

1 **Guppies (*Poecilia reticulata*) discriminate among two quantities of food items**
2 **but prioritise item size over total amount**

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5 Tyrone Lucon-Xiccato^{1*}, Maria Elena Miletto Petrazzini¹, Christian Agrillo^{1,2}, Angelo Bisazza^{1,2}

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8 ¹ Dipartimento di Psicologia Generale, Università di Padova, Italia

9 ² Centro di Neuroscienze Cognitive, Università di Padova, Italia

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12 * Correspondence: T. Lucon-Xiccato, Dipartimento di Psicologia Generale, Via Venezia 8, 35131,
13 Padova, Italy. Phone: +39 0498276635; fax: +39 0498276600; e-mail:
14 tyrone.luconxiccato@studenti.unipd.it

25 **ABSTRACT**

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27 When two food patches are available, individuals of many animal species feed on the larger one,
28 a preference frequently used to study numerical abilities in mammals and birds. We employed this
29 method to investigate, for the first time, food quantity discrimination and its underlying
30 mechanisms in a fish, the guppy (*Poecilia reticulata*). Guppies facing two sets of similar-sized food
31 items successfully discriminated numerosity up to a 0.5 ratio (1 versus 4 and 2 versus 4 items, but
32 not 2 versus 3 or 3 versus 4 food items). A further experiment suggested that guppies attended to
33 cumulative surface area of food items rather than number to select the larger quantity. Moreover, in
34 a 2 versus 4 discrimination where the cumulative surface area occupied by food was matched by
35 using larger items in the set with fewer items, guppies unexpectedly showed a preference for the
36 smaller numerosity. Since this result might be explained by assuming that guppies selected the
37 larger food item, we performed additional experiments to test this hypothesis. Guppies were
38 observed to be very accurate in estimating item size, being able to discriminate between two food
39 items that differed by a ratio of 0.75 in surface area. The attraction to the larger food item was so
40 strong that guppies preferred the set containing the largest item even when the other set contained a
41 double quantity of food. Since guppies in the wild forage in groups and compete for food, we
42 hypothesised that in this species natural selection has favoured cognitive mechanisms allowing a
43 rapid and efficient choice of the most profitable food item within the patch.

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48 **Keywords:** fish cognition; food choice; guppy; numerical cognition; *Poecilia reticulata*; quantity
49 discrimination.

50 **INTRODUCTION**

51

52 Many animals are capable of estimating and comparing quantities, an ability that drives
53 decision making in several contexts and confers important fitness advantages. For instance, female
54 freshwater gobies (*Padogobius bonelli*) choose male nests with greater surface available for egg
55 deposition (Bisazza, Marconato, & Marin, 1989), and female swordtails (*Xiphophorus helleri*)
56 prefer males with the longest ornament (Basolo, 1990). Salamanders (*Plethodon cinereus*) and
57 spiders (*Portia africana*) use quantification mechanisms to increase predation success (Nelson &
58 Jackson, 2012; Uller, Jaeger, Guidry, & Martin, 2003). Because of the broad relevance in decisional
59 processes, researchers have made a great effort to understand the ability to discriminate quantity in
60 animals.

61 The quantity to be assessed is sometimes continuous (e.g., the area of the nest), but, in other
62 situations, it is discrete and animals are required to assess the number of items contained in a set
63 (e.g., the number of preys). However, even two sets with a different numerosity usually differ by
64 other continuous quantities (often called perceptual variables) that co-vary with number, such as the
65 cumulative surface area or the total volume occupied by items. An animal could therefore infer the
66 number of items in a set using number, continuous quantities or both cues. For example, in the
67 wood duck (*Aix sponsa*), parasitic females lay more eggs in host nests with small clutches (Odell &
68 Eadie, 2010), but it is not necessary to assume that they can count egg number, as more eggs, for
69 example, occupy a larger volume in the nest. Similarly, striped field mice (*Apodemus agrarius*)
70 prefer to prey on small groups of ants because as high-density ants may bite them (Panteleeva,
71 Reznikova, & Vygonyailova, 2013). This task could be accomplished by counting ants as well as by
72 estimating the cumulative surface area and/or the amount of movement. To fully comprehend
73 decisional mechanisms, it is important to understand the exact ways an animal acquires and uses

74 information (e.g., if that species prefers to use numerical or perceptual cues to infer the number of
75 items in a set).

76 For these reasons, the study of quantity discrimination in animals often requires researchers
77 to devise complex experiments in laboratory settings with controlled continuous or numerical
78 information. For example, chimpanzees (*Pan troglodytes*) showed remarkable accuracy in selecting
79 the larger of two sets of discrete items presented in two dishes in front of them (Hanus & Call,
80 2007). Beran and Beran (2004) gave to chimpanzees the choice of two opaque containers in which
81 pieces of food have been inserted item-by-item to prevent them to glimpse the whole quantity.
82 Chimpanzees could still tell the difference, suggesting that they enumerate each item sequentially
83 presented. A typical behaviour adopted by prey fish to dilute predation risk consists in joining the
84 largest available shoal (Agrillo, Piffer, Bisazza, & Butterworth, 2012; Buckingham, Wong, &
85 Rosenthal, 2007). A number of different cues can be used to estimate shoal size. Experimental
86 manipulation of these cues has shown that fish use density, cumulative area, and amount of activity
87 to estimate how numerous shoal mates are in a group (Agrillo, Dadda, Serena, & Bisazza, 2008;
88 Gomez-Laplaza & Gerlai, 2013a; Gomez-Laplaza & Gerlai, 2013b; Pritchard, Lawrence, Butlin, &
89 Krause, 2001), but that they can also base their choice solely on numerical information when they
90 are prevented to use other cues (Bisazza, Piffer, Serena, & Agrillo, 2010; Dadda, Piffer, Agrillo, &
91 Bisazza, 2009).

92 The ability to estimate quantities plays a major role in foraging activities. Although in a few
93 cases small groups of prey are more profitable than large ones (Panteleeva et al., 2013), generally
94 foragers would be expected to benefit from recognising and selecting larger food sources.
95 Depending on the context, this may imply choosing the larger food item (Beran, Evans, & Harris,
96 2008), the patch with more food items—i.e. the larger number of items (Garland, Low, & Burns,
97 2012) — or the patch with the overall larger amount of food irrespective to the number of items
98 (Bogale, Aoyama, & Sugita, 2014).

99 Determining that an animal expresses a preference for the larger food quantity can be
100 especially useful evidence of the quantitative abilities of the species. Most of the studies have
101 focused on the ability to compare discrete quantity. Parrots (*Psittacus erithacus*) and jungle crows
102 (*Corvus macrorhynchos*) discriminate between sets of food items when the ratio between the
103 smaller and larger group is equal to 0.75 (Al Ain, Giret, Grand, Kreutzer, & Bovet, 2009; Bogale et
104 al., 2014), while apes can discriminate even a 0.90 ratio (Hanus & Call, 2007). Wolves (*Canis*
105 *lupus*) could enumerate 3 versus 4 food items sequentially inserted in two containers, suggesting
106 they have proto-mathematical skills (Utrata, Virányi, & Range, 2012). Salamanders (genus
107 *Plethodon*) and frogs (*Bombina orientalis*) chose the larger amount of food when presented 8 versus
108 16 and 4 versus 8 prey, respectively (Krusche, Uller, & Dicke, 2010; Stancher, Rugani, Regolin, &
109 Vallortigara, 2015).

110 Some studies have tried to disentangle the role of numerical and continuous information in
111 food quantity discrimination. A common procedure is to match the amount of food in the two sets
112 by placing individually larger items in the set with fewer items. Mixed results have been obtained
113 with this method. Some species select the set with more food items, indicating that their choice is
114 mainly driven by numerical information (Hauser, Carey, & Hauser, 2000; Rodríguez, Briceño,
115 Briceño-Aguilar, & Höbel, 2015; Uller & Lewis, 2009). Others appear to choose randomly,
116 suggesting their choice is primarily driven by continuous information, such as the cumulative
117 surface area occupied by food in the sets (Bogale et al., 2014; Feigenson, Carey, & Spelke, 2002;
118 Krusche et al., 2010). Finally, in some cases, animals appear to prefer the set with fewer food items,
119 probably because their choice is driven by a preference for the larger single-food item present in it
120 (Boysen, Berntson, & Mukobi, 2001). These differences could be due to differences in foraging
121 ecology of the species, but, to date, no hypothesis has been formulated to explain this variation in
122 result.

123 Studies done with other methodologies indicated that the ability of teleost fish to
124 discriminate quantities is often comparable to that determined for birds and mammals. Guppies
125 (*Poecilia reticulata*), for example, when tested in spontaneous choice for the larger group of
126 conspecifics, can discriminate 3 versus 4 fish (Agrillo et al., 2012) and with training some
127 individuals can detect a 5 versus 6 item discrimination using numerical information only (Bisazza,
128 Agrillo, & Lucon-Xiccato, 2014). Surprisingly, the food choice task, probably the most used
129 paradigm for investigation of quantitative abilities in vertebrates, has never been studied in fish, a
130 circumstance that prevents a proper comparison with other species.

131 In this study, we observed guppies in four experiments of spontaneous food choice aimed to
132 investigate for the first time quantity estimation abilities during foraging and its mechanisms in a
133 fish. In experiment 1, we studied whether guppies discriminate between sets of discrete food items
134 with homogeneous size, reproducing the paradigm most used in other vertebrates; in experiment 2,
135 we assessed the relative importance of number and cumulative surface area in food quantity
136 discrimination. Since results of these two experiments are better explained by assuming that guppies
137 pay special attention to the size of individual food items, we hypothesised that guppies prioritise
138 item size over total amount in food choice and we performed two further experiments. In
139 experiment 3, we investigated the ability to discriminate between two food items differing in size
140 and in experiment 4, we tested if the preference of guppies for the larger food item was stronger
141 than their preference for the larger food set.

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143

144 **METHODS**

145

146 *Subjects*

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148 The experimental subjects were adult male and female guppies of an outbreed domestic
149 strain reared in our laboratory at Dipartimento di Psicologia Generale, Università di Padova. This
150 laboratory population originated from 200 individuals bought from a local pet shop in 2010. The
151 maintenance tanks were 150-l glass aquaria with natural gravel bottom and abundant natural and
152 artificial plants. Each tank housed approximately twenty individuals (sex ratio 1:1) that were free to
153 interact and breed. Water temperature was constant at 26 ± 1 °C, and 15-W fluorescent lamps
154 illuminated the aquaria from 7:30 to 19:30. The fish were fed three times per day with commercial
155 food flakes (Fioccomix, Super Hi Group, Ovada, Italy) and *Artemia salina* nauplii. Each subject
156 was randomly selected from the maintenance tanks and observed in only one experiment.

157 After the end of the experiment, each subject was anesthetised in a MS-222 bath (Sigma-
158 Aldrich, St. Louis, Missouri, US) and photographed in lateral view. The standard length (SL) of the
159 subjects was estimated from the digital images by using Image J Software (available at
160 <http://rsbweb.nih.gov/ij/download.html>).

161

162 ***Experimental apparatus and stimuli***

163

164 Each experimental apparatus was a 20 x 50 cm glass tank filled with gravel and 25 cm of
165 water. The long walls of the tank were covered with green plastic. The apparatus was shaped like an
166 hourglass (Fig. 1a) by mean of two trapezoidal lateral compartments (10 x 5 x 25 cm) made of
167 transparent plastic placed in the middle of the tank. These lateral compartments housed two aquatic
168 plants each to provide a natural and enriched environment for the subject. The guppy is a social
169 species and it usually forms groups in the wild; two immature companions were housed in each
170 lateral compartment to avoid social isolation of the subject. Two fluorescent lamps were placed
171 above the main compartments to illuminate the apparatus. Experiments were conducted in a dark
172 room. We used six identical apparatuses at the same time.

173 The stimuli were small pieces of commercial food flakes with a homogeneous brown colour
174 (GVG mix, Sera GmbH, Heinsberg, Germany) cut by using a surgical scalpel. The stimuli were
175 then pasted on 3 x 3 cm white plastic cards by adding a drop of water. The size, number, and
176 arrangements of the stimuli on each card varied according to the schedule of each experiment (Fig.
177 2). To present the stimuli to the subjects, each card was fixed to the terminal part of a transparent
178 panel (3.5 x 15 cm). The experimenter inserted the panels into the tank. Each panel was provided
179 with a support that blocked it on the tank wall so that it could be rapidly placed in the correct
180 position. The top end of the cards was 3 cm under water surface.

181

182 *Procedure*

183

184 We performed four experiments with the same apparatuses and basic procedure. Each
185 subject underwent an acclimation phase, followed by an experimental phase consisting of a series of
186 independent trials. In each trial, we presented the subject with two cards showing different
187 quantities of food.

188

189 *Acclimation phase*

190 The subject was introduced into the apparatus 7 days before the start of the experiment, with
191 the four immature companions that could freely swim in the apparatus. A preliminary experiment
192 showed that subjects apparently familiarise faster to the apparatus when they could interact with
193 other fish. For 3 days, the subject was fed 3 times a day by delivering food from alternate short
194 walls of the tank. On the 4th day, the subject was fed according to the same schedule, but, a few
195 seconds before food delivering, a single card without any stimulus was inserted into the tank near
196 one of the short wall. A Pasteur pipette was used to deliver food close to the card to allow the
197 subject to learn the association between the card and the food. To further habituate subject to the

198 experiment, in the following 2 days it was fed 6 times per day (3 in morning and 3 in the afternoon)
199 by inserting in the tank a single card with some pieces of food pasted onto it. Therefore, the subject
200 had to feed on the food pasted onto the card. Most of the subjects learned this feeding routine very
201 fast and rapidly reached the card once inserted into the water; some others did not learn, and they
202 did not approach the card, or they approached it occasionally after longer delay. These subjects
203 were not admitted to the experimental phase and were replaced with new subjects of the same sex.
204 We discarded 3 males and 2 females in experiment 1, 2 females in experiment 2, 1 male in
205 experiment 3, and 1 male in experiment 4. In experiment 4, an additional subject (a male) ceased to
206 feed on the cards after the 4th day of the experimental phase and its performance was considered
207 only up to this point.

208 To avoid how companions might influence the choice of the subject, on the 6th day of the
209 acclimation phase, they were removed from the main compartment of the tank and inserted into the
210 two lateral compartments. The subject could still see them when in middle portion of the apparatus,
211 but not while approaching the stimuli. The last day of the acclimation phase, the subject was not
212 fed.

213

214 *Experimental phase*

215 In each experimental trial, two cards that differed in number and/or size of food items (see
216 next paragraph) were inserted simultaneously into the corners of one of the short walls of the tank
217 (Fig. 1b). Before inserting the cards, we waited until the subject was in the opposite half of the tank.
218 This way, fish could see both stimuli before choosing. After the subject chose one of the cards, the
219 other was gently removed from the water. The chosen card was left into the water until the subject
220 consumed all of the food on it, which normally took around 20-30 seconds. The following trial
221 began after 5 minutes. Eight trials were administered each day; 4 in the morning (9:00 – 10:00) and
222 4 in the afternoon (15:00 – 16:00). A preliminary experiment with this schedule showed guppies'

223 performance was not affected by the order of the trial within each day. The side of the tank in which
224 we inserted the cards and the relative position (right or left) of the card with the larger amount of
225 food alternated according to a pseudo-random pre-set scheme, as did the presentation order of the
226 different types of discriminations. The spatial configuration of the food items was varied according
227 to a fixed sequence to prevent fish from using pattern recognition across trials.

228

229 *Description of the single experiments*

230 Experiment 1

231 This experiment investigated the ability of guppies to discriminate between discrete food
232 quantities by presenting two sets with different numbers of food items. We administered four
233 discriminations: 1 versus 4, 2 versus 4, 2 versus 3, and 3 versus 4 food items (numerical ratios:
234 0.25; 0.50; 0.67, and 0.75, respectively) (Fig. 2). All food items were the same size (1.5 x 1.5 mm).
235 The experimental phase lasted 10 days, for a total of 80 trials (20 for each discrimination).
236 Experiments were performed 5 days per week, from Monday to Friday. We observed 20 subjects,
237 10 males and 10 females.

238

239 Experiment 2

240 The food items used in experiment 1 were the same size; therefore, the card with more food
241 items had also the larger amount of food. This experiment did not provide information about
242 whether guppies selected the larger quantity by enumerating food items or using continuous
243 variables, such as cumulative surface area. As in other studies of this type (Bogale et al., 2014;
244 Piffer, Miletto Petrazzini, & Agrillo, 2013), in experiment 2, we studied the relative importance of
245 these two types of information by presenting two novel discriminations in which either numerosity
246 or total surface were made irrelevant (Fig. 2). In the first discrimination we presented the choice
247 between 3 versus 3 food items, but one card had food items, on average, twice as large as the other.

248 In the second discrimination, we presented a choice between 2 versus 4 food items with the
249 numerically smaller group having food items, on average, twice the size, making food surface areas
250 equal. The size of the food items used ranged from 1.5 x 1.5 mm to 3 x 3 mm. The experimental
251 phase lasted 5 days (a total of 40 trials, 20 for each discrimination). We observed 10 subjects, 5
252 males and 5 females.

253

254 Experiment 3

255 We proposed that the results of experiment 2 are better explained by a hypothesis that
256 guppies pay special attention to the size of individual food items within the set. In experiment 3, we
257 investigated the ability of guppies to discriminate between two food items of different size, using an
258 experimental design similar to that of experiment 1. Subjects were presented with pairs of food
259 items (one on each card) with four size ratios: 0.25, 0.50, 0.67, and 0.75, the same ratios used in
260 experiment 1 (Fig. 2). The size of the food items used was 1.5 x 1.5 mm, 2.1 x 2.1 mm, 2.6 x 2.6
261 mm, and 3 x 3 mm. The experimental phase lasted 10 days, for a total of 80 trials (20 for each
262 discrimination). Experiments were performed 5 days per week, from Monday to Friday. We
263 observed 10 subjects, 5 males and 5 females.

264

265 Experiment 4

266 Experiment 2 and 3 indicated that the size of the single food item has a strong influence on
267 guppies' food choice. In this experiment, we contrasted the total amount of food with the size of the
268 largest food item to determine if this preference could lead to suboptimal decisions (such as
269 choosing the card with less food overall). In each trial, all the food items were the same size, except
270 one item twice as large as the other. In half of the trials, the small food items were 1.5 x 1.5 mm and
271 the large one 2.1 x 2.1 mm; in the remaining trials, the small food items were 2.1 x 2.1 mm and the
272 large one 3 x 3 mm. We presented the subjects with two discriminations in which the largest food

273 item was always on the card with the smaller food quantity (Fig. 2). The first discrimination
274 presented 2 versus 6 food items (twice the food in the card without the largest item). In the second
275 discrimination we presented 3 versus 6 food items (1.5 times the food in the card without the largest
276 item). To keep the subject from learning that the largest food item was always associated with the
277 smaller food quantity, 2 out of 8 trials presented a reversed condition (with the larger food items in
278 the card with the larger food quantity). These trials were not included in the analysis. The
279 experimental phase lasted 6 days for a total of 36 trials (18 for each discrimination discounting the
280 12 with the reversed condition). We used 10 subjects, 5 males and 5 females.

281

282 *Statistical analysis*

283

284 Statistical analysis was performed in R (R Core Team, version 3.0.2). All statistical tests
285 were two-tailed and significance threshold set at $p = 0.05$, unless stated otherwise. To evaluate the
286 performance of the subjects, we computed the proportion of choice of the card with the larger food
287 quantity. This variable was reported in text as percentages, and was always arcsine square root
288 transformed before analysis (Sokal & Rohlf, 1995). We initially tested for a sex difference in the
289 size of the subjects (SL) using independent sample t -test. As females were generally larger than
290 males, we tested for sex and SL effect on the food choice performance independently: the effect of
291 the SL was assessed with Pearson correlation test, whereas the effect of sex was examined with the
292 linear mixed model (LMM). In experiment 1, the SL was log-transformed to achieve normality
293 assumptions. To assess whether the proportion of choice of the larger food quantity was different
294 from the one expected by chance (50%), we used one sample t -test. Pearson correlation test was
295 used to assess the correlation between the performances of the subjects in the discriminations. A
296 LMM ('lme' function from the 'nlme' R package) fitted with the identifier name of the subject
297 (subject ID) as random factor was used to study the possible effect of sex and discrimination in each

298 experiment. Trend analysis in experiments 1 and 3 was performed according to Logan (2011). To
299 compare the discrimination abilities of guppies in experiments 1 and 3, we fitted the pooled data
300 into a LMM model with experiment (1 and 3), sex, and quantity ratio (0.25, 0.50, 0.67, and 0.75) as
301 fixed factors, and subject ID as random factor. The text gives means \pm standard deviations. Finally,
302 we used the Bayesian information criteria of the LMM models with and without the effect of sex to
303 approximate a Bayes factor (Schwarz, 1978). The Bayes factor estimates relative strength of
304 evidence for the two competing models even in the case of non-significant results and small sample
305 size (Dienes, 2014).

306

307 *Ethical note*

308

309 Our experiments consisted in observations of fish behaviour without manipulation of the
310 subjects. Fish spontaneously participated in the experiments, otherwise they were substituted.
311 Experimental tanks were provided with natural plants, bottom gravel and social companions to
312 minimise differences from maintenance tanks. None of the subjects expressed distress during
313 observation. At the end of the experiment, subjects were released in maintenance tanks identical to
314 the ones previously described, and kept only for breeding purpose. Experiments comply with the
315 law of the country (Italy) in which they were performed (Decreto legislativo 4 marzo 2014, n. 26).
316 The experimental procedures have been approved by Università di Padova Ethical Committee
317 (protocols n. 09/2012 and 108660).

318

319

320 **RESULTS**

321

322 *Experiment 1*

323

324 Subjects measured 24 ± 3 mm. Female subjects were significantly larger than male (females
325 SL: 26 ± 3 mm; males SL: 22 ± 1 mm; independent sample *t*-test: $t_{18} = 3.879$, $P = 0.001$). There was
326 no significant correlation between SL of subjects and proportion of choice of the card with more
327 food items (Pearson correlation: $r_{18} = -0.021$, $P = 0.983$), suggesting that the body size did not
328 affect the results of the experiment.

329 Subjects chose the card with more food items in $55.25 \pm 7.56\%$ of the trials, a preference
330 significantly greater than chance (one sample *t*-test: $t_{19} = 3.109$, $P = 0.006$). However, separate
331 analysis for each discrimination found the ratio between quantities important. Subjects significantly
332 discriminated 1 versus 4 ($63.25 \pm 14.89\%$, $t_{19} = 3.907$, $P < 0.001$) and 2 versus 4 food items ($57.5 \pm$
333 8.51% , $t_{19} = 3.916$, $P < 0.001$), but not 2 versus 3 ($53.00 \pm 11.52\%$, $t_{19} = 1.174$, $P = 0.255$) or 3
334 versus 4 food items ($47.25 \pm 11.18\%$, $t_{19} = 1.104$, $P = 0.283$) (Fig. 3). The proportion of choice of
335 the card with more food items significantly correlated between the 1 versus 4 and 2 versus 3
336 discrimination (Pearson correlation: $r_{18} = 0.526$, $P = 0.017$) and between the 2 versus 4 and 3 versus
337 4 discrimination ($r_{18} = 0.472$, $P = 0.036$). There was no significant correlation between the
338 remaining discriminations (all P values > 0.300).

339 The LMM on the proportion of choice of the card with more food items revealed a
340 significant effect of discrimination ($F_{3,54} = 8.721$, $P < 0.001$). A polynomial trend analysis
341 suggested that the proportion of choice of more food items decreased linearly with the increase of
342 the ratio of the discrimination ($P < 0.001$) (Fig. 3). No significant effects of sex ($F_{1,18} = 1.613$, $P =$
343 0.220) nor significant sex by discrimination interaction ($F_{3,54} = 1.021$, $P = 0.391$) were found in the
344 model. The approximate Bayes factor indicated that the LMM model without the effect of sex was
345 42.612 times more likely to explain the performance of the subjects than the model with the effect
346 of sex.

347

348 **Experiment 2**

349

350 Subjects measured 22 ± 2 mm. Females were significantly larger than males (females SL: 23
351 ± 1 mm; males SL: 21 ± 1 mm; independent sample t -test: $t_8 = 3.795$, $P = 0.005$). There was no
352 significant correlation between SL and proportion of choice of the card with the larger food area in
353 the 3 versus 3 discrimination (Pearson correlation: $r_8 = -0.001$, $P = 0.997$) or of the card with more
354 food items in the 2 versus 4 discrimination ($r_8 = 0.113$, $P = 0.756$), suggesting that body size did not
355 affect the results of the experiment.

356 In the 3 versus 3 discrimination with different food area, subjects chose the larger area in
357 $68.00 \pm 14.57\%$ of the trials, a preference that was significantly greater than chance (one sample t -
358 test: $t_9 = 3.791$, $P = 0.004$) (Fig. 4). In the 2 versus 4 discrimination with equal food area, subjects
359 chose the more food items in $33.00 \pm 11.60\%$ of the trials, a preference significantly smaller than
360 chance ($t_9 = 4.329$, $P = 0.002$) (Fig. 4). There was no significant correlation between the proportion
361 of choice of the larger food area in the 3 versus 3 discrimination and the proportion of choice of the
362 more food items in the 2 versus 4 discrimination (Pearson correlation: $r_8 = -0.428$, $P = 0.217$).

363 The LMM on the proportion of choice of the larger food area/more food items revealed a
364 significant effect of discrimination ($F_{1,8} = 29.704$, $P < 0.001$). No significant effects of sex ($F_{1,8} <$
365 0.001 , $P = 0.995$) nor sex by discrimination interaction ($F_{1,8} = 0.610$, $P = 0.457$) were found. The
366 approximate Bayes factor indicated that the LMM model without the effect of sex was 22.029 times
367 more likely to explain the performance of the subjects than the model with that effect.

368

369 **Experiment 3**

370

371 Subjects measured 23 ± 2 mm. Females were significantly larger than males (females SL: 25
372 ± 2 mm; males SL: 21 ± 1 mm; independent sample t -test: $t_8 = 3.860$, $P = 0.005$). There was no

373 significant correlation between SL and proportion of choice of the card with the larger food item
374 (Pearson correlation: $r_8 = -0.107$, $P = 0.768$), suggesting that body size did not affect the results of
375 the experiment.

376 Subjects chose the card with the larger food item in $74.38 \pm 5.72\%$ of the trials, a preference
377 significantly greater than chance (one sample t -test: $t_9 = 11.316$, $P < 0.001$). A separate analysis for
378 each discrimination revealed the proportion of choice of the larger food item was significant in all
379 quantity ratios (0.25 ratio: $88.50 \pm 5.80\%$, $t_9 = 15.306$, $P < 0.001$; 0.50 ratio: $79.00 \pm 4.59\%$, $t_9 =$
380 16.157 , $P < 0.001$; 0.67 ratio: $65.00 \pm 11.3\%$, $t_9 = 3.851$, $P = 0.004$; 0.75 ratio: $65.00 \pm 12.69\%$, $t_9 =$
381 3.660 , $P = 0.005$) (Fig. 3). The proportion of choice of the larger food item was significantly
382 correlated only between the 0.50 and 0.67 discrimination (Pearson correlation: $r_8 = 0.705$, $P =$
383 0.023). There was no significant correlation between all the remaining discriminations (all P values
384 > 0.100).

385 The LMM on the proportion of choice of the larger food item revealed a significant effect of
386 discrimination ($F_{3,24} = 18.911$, $P < 0.001$). A polynomial trend analysis suggested that the
387 proportion of choice of the larger food item decreased linearly with the increase of the ratio ($P <$
388 0.001) (Fig. 3). No significant effect of sex ($F_{1,8} = 0.011$, $P = 0.920$) or significant sex by
389 discrimination interaction ($F_{3,24} = 0.441$, $P = 0.726$) were found. The approximate Bayes factor
390 indicated that the LMM model without the effect of sex was 48.565 times more likely to explain the
391 performance of the subjects than the model with that effect.

392

393 ***Comparison of experiments 1 and 3***

394

395 The LMM model that compares experiments 1 and 3 revealed a significant effect of
396 experiment ($F_{1,26} = 52.252$, $P < 0.001$) and ratio ($F_{3,78} = 22.889$, $P < 0.001$), but also a significant
397 experiment by ratio interaction ($F_{3,78} = 3.368$, $P = 0.023$). We explored the nature of this interaction

398 by comparing each ratio between the two experiments using multiple t -tests with α -level corrected
399 with Bonferroni method. In all the ratios, subjects achieved a performance significantly better in
400 experiment 3 (all P values < 0.0125). Therefore, it seems reasonable that guppies were more
401 accurate in the comparison of the single item with the respect of multiple items. The effect of sex
402 and the remaining interactions in the LMM model were not significant (sex: $F_{1,26} = 1.248$, $P =$
403 0.274 ; interactions: all P values > 0.300). The approximate Bayes factor indicated that the LMM
404 model without the effect of sex was 79.166 times more likely to explain the performance of the
405 subjects than the model with the effect of sex.

406

407 *Experiment 4*

408

409 Subjects measured 23 ± 3 mm, and there was no significant difference between the two
410 sexes (females SL: 25 ± 1 mm; males SL: 22 ± 3 mm; independent sample t -test: $t_8 = 1.966$, $P =$
411 0.085). There was no significant correlation between SL of the subjects and preference for the set
412 with the larger food item in either the 2 versus 6 discrimination (Pearson correlation: $r_8 = -0.291$, P
413 $= 0.414$) or the 3 versus 6 discrimination ($r_8 = 0.112$, $P = 0.758$), suggesting that body size did not
414 affect the results of the experiment.

415 In the 2 versus 6 discrimination, subjects chose the set with the larger food item in $58.67 \pm$
416 10.31% of the trials, a preference significantly greater than chance (one sample t -test: $t_9 = 2.621$, P
417 $= 0.028$) (Fig. 4). In the 3 versus 6 discrimination, the preference for the larger food item ($64.78 \pm$
418 8.99%) was also significantly greater than chance ($t_9 = 5.025$, $P < 0.001$) (Fig. 4). Discrimination of
419 2 versus 6 and 3 versus 6 were not significantly correlated (Pearson correlation: $r_8 = 0.621$, $P =$
420 0.055).

421 The LMM on the proportion of choice of the set with the larger food item revealed no
422 significant effect of discrimination ($F_{1,8} = 4.691$, $P = 0.062$), sex ($F_{1,8} = 1.357$, $P = 0.278$), or

423 significant sex by discrimination interaction ($F_{1,8} = 0.408$, $P = 0.541$). The approximate Bayes
424 factor indicated that the LMM model without the effect of sex was 13.107 times more likely to
425 explain the performance of the subjects than the model with the effect of sex.

426

427

428 **DISCUSSION**

429

430 In experiment 1, guppies were administered four discriminations between discrete food
431 quantities, from 1 versus 4 up to 3 versus 4. Overall, subjects selected the larger food quantity, but
432 their performance was affected by the numerical ratio. They had a significant preference only in the
433 two easier discriminations (1 versus 4 and 2 versus 4 food items), but showed a near-chance
434 performance in the remaining discriminations (2 versus 3 and 3 versus 4 food items). The ratio
435 dependence of the accuracy aligns with previous literature in mammals (Ward & Smuts, 2007) and
436 birds (Al Aïn et al., 2009) in the same numerical ratios. To explain this phenomenon, several
437 authors have hypothesised the existence of an approximate number system for discrimination in the
438 whole numerical range whose accuracy is set by Weber's law (Cantlon & Brannon, 2007).
439 However, the performance of guppies in food choice appears to be lower than that found in studies
440 of other species (chimpanzee: Beran, 2006; orangutan: Call, 2000; macaque: Hauser et al., 2000;
441 New Zealand robin: Hunt, Low, & Burns, 2008; salamander: Uller et al., 2003) and similar only to
442 dogs (Ward & Smuts, 2007). Interestingly, the upper limit of the discrimination ability we observed
443 in food choice test was also lower than the one reported in shoal choice experiments, where guppies
444 discriminated up to 3 versus 4 conspecifics (Agrillo et al., 2012), or in experiments that used
445 training procedures where some guppies achieved a 4 versus 5 items discrimination (Bisazza et al.,
446 2014). The different thresholds in numerical acuity of guppies in different tasks is worth noting and
447 points to the existence of multiple, context-dependent numerical systems instead of a single cross-

448 modal system to process quantity in every context (Miletto Petrazzini, Agrillo, Piffer, & Bisazza,
449 2014; Spelke, 2000;).

450 In relative quantity judgments, animals can use both numerical and non-numerical
451 information that co-varies with number (Cantlon & Brannon, 2007; Gomez-Laplaza & Gerlai,
452 2013a). For instance, two groups of food items could be discriminated by using their cumulative
453 surface area instead of their number. In experiment 2, we investigated the relative importance of
454 these two types of information by presenting the choice between 3 versus 3 food items with a 2:1
455 surface area and between 2 versus 4 food items with cumulative surface area matched (because the
456 items in the smaller set were of larger size). Guppies preferred the larger quantity in the first
457 discrimination but not in the second. In this species, the cumulative surface area occupied by food
458 appears to be more important than the number of food items in quantity estimation during foraging.
459 Analogous results have been found in other organisms. For instance, jungle crows showed no
460 preference for small or large quantities of food items when the total volume between sets was
461 equalised (Bogale et al., 2014). Human infants presented with sets of crackers chose at chance when
462 the total surface area was equated (Feigenson et al., 2002). However, the preference for continuous
463 variables over number in food quantity discrimination has not been found in all species
464 investigated. For instance, rhesus monkey (*Macaca mulatta*) and horses (*Equus caballus*) privilege
465 number of items rather than overall volume in selecting the larger food quantity (Hauser et al.,
466 2000; Uller & Lewis, 2009). To date, it is not clear whether these differences can be ascribed to
467 different experimental methodologies or different foraging strategies.

468 Intriguingly, in the second discrimination of experiment 2 (2 versus 4 food items with
469 matched area), guppies did not choose the two options with the same frequency but instead showed
470 a marked preference for the set with fewer food items. To equate the area of the two options, the set
471 with fewer food items contained, on average, larger food pieces, and in the 90% of the trials the
472 largest food item was contained in this set. Therefore, a possible explanation for our results is that

473 guppies have a strong preference for larger food items. Our hypothesis implies that guppies should
474 possess an excellent ability to estimate and compare the area of two food items. There is indeed
475 some evidence that fish have this ability. Female freshwater gobies lay eggs on the larger nest
476 available (Bisazza et al., 1989), and female guppies prefer to mate with males showing larger area
477 of carotenoid pigmentation (Houde, 1997). However, to our knowledge, no study has assessed the
478 accuracy of area discrimination in fish.

479 In experiment 3, we investigated the ability of guppies to discriminate between two food
480 items differing in area, using the same ratios as in experiment 1 (0.25, 0.50, 0.67, and 0.75). Here
481 the subjects performed much better than in experiment 1 and exhibited a significant preference for
482 the larger food quantities, even in the 0.75 ratio discrimination. Again, the accuracy of the subjects
483 appeared to decrease with increasing ratio, suggesting Weber's law sets the accuracy of this task as
484 well. So guppies discriminate up to a 0.67 and 0.75 ratio of quantity, but only if these quantities are
485 not fragmented into more units. Further investigation should test this effect in other tasks.

486 Given their remarkable ability in area discrimination, it is not surprising that guppies in
487 experiment 2 used the food area as a prominent cue to drive their food choices. What still remains
488 unclear is why guppies are so accurate in comparing the area of single food items compared to
489 multiple discrete items and why they are so attracted by large food items. In the natural
490 environment of guppies, a simultaneous encounter of two patches of food is probably a rare event.
491 Conversely, wild guppies often move in shoals (Magurran & Seghers, 1991); thus, many can
492 discover and exploit a single food patch at once. While an individual is processing one food item in
493 the patch, its shoal mates are probably eating the residual items. In such a scenario, there is an
494 advantage for the individual that detects and consumes the largest food item first. Therefore, natural
495 selection should promote abilities that accurately estimate and compare the size of single food items
496 and decision mechanisms that prioritise the search of larger food items rather than the search of
497 patches containing more overall food. If our hypothesis is correct, the preference for the larger food

498 item should prevail over other choice criteria. Guppies should choose the patch with the larger food
499 item even when the overall food quantity is smaller than the other option. We tested this possibility
500 in experiment 4, finding support for our hypothesis. Guppies preferred the larger food item even
501 when this led them to the suboptimal choice of a set with overall less food. Interestingly, two other
502 social species have a similar pattern of food selection: chimpanzee presented with two sets of food
503 items reliably selected the largest, but showed a bias toward the smaller one when it contained the
504 largest single food item (Beran et al., 2008; Boysen et al., 2001); cotton-top tamarins (*Saguinus*
505 *oedipus*) showed a similar preference for sets with the largest single food items (Stevens, Wood,
506 Hauser, 2007). Like guppies, those two monkeys forage in groups and compete for food (Pusey &
507 Schroepfer-Walker, 2013; Tardif & Richter, 1981; Wittig & Boesch, 2003), supporting our
508 hypothesis that the preference for the larger food item could arise from social foraging habits.

509 Although our study was not designed to investigate cognitive sex differences, we used males
510 and females in all experiments, which allows us to compare sexes and to increase knowledge about
511 an issue which is almost neglected in fish (but see Lucon-Xiccato & Bisazza, 2014). Sex differences
512 in quantity discrimination abilities have been studied only in salamanders (*Plethodon cinereus*) and
513 humans (Benbow & Stanley, 1983; Gallagher et al., 2000; Uller et al., 2003). In the four
514 experiments of the present study, we found no evidence of differences between male and female
515 guppies, suggesting the sexes have comparable quantity discrimination abilities and mechanisms for
516 food choice. This result appears quite robust, since the Bayesian approach indicated a strong (*sensu*
517 Jeffreys, 1998) evidence against the hypothesis of a sex difference in guppies' performance. In the
518 guppy, the two sexes have the same diet and exhibit only minor differences in foraging behaviour
519 (Dussault & Kramer, 1981; Magurran, 2005; Nikolaeva & Kasumyan, 2000). Therefore, the
520 selective pressures imposed on cognitive mechanisms controlling food choice are likely to be
521 similar in the two sexes.

522 To summarise, we provide evidence that guppies discriminate the larger quantity of food by
523 using primarily non-numerical cues and that they prioritise the selection of the largest food item
524 over the total number of items and the total amount of food. We hypothesised that this might occur
525 because of shoaling habits that bring them to compete for food and hence favour strategies that
526 maximise the chance of consuming larger food items before their companions. Further studies
527 investigating such feeding strategies in species that do not form shoals are welcome to verify this
528 hypothesis.

529

530

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532

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718

719 **Figure 1.**

720 **Experimental apparatus.** Aerial (a) and frontal (b) view. The subject was housed in the apparatus
721 for the entire experiment. In each trial, two cards with items differing in number and/or size were
722 simultaneously inserted at the corners of one of the short walls. The subject was allowed to select
723 only one card while the other was removed after the choice.

724

725 **Figure 2.**

726 **Examples of cards with stimuli used in the four experiments.** In experiment 1, the two cards
727 differed in the number of food items. Experiment 2 sequentially controlled the number of food
728 items and surface area of the food in two discriminations. In experiment 3, the two food items
729 differed in size. In experiment 4, the set with the smaller food quantity had a larger food item.

730

731 **Figure 3.**

732 Preference for the set with more food items (experiment 1, dark line) and for the larger food item
733 (experiment 3, grey line). Data points represent mean \pm SEM percentage of choice for the larger
734 food quantity.

735

736 **Figure 4.**

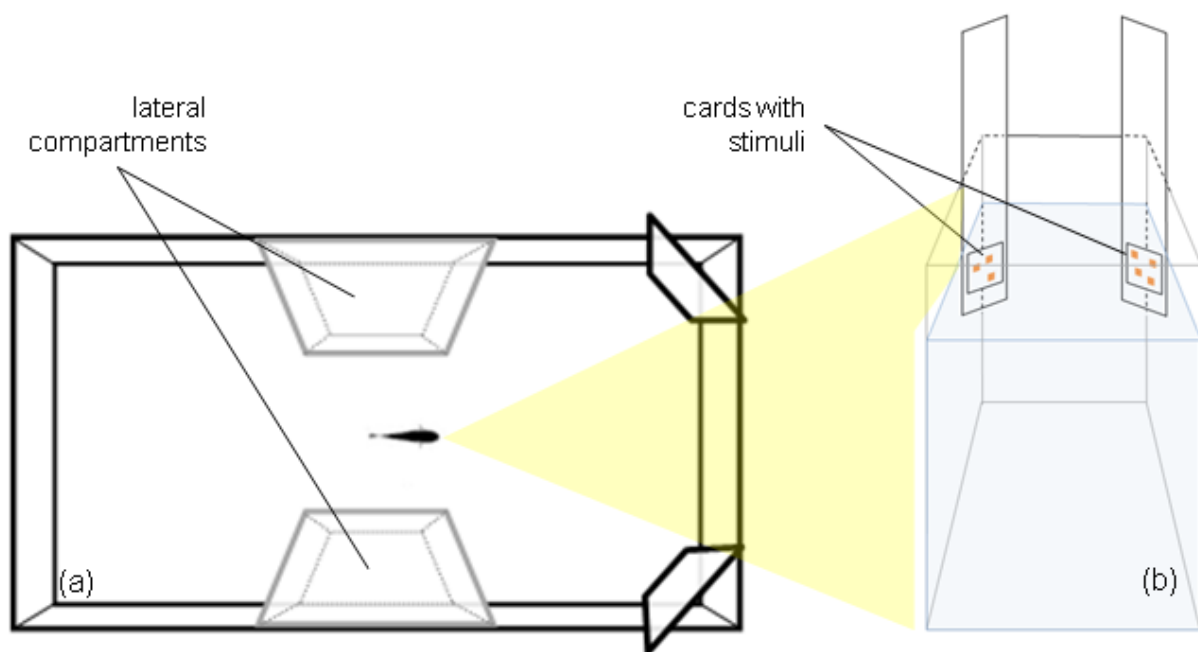
737 Preference for the larger food quantity in experiment 2 (left panel), and for the larger food item in
738 experiment 4 (right panel). Data points represent mean \pm SEM percentage of choice.

739

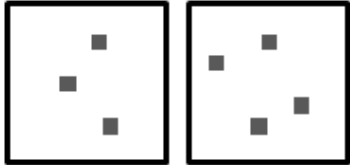
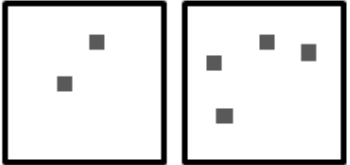
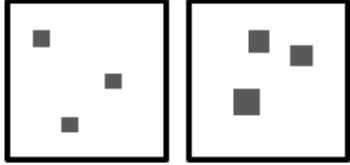
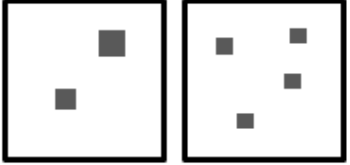
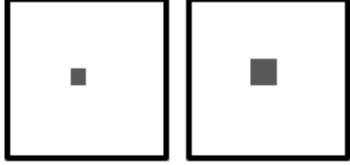
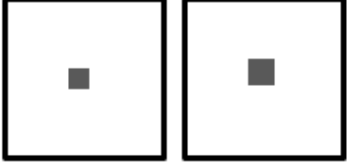
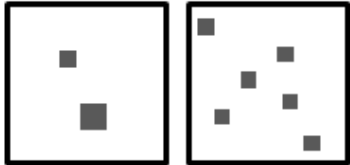
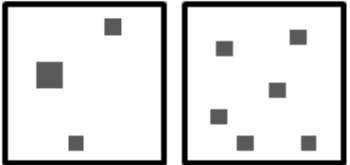
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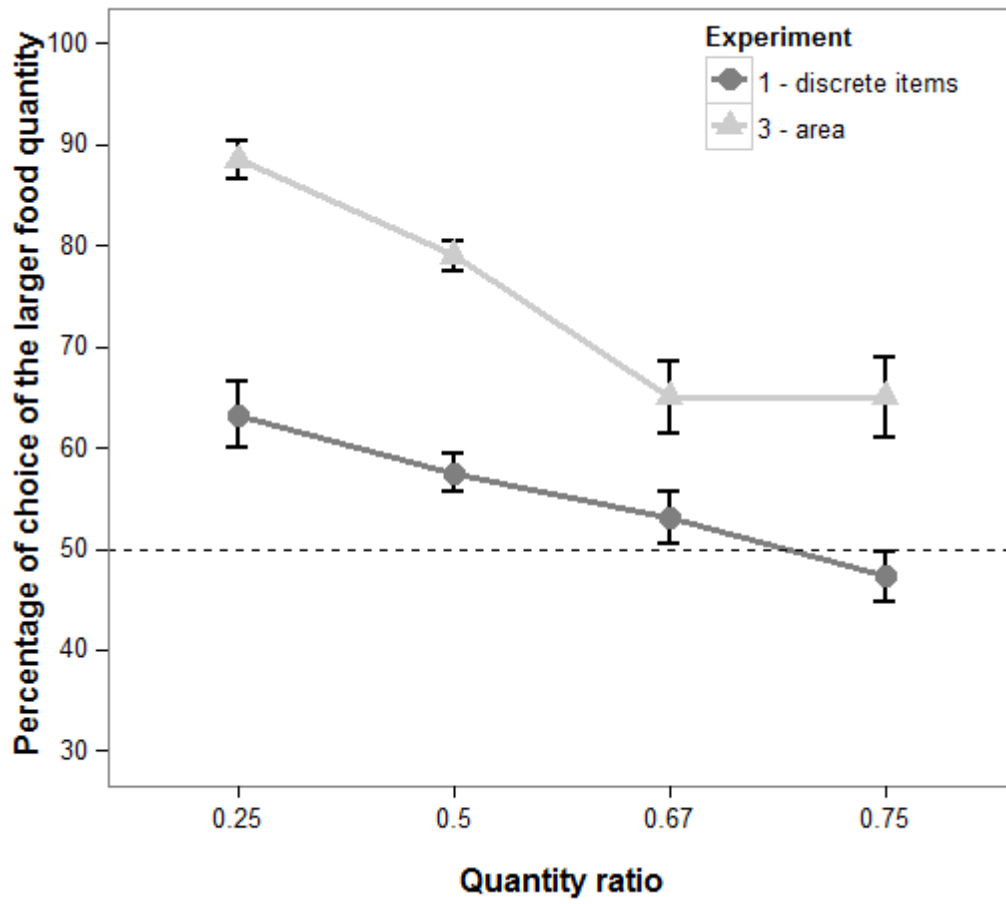


743

Experiment 1		
Experiment 2		
Experiment 3		
Experiment 4		

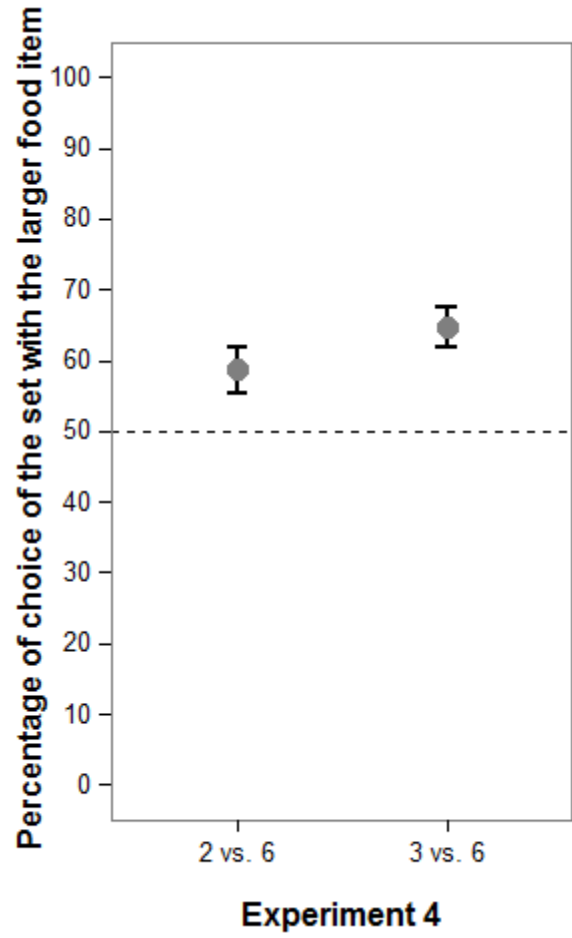
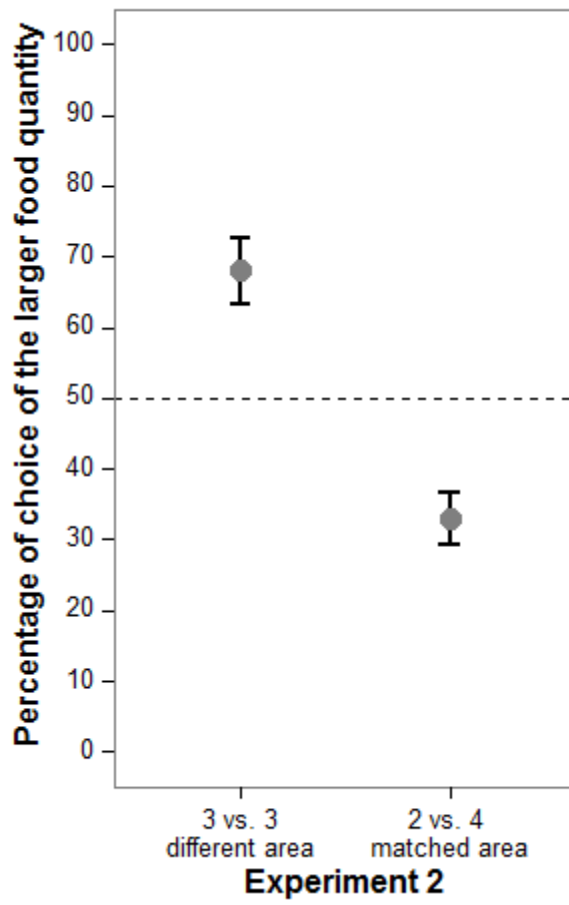
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