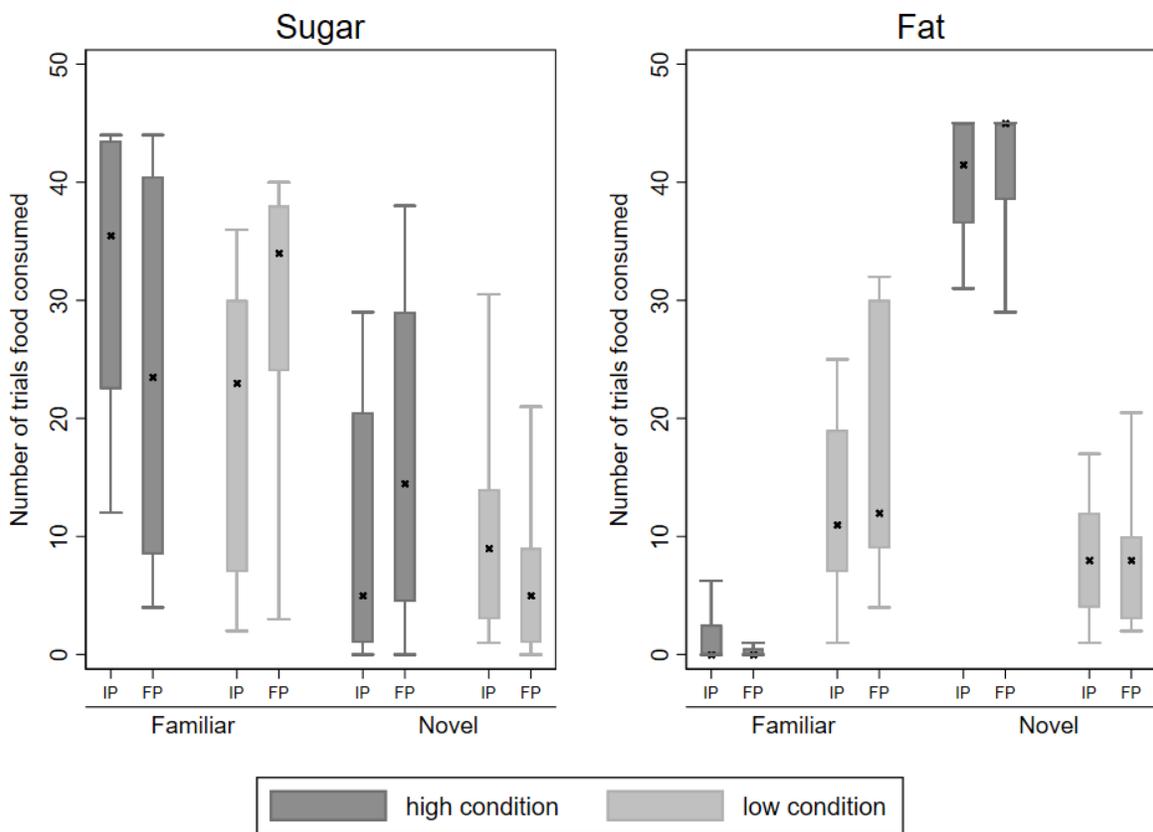
| | | Experiment 2a (fat manipulation) | | | Experiment 2b (sugar manipulation) | | |
|--|-----------|----------------------------------|----------------------------------|---------------------------------|------------------------------------|----------------------------------|---------------------------------|
| | | Group 1 (L exp, L/H2 Ch) | Group 2 (H2 exp, H1/H2 Ch) | Group 3 (H2 exp, H2/L Ch) | Group 1 (L exp, L/H2 Ch) | Group 2 (H2 exp, H1/H2 ch) | Group 3 (H2 exp, H2/L ch) |
| Novel food consumption | IP | 34 (3) | 32 (22) | 21.5 (18) | 39.5 (9) | 37.5 (19) | 10.5 (11) |
| | FP | 29.5 (27) | 21 (24) | 18 (15) | 30.5 (7) | 27 (25) | 7.5 (20) |
| Familiar food consumption | IF | 9.5 (3) | 12.5 (16) | 23.5 (22) | 3.5 (9) | 7 (20) | 21.5 (11) |
| | FP | 14 (24) | 23 (22) | 25.5 (15) | 14.5 (5) | 18 (24) | 30 (19) |

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629 Figure 1. Consumption frequency of novel and familiar food items among high (N=8) and low
 630 (N=9) macronutrient groups across Experiment 1a (fat) and Experiment 1b (sugar). Initial
 631 phase (IP) refers to sessions 1-3; final phase (FP) refers to Sessions 8-10. X: median
 632 number of trials food consumed; boxes: 25-75 percentile; whiskers: lower and upper
 633 adjacent values defined as $[Q1 - 1.5 \times IQR]$ and $[Q3 + 1.5 \times IQR]$; Group 1 (high
 634 condition). IQR, interquartile range.



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