Animal Cognition

To free, or not to free: Social reinforcement effects in the social release paradigm with rats
--Manuscript Draft--

Manuscript Number:	
Full Title:	To free, or not to free: Social reinforcement effects in the social release paradigm with rats
Article Type:	Original Article
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Corresponding Author's Institution:	Cornell University
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Funding Information:	National Institute on Drug Abuse (026127) — Dr. Timothy D Hackenberg

Abstract:	The aim of the present research was to measure social reinforcement in rats, using a social-release procedure in which lever presses permitted 10-s access to a familiar social partner. The work requirements for reinforcement increased systematically with each earned reinforcer according to progressive-ratio (PR) schedules. Social reinforcers were compared against food reinforcers, either across blocks of sessions (Experiment 1) or concurrently, within the same sessions (Experiment 2). To assess the impact of motivational variables, PR breakpoints (last completed ratio each session) and response rates for both reinforcers were studied under food restriction, social restriction, and combined food and social restriction. Responding was maintained by both reinforcers, albeit at significantly higher levels for food than for social access. Responding for social access decreased to low levels when the contingency between lever pressing and access was discontinued (extinction), demonstrating functional control by the social reinforcement contingency. Food-reinforced behavior was more sensitive to deprivation conditions (i.e., it occurred at higher levels when food was restricted than when it was not), than was socially-reinforced behavior (i.e., generally comparable across deprivation conditions). Sensitivity to social deprivation was seen in some conditions in Experiment 2, in which social reinforcers were earned earlier in the session (at lower food prices) under social restriction than under the other deprivation conditions. Altogether, the results are consistent with a social reinforcement conceptualization, and demonstrate an important role for social contact in social release behavior. More generally, the study illustrates a promising set of methods for analyzing and quantifying social reinforcement.

Suggested Reviewers:	Alan Silberberg American University asilber@american.edu Dr. Silberberg has previously published on relevant topics, including the investigation of quantitative methods for assessing social reinforcement in rats. His knowledge of the subject matter as well as his expertise in behavioral economics makes him an

	appropriate choice as a reviewer.
	Michael J Beran Georgia State University mberan1@gsu.edu Dr. Beran's extensive knowledge of comparative cognition, learning, and decision-making in animal models makes him an ideal reviewer for this work. In addition, his emphasis on finding parsimonious explanations for complex behavioral phenotypes resonates with the aims of our submission.
Opposed Reviewers:	

1   To free, or not to free: Social reinforcement effects in the social release paradigm

2   with rats

3

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21   **Abstract**

22   The aim of the present research was to measure social reinforcement in rats, using a

23   social-release procedure in which lever presses permitted 10-s access to a familiar social

24   partner. The work requirements for reinforcement increased systematically with each

25   earned reinforcer according to progressive-ratio (PR) schedules. Social reinforcers were

26   compared against food reinforcers, either across blocks of sessions (Experiment 1) or

27   concurrently, within the same sessions (Experiment 2). To assess the impact of

28   motivational variables, PR breakpoints (last completed ratio each session) and response

29   rates for both reinforcers were studied under food restriction, social restriction, and

30   combined food and social restriction. Responding was maintained by both reinforcers,

31   albeit at significantly higher levels for food than for social access. Responding for social

32   access decreased to low levels when the contingency between lever pressing and access

33   was discontinued (extinction), demonstrating functional control by the social

34   reinforcement contingency. Food-reinforced behavior was more sensitive to deprivation

35   conditions (i.e., it occurred at higher levels when food was restricted than when it was

36   not), than was socially-reinforced behavior (i.e., generally comparable across deprivation

37   conditions). Sensitivity to social deprivation was seen in some conditions in Experiment

38   2, in which social reinforcers were earned earlier in the session (at lower food prices)

39   under social restriction than under the other deprivation conditions. Altogether, the

40   results are consistent with a social reinforcement conceptualization, and demonstrate an

41 important role for social contact in social release behavior. More generally, the study

42 illustrates a promising set of methods for analyzing and quantifying social reinforcement.

43

44 **Key words** social reinforcement, food reinforcement, social behavior, progressive ratio

45 schedules, lever press, rats

46

47   **Introduction**

48   Several recent studies with rats have investigated what might be termed *social*

49   *release*, in which one rat works to release another rat from a restraint (Bartal, Decety &

50   Mason, 2011; Silberberg, Allouch, Sandfort, Kearns, Karpel, & Slotnik, 2014). In the

51   Ben-Ami Bartal et al. (2011) study, for example, two familiar (cagemate) rats were

52   placed in an arena, one of which began each session in a transparent tube-like restrainer.

53   A second rat was unrestrained, and could move freely around the rest of the arena. A

54   latch on one side of the restrainer could be lifted, releasing the restrained rat, for the

55   remainder of the 60-min session. No explicit training was provided, though the response

56   was prompted by lifting the door halfway up at the 30-min mark. After an average of 7

57   sessions, 23 of the 30 rats acquired the door-opening response; and once the response was

58   acquired, it generally continued to occur in subsequent sessions and with shorter latencies

59   (i.e., earlier in the session). The door-opening response was also selective, in that it

60   occurred only under conditions with a live rat in the restraint; it did not occur when the

61   restraint was empty or occupied by a toy rat. Door opening under these conditions thus

62   appears to be a learned social response, but its mechanisms are not well understood.

63   Bartal et al. (2011) favored an empathy-based explanation, according to which the

64   restrained rat, in acute distress, passed its distress to the other rat; opening the door and

65   releasing the rat alleviated the stress; the actions of the non-restrained rat were therefore

66   motivated by empathic concern for the restrained rat (see also Bartal et al., 2014; Sato,

67   Tan, Tate, & Okada, 2015). An alternative, and far simpler, explanation is that door

68   opening for the unrestrained rat is an operant response, established and maintained by

69   social reinforcement (access to the other rat). This possibility was considered but

70   rejected by Bartal et al. (2011), largely on the basis of a control condition, in which door

71   opening permitted release but precluded direct social contact with the other rat (which

72   was released into an adjacent chamber). Rats in these no-contact conditions continued to

73   respond, despite the absence of direct social contact.

74   Although this result is seemingly inconsistent with the social reinforcement

75   hypothesis, the rats in these no-contact conditions all had prior social reinforcement

76   histories (i.e., histories in which responding produced direct social contact with the other

77   rat). Silberberg et al. (2014) showed that, without such a history of social contact, social

78   release is not acquired. Once social release is established, however, under conditions

79   with direct social contact, it can be maintained at moderate levels even without direct

80   social contact. This may be due to conditioned reinforcement effects (i.e., the presence of

81   stimuli correlated with prior social release). It may also be due to uncontrolled sources of

82   social contact. In the Silberberg et al. study, for example, restrained rats frequently

83   remained in or returned to the restrainer. This is inconsistent with a view of the restraint

84   as aversive and stress-inducing, but can be understood in terms of social proximity.

85   Because the restraint was enclosed within the chamber containing the unrestrained rat

86   (with the door opening into an adjacent chamber), leaving the tube increased social

87   distance whereas remaining in the tube reduced it.   Social contact may thus serve

88   important functions even in conditions designed to minimize its impact. At the very

89   least, these findings cannot rule out a potentially crucial role for social contact in prior

90   results in the social release paradigm with rats.

91   Conceptualizing social release in terms of social reinforcement has several

92   advantages. First, it is consistent with a longstanding body of literature showing that

93   contingent access to social stimuli can function as a reinforcer across a variety of

94   procedures and in a range of species, including chimpanzees (Mason, Hollis, & Sharpe,

95   1962), capuchin monkeys (Dettmer & Fragaszy, 2000), horses (Sondergaard, Jensen &

96   Nicol, 2011), foxes (Hovland, Akre, Flø, Bakken, Koistinen & Mason, 2011), calves

97   (Holm, Jensen, & Jeppesen, 2002), sows (Kirkden & Pajor, 2006), mice (Martin, Sample,

98   Gregg, & Wood, 2014), and rats (Evans, Duvel, Funk, Lehman, Sparrow, Watson &

99   Neuringer, 1994; Wilsoncroft, 1968).

100   Second, a social reinforcement view opens questions to sharper methods for

101   assessing reinforcing value, more generally.   For example, Evans et al. (1994) used

102   operant methods to assess the value of food and social reinforcement in rats. Lever

103   pressing by two groups of female rats produced either 45-s access to another rat (a

104   castrated male cagemate) or 45-s access to food, according to a fixed-ratio (FR) 3

105   schedule, in which each 3rd press produced food or social access. Lever pressing was

106   acquired, maintained, and extinguished in both groups of rats, consistent with operant

107   functions. Moreover, social and food access appeared to be about equally effective as

108   reinforcers, as there were no significant differences between groups in the number of

109   responses under reinforcement or extinction conditions.

110   The present study further explores the reinforcing value of social contact in rats.

111   The procedures were designed partly after the Bartal et al. (2011, 2014) studies, but with

112   free-operant methods like those of Evans et al., (1994) to provide a more detailed analysis

113   of reinforcer value. As in the Bartal et al., study, the rats were cagemates of the same

114   sex. The restrained rat was in a transparent tube restraint identical to that used by Bartal

115   et al., but the door on one end could be opened by lever presses by the unrestrained rat, as

116   in Evans et al. (1994). Also similar to the Evans et al. study, following a specified period

117   of social interaction, the rats were separated and a new trial started. This permitted

118   repeated opportunities to respond within a session, and a more refined and graded

119   measure of reinforcer value. This contrasts with the binary (all-or-none) measure

120   permitted by Bartal et al., in which only a single response was permitted each session

121   (i.e., the door was either opened or it was not).

122   As a result, the duration of social contact in the Bartal et al. study was not

123   controlled; once the door had been opened, the two rats remained together for the

124   remainder of the 60-min session. The amount of social contact thus varied depending on

125   the time in the session when the response occurred. From a social reinforcement

126   perspective, social contact is *the* relevant consequence. Therefore, a procedure in which

127   the duration of this variable (akin to reinforcement magnitude) varies so widely between

128   sessions and subjects is not optimal. Thus, in line with some prior research (e.g., Evans

129   et al., 1994; Holm et al., 2006), we carefully controlled the duration of social contact.

130   To measure reinforcer value, we used progressive ratio (PR) schedules, in which

131   the price varies within each session. More specifically, the price of a reinforcer increases

132   systematically following each reinforcer, until a price is reached at which the subject

133   stops responding. The last completed ratio, or breakpoint (BP), provides a quantitatively

134   precise measure of reinforcer value. PR schedules have been used widely to assess the

135   incentive value of a range of reinforcers and motivational conditions (Hodos & Kalman,

136   1963), including food and drink (Pickering, Alsiö, Hulting, & Schiöth, 2009; Stafford &

137   Branch, 1998), sucrose (Sclafani & Ackroff, 2006; Weatherly, King, & Uran, 2003),

138   alcohol (Maccioni et al., 2009; Rodd et al., 2003), nicotine (Donny et al., 1999), and

139   others drugs of abuse (Carroll, Batulis, Landry, & Morgan, 2005; Grasing, Li, He,

140   Parrish, Delich, & Glowa, 2003; Spear & Katz, 1991).

141   Because social reinforcers have been studied far less extensively than other

142   reinforcers, we compared them to more common food reinforcers. Some studies have

143   reported higher levels of responding for food than for social reinforcers. Gilbertson

144   (1975), for example, found that pigeons responded at a higher rate for access to food than

145   to visual access to their mate. Similarly, foxes (Hovland et al., 2011) and mice (Martin et

146   al, 2014) paid higher prices for food than for social access to a same-sex conspecific.

147   Other studies, however, with capuchin monkeys (Dettmer & Fragaszy, 2000) and rats

148   (Bartal et al., 2011; Evans et al., 1994; Sato et al., 2015), have reported comparable value

149   of social and food reinforcers.

150   In the Bartal et al. and Sato et al. studies, rats were given choices between two

151   doors—one permitting access to a partner rat and one permitting access to a preferred

152   food item (pieces of chocolate). The average latencies were similar between social and

153   food, prompting the authors of both studies to conclude equivalent reinforcer value,

154   although only Sato showed preference data (which door was opened first). Preference

155   depended on the rats' training histories: when trained with social reinforcement,

156   approximately 70% of the initial choices favored social over food, but when trained with

157   food reinforcement, initial choices were equally divided between social and food. These

158   results suggest that social reinforcers may, under some circumstances, compete

159   successfully with food reinforcers (although it is worth noting that in neither the Bartal et

160 al. or Sato et al. studies were rats socially or food restricted). Similar results were

161 reported by Evans et al. (1994) with more robust procedures that provided repeated

162 choices, extended exposure to outcomes, and deprivation from the relevant reinforcers.

163 In that study, response rates for a group of rats responding for social reinforcers were

164 comparable to those for a second group responding for food reinforcers.

165 In the present study, we used PR schedules to measure reinforcer value of food

166 and social contact on a within-subject basis within the same experiment.   In Experiment

167 1, social and food reinforcers were studied separately on PR schedules, with BP and

168 response rates providing quantitatively precise measures of reinforcer value. In

169 Experiment 2, social and food reinforcers were studied concurrently, providing an

170 additional measure of value: reinforcer preference. In both experiments, we also

171 explored deprivation effects, by restricting access to social and/or food reinforcers

172 outside the sessions. Together, the two experiments were directed to an experimental

173 analysis of social contact as a reinforcer, measured in multiple ways, relative to food

174 reinforcers, and as a function of price and motivational variables.

175 **Experiment 1**

176 **Methods**

177 *Subjects*

178 Six male Long-Evans rats (*Rattus norvegicus*), approximately 13 weeks of age,

179 were used in this experiment. All rats were previously trained to lever-press in operant

180 chambers during an introductory psychology class before assignment to this study. The 6

181 rats were divided into three pairs (designated Green, Purple, and Orange) with one rat

182 from each pair designated the unrestrained rat, and the other the restrained rat. When not

183   in the experiment, rats lived in a temperature and light-controlled (12:12 light/dark cycle)

184   colony room, with unrestricted access to water. Depending on the condition of the

185   experiment, rats were housed either individually or together, and with either unrestrained

186   or restricted access to food, as described below.

187   *Apparatus*

188   The experimental apparatus is shown in Figure 1. It consisted of three adjoining

189   operant conditioning chambers, each measuring 31 cm x 25 cm x 22 cm, and all

190   containing a grid floor. The two rightmost chambers contained a lever (5 cm x 1.5 cm x

191   1.5 cm) a pellet receptacle (2 cm diameter), and small light (2 cm diameter) mounted

192   above each lever. The leftmost chamber contained a Plexiglas rodent restrainer (25 by

193   8.75 by 7.5 cm, Harvard Apparatus, Holliston, MA), separated by a mechanical metal

194   door that opened into the center chamber. The apparatus was controlled VB.net program

195   run on a Macintosh computer located to the right of the chambers.

196   *Preliminary Training*

197   *Escape Training*. To minimize the delay between lever pressing and social

198   contact, restrained rats were trained to escape (i.e., leave the restraint) soon after the door

199   was opened. Following one 30-min adaptation session with free access to all

200   compartments and the restrainer, the rats underwent a series of conditions in which the

201   restraint door was lifted response-independently (accompanied by a 1 kHz tone of 1 s

202   duration). Escape was defined as the entire body of the rat (except the tail) outside the

203   restrainer. Once in the chamber, rats were allowed to explore for 10 s before being

204   returned to the restrainer for the next trial. Sessions lasted for 10 trials. When escape

205   occurred consistently and with short latencies, the time spent in the restrainer prior to

206   door opening was incrementally increased across sessions according to a variable-time

207   (VT) schedule, with an average delay of 10 s (3 sessions), 20 s (3 sessions), and 30 s (14

208   sessions).

209   *Food Reinforcement Training*. Unrestrained rats were trained in four 15-min

210   sessions to press the left lever for sucrose banana pellets under a fixed ratio (FR) 1

211   schedule, in which each lever press produced food. During these sessions, only the left

212   lever was active and only the left light was illuminated. The schedule was then changed

213   to a PR 1 schedule, in which the response requirement increased by one response after

214   each food reinforcer. Sessions lasted 30 min in this and all subsequent conditions. After

215   food training, all rats were immediately switched to social reinforcement training.

216   *Social Reinforcement Training*. Both rats were placed in the apparatus, the

217   restrained rat in the restrainer and the unrestrained rat in the center of the open part of the

218   chamber. When the light above the right lever was on, lever presses produced the 1-s

219   tone and opened the door to the restrainer. (The left lever light was off and left lever

220   presses produced no scheduled consequences during this training condition.) When the

221   restrained rat left the restraint and entered the chamber, the door was closed and this

222   started the 10-s social interaction period, after which the restrained rat was removed and

223   returned to the restrainer for the next trial. During the social interaction period, both

224   levers were temporarily inactivated and the lights extinguished. All pairs received 7

225   sessions of training on a FR 1 schedule, then were moved onto a PR 1 schedule of

226   reinforcement, like that described above for food reinforcement training.

227   *Experimental procedures*

228   By the end of training, restrained rats were leaving the restraint quickly and

229   reliably, and unrestrained rats had experience with PR 1 schedules of food and social

230   reinforcement (10-s period of social interaction).   The rats were then studied under food

231   and social reinforcement across different deprivation conditions. The deprivation

232   conditions limited access to the relevant reinforcer outside the sessions, and were

233   designed to be as equivalent as possible. In *Food-restriction* conditions, rats received 60

234   min access to food after each session, but were otherwise restricted; they had continuous

235   access to their cagemate. In *Social-restriction* conditions, rats had 60-min post-session

236   access to their cagemate, but were otherwise separated in different cages; they had

237   continuous access to food. In *Combined-restriction* conditions, rats had 60-min post

238   session access to both food and their cagemate, but had otherwise restricted access to

239   these reinforcers outside the sessions.

240   Table 1 shows the sequence of experimental conditions and the number of

241   sessions conducted at each.   Phase 1 (the first 6 conditions listed in Table 1) constitutes a

242   2 x 3 within-subject experimental design, with reinforcer type (*Food*, *Social*) and

243   deprivation type (*Food-restriction*, *Social-restriction*, and *Combined-restriction*) as

244   variables. The sequence of conditions was selected so as to change only one variable at a

245   time, and each pair of rats was exposed to all 6 combinations of reinforcer type and

246   deprivation in the same order.

247   Conditions 7-8 were control procedures, designed to assess the contribution of

248   additional variables to ongoing performance. The first was an *Extinction* procedure, in

249   which right lever presses were no longer effective in releasing the restrained rat; the

250   restrained rat was present, but responses neither opened the door nor produced the tone.

251   The second was a *Conditioned reinforcement* assessment, in which lever presses opened

252   the door and produced the tone, but the restraint was empty and entry was precluded by a

253   second transparent door; the only consequences of responding were the stimuli

254   previously correlated with social release (door opening, tone). Between the two control

255   conditions, lever pressing on the social lever was reinstated for one baseline session on an

256   FR 1 schedule with 10-s social interaction as the reinforcer. Both control conditions (and

257   the baseline sessions that preceded them) were conducted under social restriction.

258   Conditions 9-10 were replications of the *Food* reinforcer conditions under *Food-*

259   *restriction* and *Combined-restriction* conditions.

260   When a change in condition included switching of the reinforcer type,

261   unrestrained rats were exposed to a single session under an FR 1 schedule to extinguish

262   responses on the now inactive lever and promote responding on the alternative lever for

263   the newly available reinforcer. Following this transitional session, sessions were

264   conducted in each condition until stability was achieved, defined as (a) minimum of 3

265   sessions, and (b) absence of monotonic trends in session-to-session PR breakpoints

266   (highest completed ratio in the session).

267   A mechanical error during the *Social reinforcement* condition under *Social-*

268   *restriction* required Rat Purple to undergo additional sessions to achieve stability. These

269   additional sessions included a 1-min socialization period in the operant chamber prior to

270   the beginning of the sessions to help instigate responding on the social reinforcement

271   lever.

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273

274   **Results and Discussion**

275   Figure 2 shows mean breakpoints under food and social reinforcement across the

276   three deprivation conditions for individual subjects and for the aggregate data (bottom

277   right panel). A linear mixed model was used with rank-transformed values, appropriate

278   to the small sample size and non-parametric data. A large factor was created using all

279   pairwise combinations of reinforcer type and deprivation type to specify condition.

280   Condition was included in the mixed-effects model as a fixed factor, while subject was

281   included as a random factor. An ANOVA was run on the model, and a significant

282   omnibus effect of condition was subsequently analyzed using pairwise contrasts with a

283   false discovery rate correction for multiple comparisons.

284   The data were remarkably consistent across subjects: BPs were consistently

285   higher under food than under social reinforcement conditions under all 3 restriction

286   conditions. There was a significant effect of condition ($p < 0.001$) on the group mean BP

287   (bottom right panel in Figure 2), such that the BP was greater for food reinforcement than

288   social reinforcement under all three deprivation conditions: food restriction ($p < 0.001$),

289   social restriction ($p < 0.001$), and combined ($p < 0.001$).

290   Breakpoints under food reinforcement were sensitive to deprivation, higher in

291   conditions involving food restriction (*Food*, *Combined*) than in conditions without

292   restriction (*Social*), generally peaking under *Combined* restriction. These differences

293   were seen in all three rats and were statistically significant at the group mean level:

294   *Combined restriction* differed from *Food restriction* alone ($p < 0.001$) and from *Social*

295   *restriction* alone ($p < 0.001$). Mean breakpoints for food also differed significantly

296   between *Food restriction* only and *Social restriction* only conditions ($p < 0.001$).

297   This type of sensitivity to combined food and social deprivation was not seen

298 consistently for any of the 3 rats under *Social reinforcement* conditions, and there were

299 no significant differences across any of the deprivation conditions when social contact

300 was the reinforcer ($p > 0.05$).

301   Figure 3 shows the results from Conditions 9-10, replications of the *Food*

302 *reinforcement* conditions under *Food restriction* and *Combined restriction*. There was a

303 significant effect of condition ($p < 0.001$), replicating the original effect. The breakpoints

304 under both conditions were also substantially higher than those seen in all earlier

305 conditions of the experiment.

306   The overall breakpoints do not take account of differences in the way the two

307 reinforcers were delivered. Under *Food reinforcement* conditions, responses were

308 possible anytime, including just after reinforcement. Under *Social reinforcement*

309 conditions, on the other hand, responses were not possible during the 10-s social

310 interaction period or in the period during which the experimenter gathered and returned

311 the rat the restraint. Because the sessions were time-based rather than trial-based, these

312 differences in the timing of the reinforcers created differences in response opportunity.

313 To remedy this, we computed responses rates (lever presses per active min) as a way to

314 equalize response opportunity for both reinforcers.

315   As shown in Table 2, the results obtained with response rates mirrored all of the

316 major results seen with breakpoints for food reinforcement, including statistical

317 significance. The same linear mixed model was used to analyze the response rate data,

318 with the exception of rank-transformed response rate added as the fixed factor, as shown

319 in Table 3. An ANOVA was run on the model, and a significant omnibus effect was

320   subsequently analyzed using pairwise contrasts, with a false discovery rate correction for

321   multiple comparisons. There was significant main effect of condition on response rates (p

322   < 0.001). Response rates for social reinforcement alone did not differ significantly

323   between deprivation conditions. Figure 4 shows response rates across sessions in the

324   *Extinction* condition, when lever presses were ineffective. The unconnected point to the

325   left represents the rate under baseline conditions (PR 1 schedule of 10-s social contact)

326   just prior to extinction. Relative to baseline, responding declined substantially for all 3

327   rats, requiring 4-6 sessions to reach low (< 20% of baseline) levels.

328   Figure 5 shows response rates on the social lever in the second control condition,

329   designed to assess the contributions of stimuli correlated with social release. Social

330   release was not only ineffective, as in the *Extinction* condition, but was not even possible

331   (no rat in the restraint). Relative to the baseline session (left unconnected point) with

332   social release possible, responding persisted at moderate levels for several sessions, in

333   some cases equal to or exceeding baseline. Although responding eventually declined for

334   all 3 rats, it continued to occur at low to moderate levels for some time, requiring 9-12

335   sessions for 2 rats to reach low levels; for a third rat, the condition ended after 14

336   sessions, at which point responding had stabilized at approximately 50% of baseline.

337   **Experiment 2**

338   In Experiment 1, relative reinforcing value of food and social reinforcers was

339   compared across conditions. Another way to assess the relative value is to arrange

340   reinforcers concurrently, as explicit choices. In Experiment 2, rats were given repeated

341   choices between food and social reinforcers in a concurrent PR-PR schedule. The PR

342   schedules operated independently for the two reinforcers, such that the PR increment

343   occurred only for whichever reinforcer had been selected on the previous trial. Thus,

344   while the response cost, or price, of the two options was initially identical, the more times

345   a reinforcer was chosen, the higher its resulting price. This enabled an assessment not

346   only of relative reinforcer value, but also of reinforcer interactions: how the value of one

347   reinforcer is affected by the price and availability of the other reinforcer.

348   **Methods**

349   **Subjects and apparatus**

350   The same three pairs of rats (*Purple*, *Orange*, and *Green*) and the same

351   experimental apparatus (Figure 1) were used for Experiment 2.

352   **Procedure**

353   The rats in each pair retained their roles (i.e., restrained rats and unrestrained rats)

354   from the first experiment. Concurrent PR-PR schedules of food and social reinforcement

355   were used; presses on the left lever were reinforced with food whereas presses on the

356   right lever were reinforced with 10-s social interaction. The schedules were initially FR

357   1 for both options, but increased by 5 responses with each reinforcer earned on a schedule

358   (PR 5); the schedules were independent, in that the PR increment only occurred for the

359   chosen schedule. An intertrial interval (ITI) separated successive trials, during which the

360   lights above each lever were off and responses had no programmed consequences. The

361   duration of the ITI varied for the two outcomes: 17 s following food reinforcement and 7

362   s following social reinforcement (accounting for the time needed for 10-s social

363   interaction and 7 s for replacing the partner rat in the restrainer). This equalized the rate

364   of trial onset, such that choices in trial *n* would not be affected by trial onset in trial *n*+1.

365   The first 4 sessions in each session were forced-choice trials, in which only one option

366   was available (signaled by light above the active lever). The initial position of the active

367   lever was determined randomly, but then strictly alternated, with two trials of each

368   reinforcer type. Sessions lasted 30 min, including the forced-choice trials, and were

369   conducted 5 days per week.

370   Preferences were assessed across the same 3 motivational conditions as in

371   Experiment 1: *Food restriction*, *Social restriction*, and *Combined restriction*, in the order

372   depicted in Table 4. Given that the highest levels of responding were obtained in the

373   *Combined restriction* conditions in Experiment 1, this was used as the baseline (A) phase

374   in an A-B-A-C-A within-subject experimental design, with social and food reinforcement

375   serving as (B) and (C) phases, respectively. Due to time constraints, Rat *Green* did not

376   undergo the final return to the *Combined restriction* condition. Conditions were run until

377   stability was achieved, defined as the absence of monotonic trends across at least three

378   sessions, as in Experiment 1.

379   **Results and Discussion**

380   Mean breakpoints across the final 3 sessions per condition are depicted in Figure

381   6. Consistent with Experiment 1, responding was maintained by both food and social

382   reinforcers, but BPs were consistently higher for food than for social reinforcers under all

383   3 deprivation conditions. The data were non-parametric, so responses were rank-

384   transformed and run in a linear mixed model, as in Experiment 1. A large factor was

385   created using all pairwise combinations of reinforcer type and deprivation type to specify

386   condition. Condition was included in the mixed-effects model as a fixed factor, while

387   Subject was included as a random factor. An ANOVA was run on the model, and a

388   significant omnibus effect was subsequently analyzed using pairwise contrasts, with a

389 false discovery rate correction for multiple comparisons. Breakpoints were averaged

390 across the three separate combined deprivation conditions. For the group, breakpoints

391 were higher for food than for social reinforcement in all deprivation conditions ($p <$

392 0.001).

393   Post-hoc comparisons revealed that breakpoints for food did not differ between

394 combined deprivation and food only deprivation ($p = .74$), but did differ between

395 combined deprivation and social deprivation ($p = 0.0028$), and between social deprivation

396 and food only deprivation ($p = 0.0055$). Breakpoints did not vary significantly for social

397 reinforcement between combined deprivation and social deprivation ($p = 0.29$) or

398 between food deprivation and social deprivation ($p = 0.12$), but they did significantly

399 differ between combined deprivation and food only deprivation ($p = 0.0057$).

400   Thus, as in Experiment 1, food and social reinforcers differed in sensitivity to

401 deprivation: BPs for social reinforcers were insensitive to deprivation (similar whether

402 the rats were socially deprived or not), whereas BPs were higher when rats were food

403 deprived (*Food restriction* and *Combined restriction*) than when they had free access to

404 food outside the session (*Social restriction*). Unlike Experiment 1, there was no evidence

405 of reinforcer interaction effects, in which responding was higher in the *Combined*

406 *restriction* conditions than in the *Food restriction* conditions: both generated comparable

407 BP and response rates in the present experiment.

408   Figure 7 shows the proportion of food and social reinforcers earned across

409 experimental conditions. Because the individual data were so similar, the data were

410 pooled across subjects. There was strong preference for the food over the social

411   reinforcers across all motivational conditions. Only in the *Social-restriction* conditions

412   did choice proportions rise to approximately 25% for the social reinforcers.

413   In addition to these global (session-wide) measures, we analyzed within-session

414   patterns of responding. As would be expected from the global measures, more food than

415   social reinforcers were selected overall, but the likelihood of selecting a social reinforcer

416   increased as a function of the price of food. Figure 8 shows the PR price of food when

417   the first social reinforcer each session was earned across the three deprivation conditions.

418   Each point is taken from each of the last three stable sessions of every subject. The points

419   in the combined restriction condition are mean PR prices across all three of the combined

420   restriction condition sessions (A). Social reinforcers were selected much earlier in the

421   session (at lower PR food prices) in *Social-restriction* conditions than in the other

422   deprivation conditions, showing sensitivity to social motivational variables not seen with

423   the more global (session-wide) measures.

424   **General Discussion**

425   The overall pattern of results show that rats' lever pressing was under functional

426   control of social reinforcement contingencies, in which responses produced access to a

427   partner rat: responding occurred at modest but consistent levels when it produced social

428   release, and quickly decreased to low levels when the social release contingency was

429   discontinued. These results are in line with those of Evans et al. (1994), who found that

430   lever pressing was maintained by social access but decreased substantially when it no

431   longer produced access to the social partner. In their study, this pattern of extinction held

432   both under conditions in which the reinforcement compartment was empty, and when it

433   contained a social partner. The latter conditions more closely resemble those used in the

434   present study, in which the social partner was present and the unrestrained rat was

435   socially deprived. Such conditions include the critical requirements for an extinction

436   procedure, in which responses are ineffective but motivational variables are in place (i.e.,

437   the response is ineffective in producing the reinforcer but the motivation to produce it

438   remains high).

439   Social contact was not the only consequence of door-opening, however; responses

440   also produced correlated stimuli (e.g., tone, door opening). Results from the *Conditioned*

441   *reinforcement* probe condition in Experiment 1 (Figure 5) show the important

442   contribution of these correlated stimuli. The continued response-dependent presentation

443   of these stimuli sustained a good deal of behavior even in absence of social release,

444   comparable to prior research (Bartal et al., 2011; Silberberg et al., 2014). Similar to these

445   previous studies, the non-social conditions always followed the social conditions. The

446   rats thus all had extensive histories of social release: 40 sessions per subject, on average

447   (all with correlated stimuli), by the time of the conditioned reinforcement probe. These

448   stimuli were presumably functioning as conditioned reinforcers, via long-term correlation

449   with social release, but additional analysis is needed to isolate specific controlling

450   variables.

451   Conceptualizing social release in social reinforcement terms is consistent with a

452   growing body of research across species showing that access to social stimuli reinforces

453   behavior that produces it (see Trezza, Campolongo, & Vanderschuren, 2011, for a

454   review). It has proven useful in studies of this sort to compare social reinforcers against

455   more common reinforcers, such as food. Prior studies with rats have found social and

456   food reinforcers to be roughly equivalent (Bartal et al., 2011; Sato et al., 2015), including

457   one (Evans et al., 1994) with operant methods and deprivation schedules similar to the

458   present study. In contrast, we found that food reinforcers generated consistently higher

459   response rates and preference than social reinforcers.

460   The differences between the present results and those of Evans et al. (1994) may

461   be due to procedural differences, such as social reinforcement magnitude: 10 s in the

462   present study vs. 45 s in Evans et al. If social contact serves a reinforcing function, then

463   increasing the duration might be expected to enhance its value as a reinforcer, as has been

464   demonstrated with food reinforcers (deVilliers, 1977). But even with food reinforcers,

465   the relationship between reinforcer magnitude and value is complex, with some studies

466   reporting a positive relationship (Bradshaw, Szabadi, & Bevan, 1978), some an inverse

467   relationship (Harzem, Lowe, & Priddle-Higson, 1978), and some both increases and

468   decreases in the same study (Reed, 1991). With less conventional reinforcers, such as

469   wheel running, there is an inverse relationship between responding and duration of

470   access, presumably due to satiation (Belke, 1997). Even less is known about how social

471   reinforcers are affected by the duration of their access. An important priority for future

472   research therefore is to map out the functions relating the value of a social reinforcer

473   value to its magnitude, both quantity (e.g., duration of social access) and quality (e.g.,

474   type of social interaction).

475   Another difference between food and social reinforcers in the present study

476   concerns the effects of motivational variables, arranged here as restricted homecage

477   access to the reinforcers. Breakpoints and response rates for food reinforcers were higher

478   when food was restricted outside the sessions, but responding for social reinforcers was

479   comparable whether or not homecage access to the social partner was provided outside

480   the sessions. An analysis of within-session patterning did reveal a sensitivity to social

481   restriction, as reflected in lower PR food prices when the initial social reinforcer was

482   selected in the session (Figure 8). On the whole, however, food-reinforced behavior was

483   far more sensitive to food deprivation than socially-reinforced behavior was to social

484   deprivation.

485   These differences, too, may have arisen from procedural differences. Although

486   we attempted to match the social deprivation procedures to more standard food

487   deprivation procedures (e.g., 60-min post-session access in both cases), the motivational

488   dynamics of food and social reinforcers may be quite different; perhaps longer, or

489   different, periods of social deprivation are needed to induce motivational changes

490   comparable to food. At present, little is known about the motivational dynamics of social

491   reinforcement – how it changes with deprivation and availability of other reinforcers.

492   This, too, is an important topic for further research.

493   Although we did not directly measure behavior during the reinforcement periods,

494   informal observations suggested that the social interactions were mutually reinforcing.

495   The restrained rat generally exited the tube shortly after the door opening, and the

496   unrestrained rat generally moved toward the tube, both of which facilitated social contact.

497   Moreover, the interactions themselves were largely positive (e.g., grooming, play).

498   Interestingly, the unrestrained rats would often enter and spend time in the restraint tube.

499   Together with observations reported by Silberberg et al. (2014), this suggests that access

500   to the tube may (perhaps in addition to social release) contribute to the lever pressing by

501   the unrestrained rat. In fact, it appeared that access to the tube was reinforcing for the

502   restrained and unrestrained rats alike, as both entered during reinforcement periods. On

503   its face, the observation that restrained rats would ever return to the restraint runs

504   contrary to the notion that the restraint is aversive (i.e., a source of acute distress). Direct

505   measurement of such behavior, however, is needed for a clearer picture of the nature of

506   the social interaction, and the degree to which social release is motivated primarily by

507   aversive or reinforcing contingencies: minimizing distress or enhancing social contact?

508   It will also prove useful in this context to supplement behavioral measures with

509   ultrasonic vocalization (USV) methods. Bartal et al. (2011) measured USV in the 23 kHz

510   range (commonly associated with distress calls) in the context of their social release

511   procedure. If social release is motivated by empathic concern for the restrained rat, then

512   one might expect door opening to occur in the presence of distress calls by the restrained

513   rat, as this is when obvious distress is most apparent. Contrary to this expectation,

514   distress calls occurred initially, but decreased over time, several sessions prior to when

515   social release began occurring. There was thus no relationship between acute distress (at

516   least as indexed by USV) and social release.

517   It would be informative to also measure USV in the 50 kHz range, as these are

518   associated with a range of positive outcomes, including food (Yuki & Okanoya, 2014)

519   and social access (Willey & Spear, 2013). If social release is governed more by access to

520   social contact than by avoiding distress, this should be reflected in the USV profile:

521   relatively higher in the 50 kHz than in the 23 kHz range. On the other hand, the reverse

522   would be true if distress was the main factor: relatively higher in the 23 kHz range. In

523   any case, detailed measurement, using both behavioral and USV methods, is a critical

524   part of a comprehensive understanding of social release.

525   The present study shows the utility of viewing social release through a social

526   reinforcement lens, grounded in established methods for quantifying the value of

527 reinforcers more generally. To identify an important role for social reinforcement,

528 however, is not to deny the importance of other variables; escaping from acute distress

529 (including that induced by another animal) and accessing social contact may each

530 contribute to social release – perhaps even at different times in the development of the

531 behavior. Determining the relative contributions of these (and possibly other)

532 mechanisms is a crucial priority for future research, to which present methods are well

533 suited. Such research is crucial to an overall analysis of social behavior, regardless of

534 one's theoretical predilections.

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565 **Notes** The data from Experiment 1 served as L.C.H.'s Senior Thesis at Reed College.

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573 **Compliance with ethical standards**

574 **Conflicts of interest** The authors declare that they have no conflicts of interest.

575

576 **Ethics statement** All applicable international, national, and/or institutional guidelines

577 for the care and use of animals were followed. All experimental procedures were

578 approved by the Institutional Animal Care and Use Committee of Reed College.

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685

686 **Figure Captions**

687 **Fig. 1** The experimental apparatus: the restrainer on the left of the apparatus held the

688 restrained rat, while the open space in the operant chambers held the unrestrained rat

689 **Fig. 2** Mean breakpoints for Food reinforcement and Social reinforcement, across

690 deprivation conditions, both for individual subjects and the group mean. Error bars are

691 standard errors. * $p < 0.05$

692 **Fig. 3** Replicated mean breakpoints for Food reinforcement under Food restriction and

693 Combined restriction conditions. Error bars are standard errors. * $p < 0.05$

694 **Fig. 4** Reponses per minute for each subject in the Baseline session (gray points to the

695 left) and extinction sessions

696 **Fig. 5** Responses per minute per session for each subject in the Social reinforcement

697 probe condition

698 **Fig. 6** Averaged breakpoints for both food reinforcement and social reinforcement

699 plotted as a function of deprivation condition. Error bars are standard errors. * $p < 0.05$

700 **Fig. 7** The bars depict the mean proportion of reinforcers earned for all subjects within

701 each condition

702 **Fig. 8** The PR price on the food lever at which the first response on the social lever was

703 made, compared across deprivation conditions

704

705 **Table Captions**

706 **Table 1** The sequence of conditions in Experiment 1 and the number of sessions

707 conducted at each

708 **Table 2** Mean response rates (responses / min) in the stable sessions for each individual

709 rat as a function of deprivation condition and reinforcer type

710 **Table 3** Statistical comparisons of mean response rates (responses / minute) between the

711 experimental conditions

712 **Table 4** The order of conditions across testing sessions from top to bottom, including the

713 states of deprivation and the number of sessions for each subject
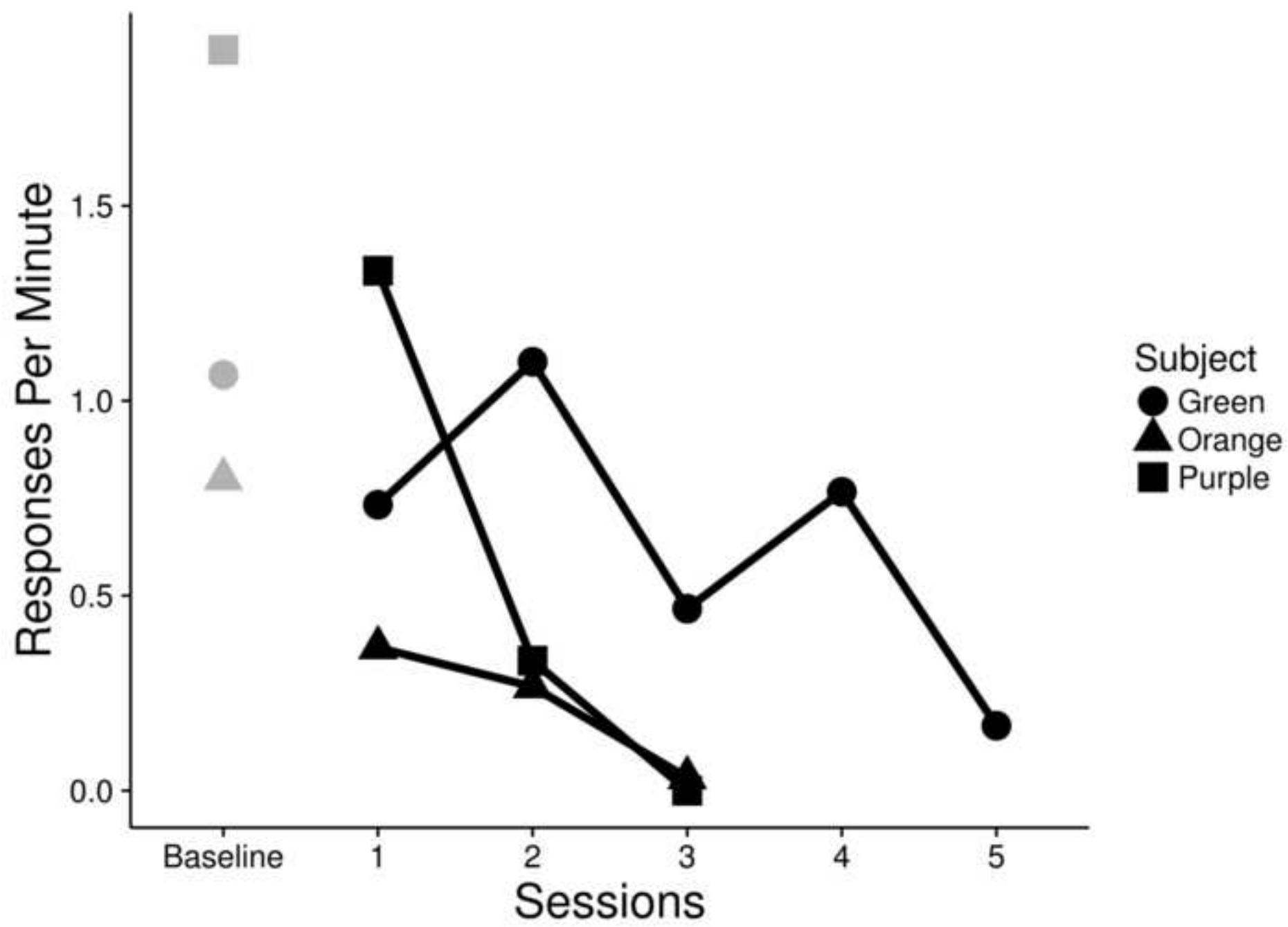
Figure 1
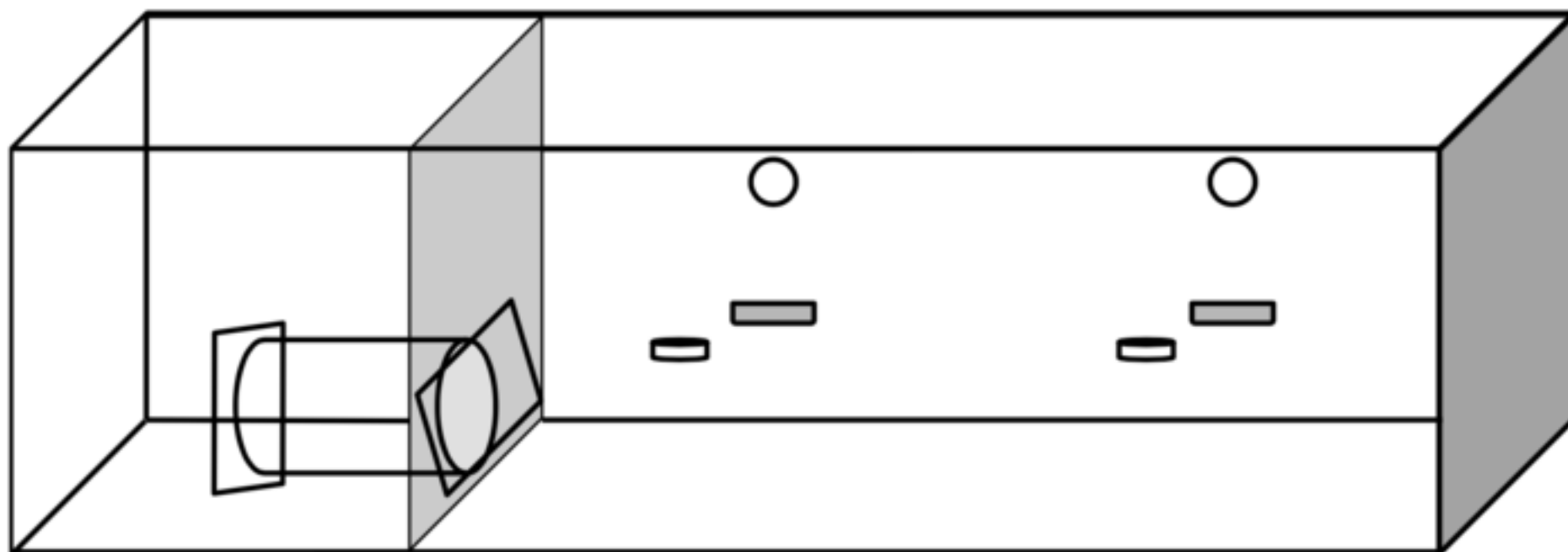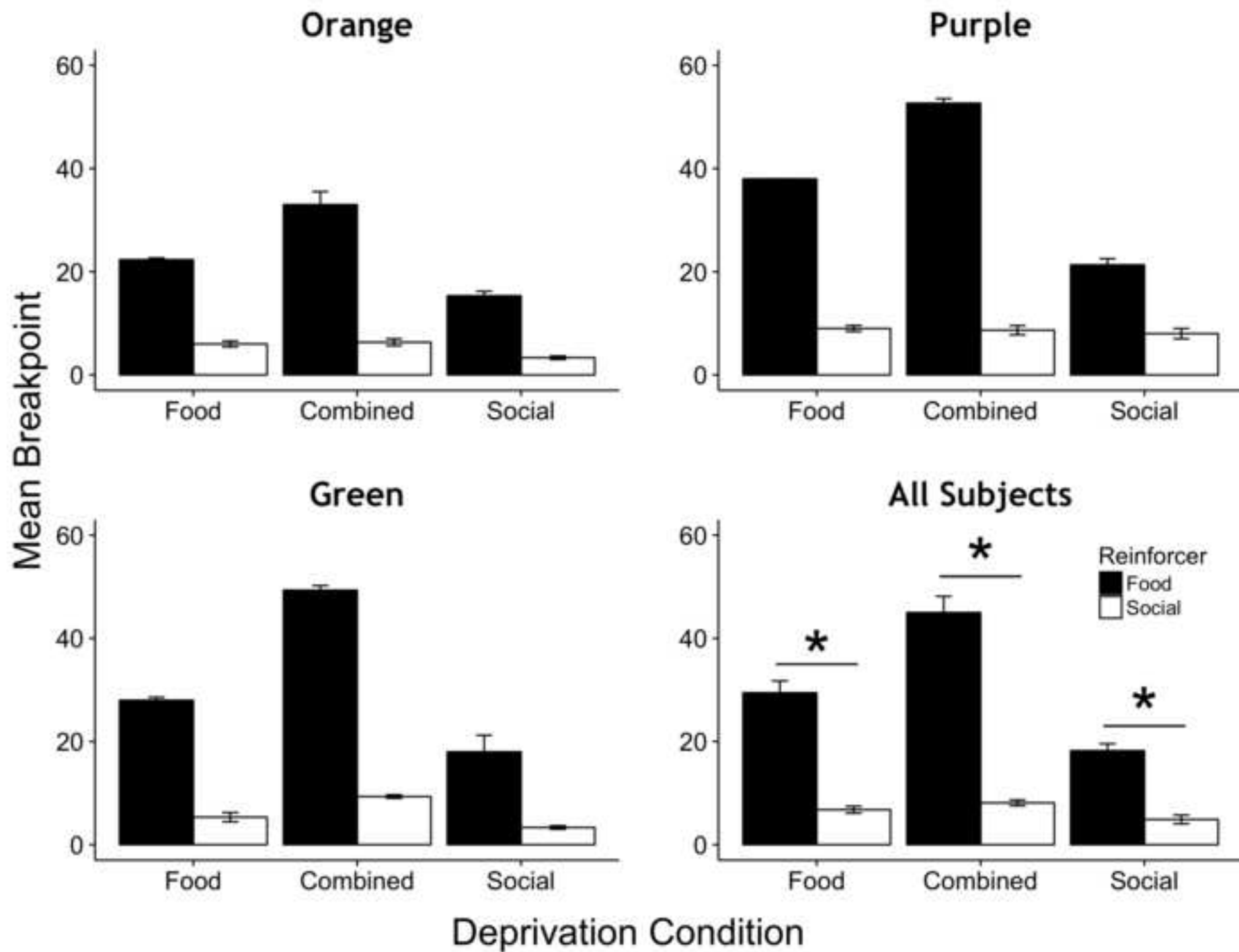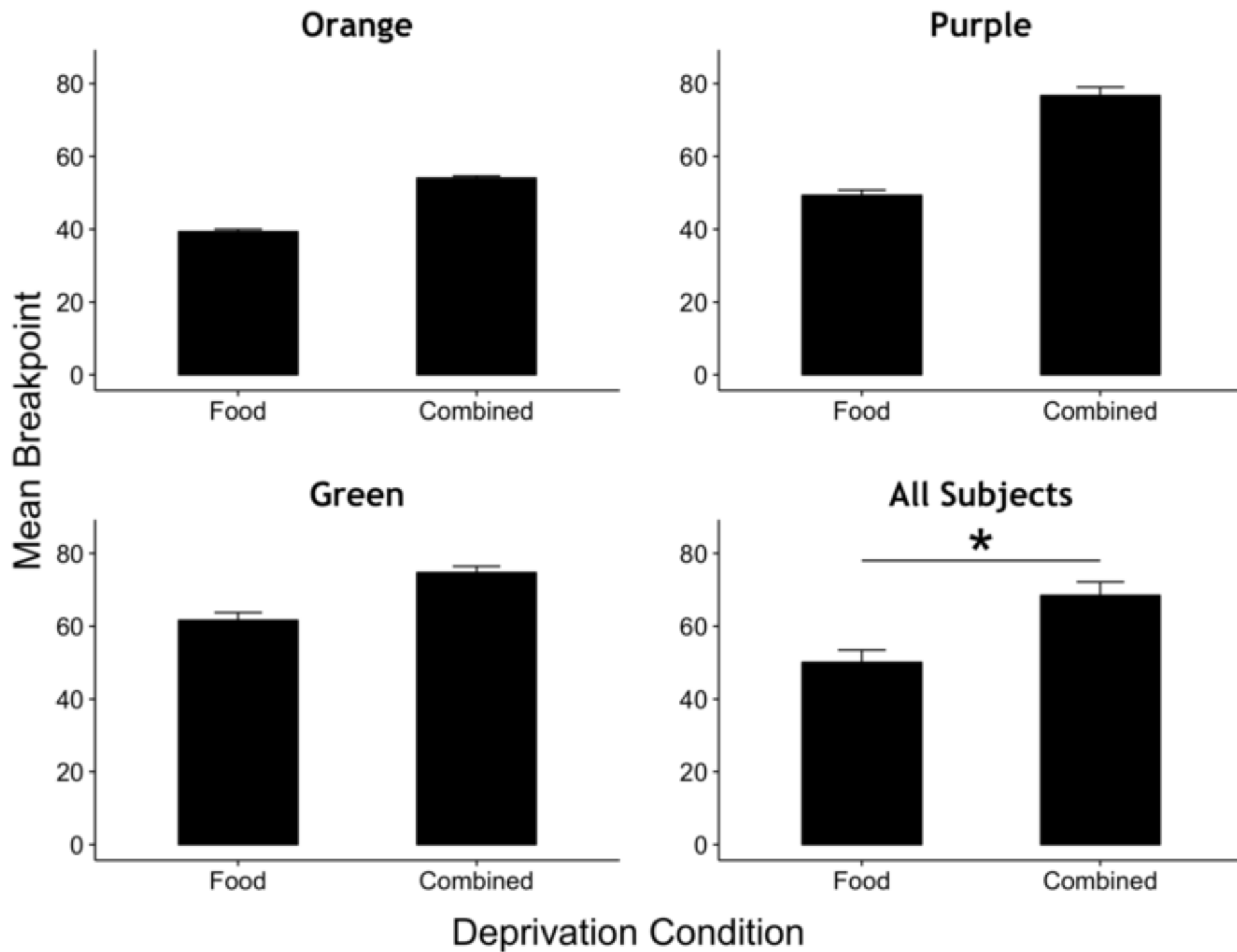
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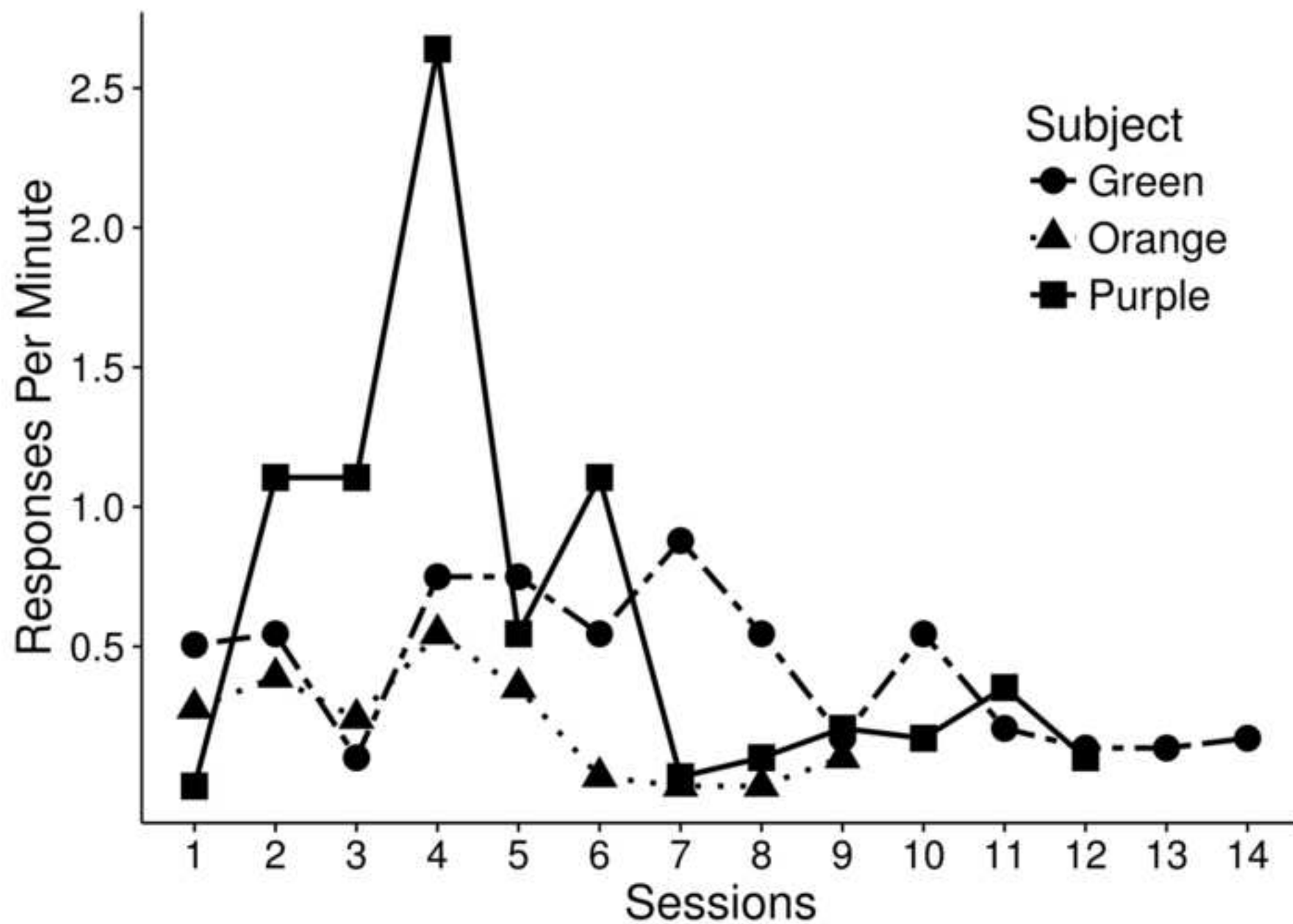
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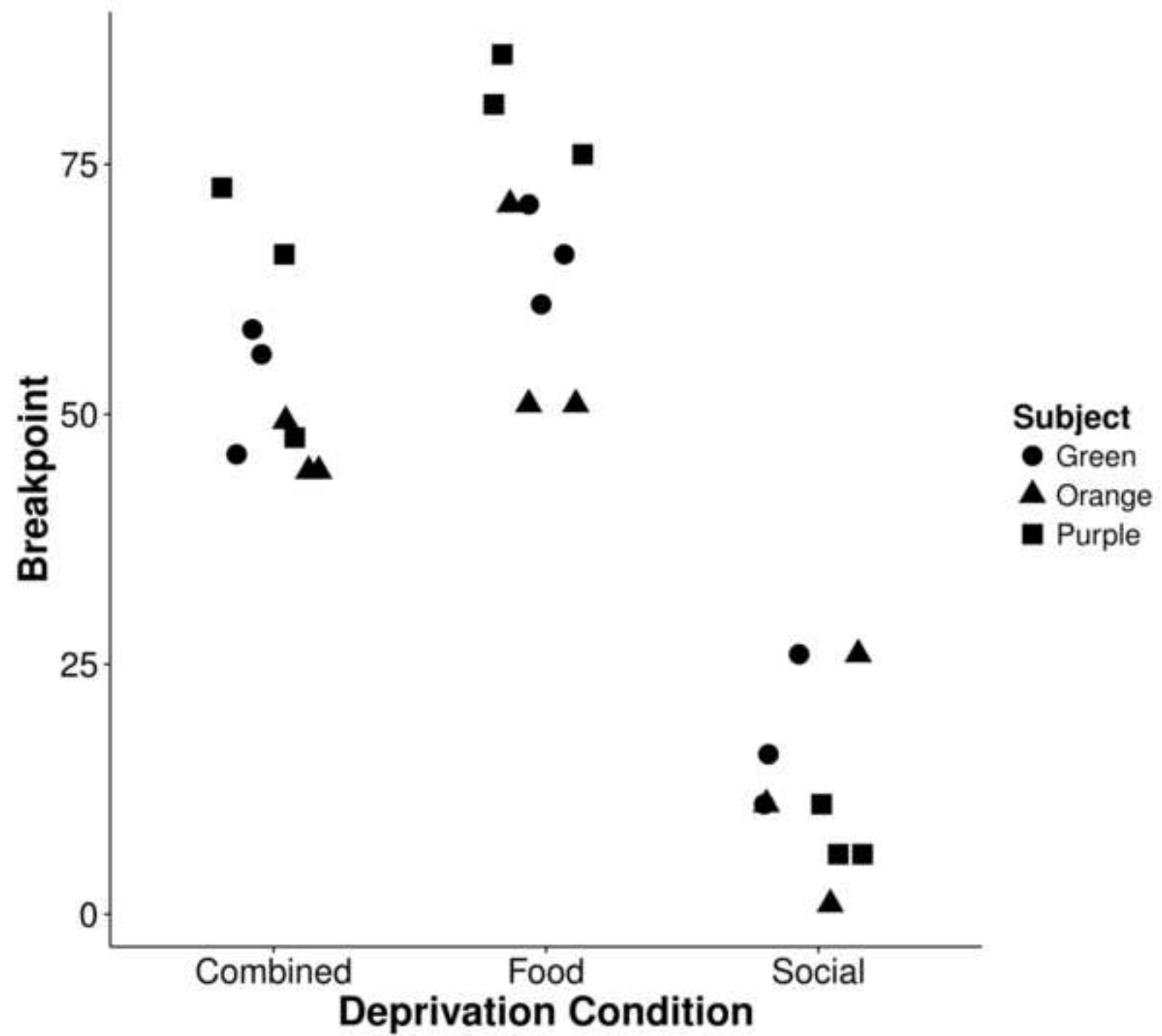Table 1   Click here to download Table Table 1.png ⬇
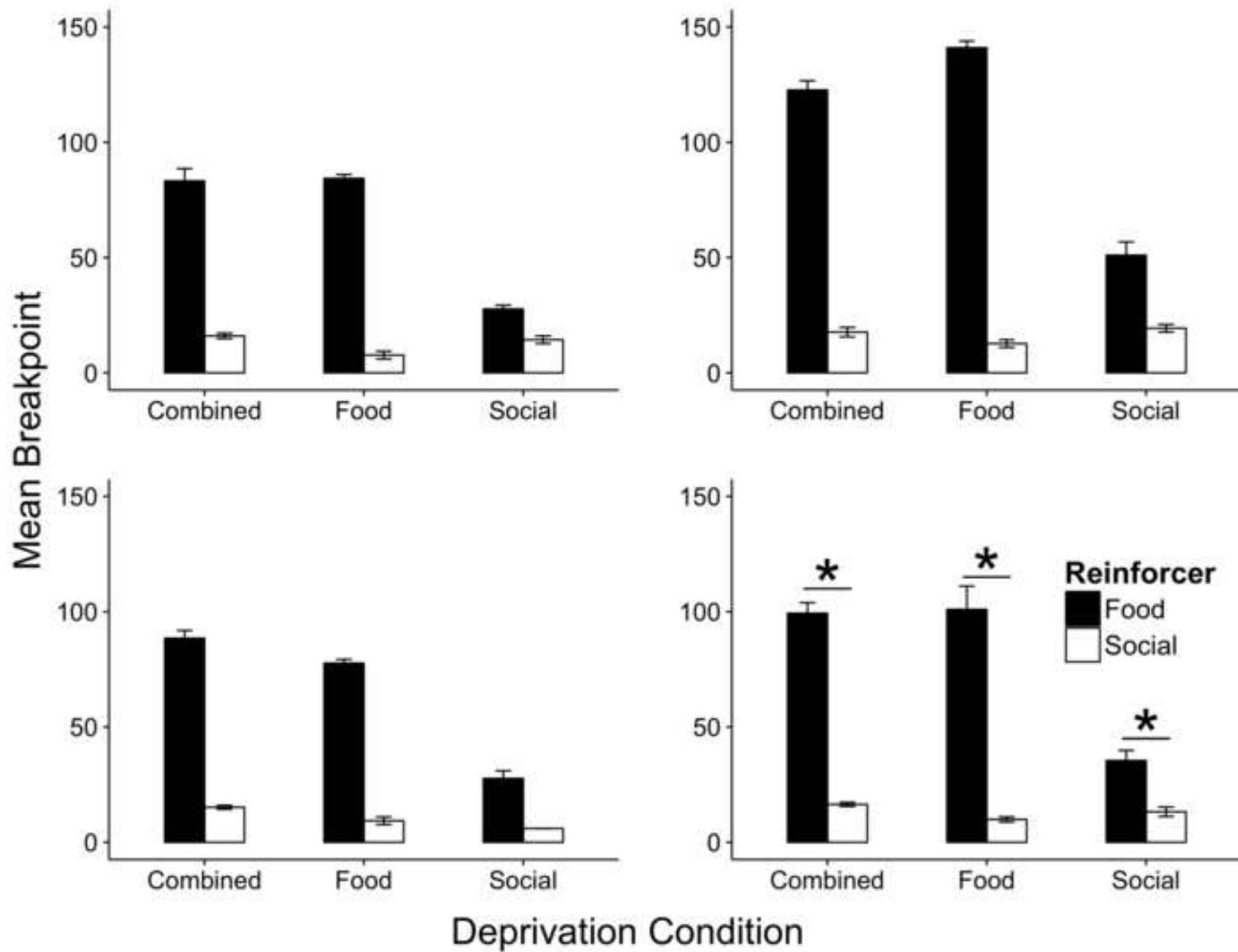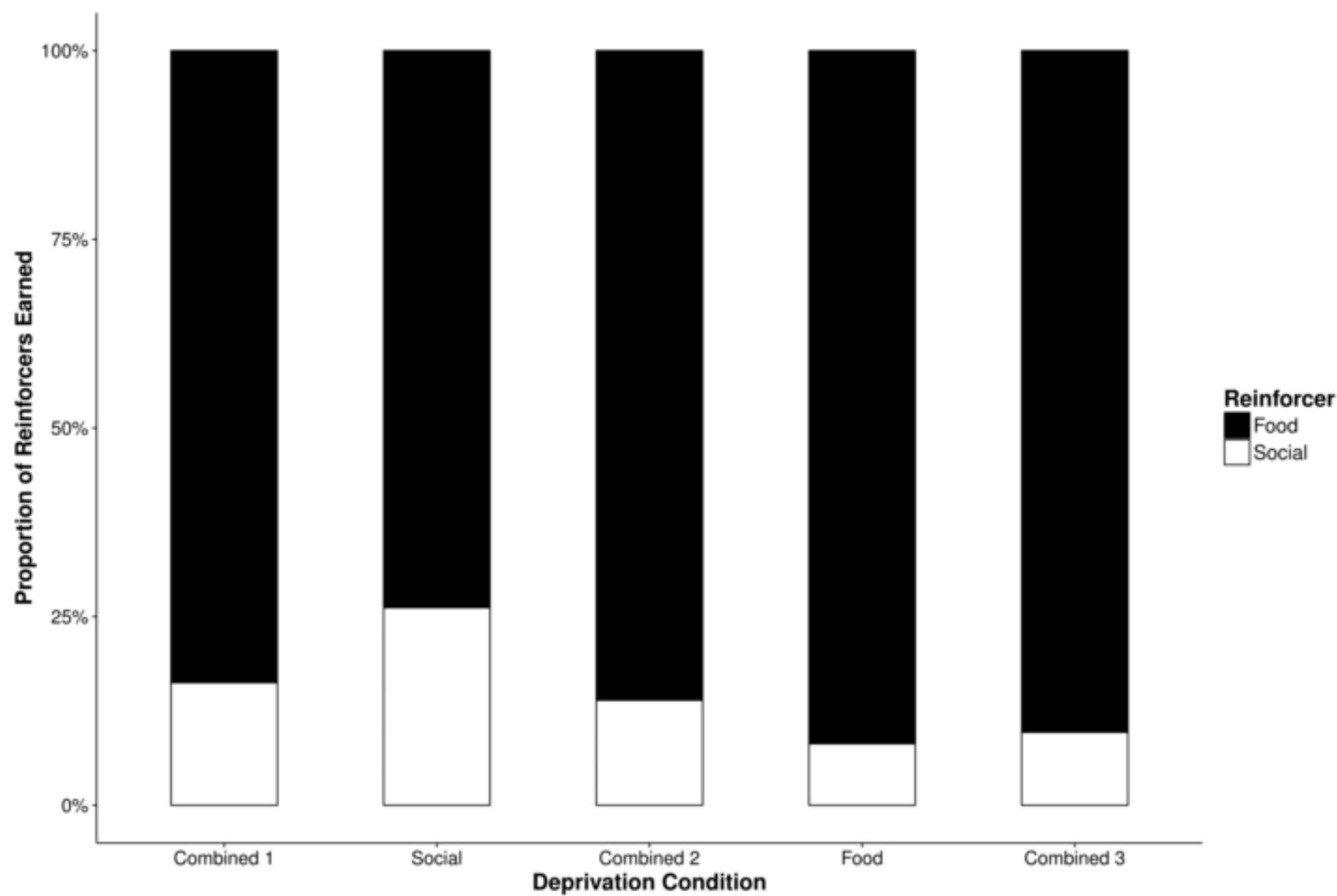
Order	Reinforcer	Deprivation	Number of Sessions		
			Green	Purple	Orange
1	Food	Food	14	14	14
2	Social	Food	14	14	14
3	Social	Combined	11	11	11
4	Food	Combined	16	14	14
5	Food	Social	11	13	13
6	Social	Social	10	21	10
7	Extinction	Social	5	3	3
8	Conditioned Social	Social	14	12	9
9	Replication Food	Replication Food	24	15	16
10	Replication Food	Replication Combined	14	19	19

Table 2

Reinforcer	Deprivation	Response Rate		
		Green	Purple	Orange
Food	Food	13.6 ± 0.55	24.0 ± 1.1	9.01 ± 0.2
Food	Combined	41.5 ± 1.41	47.2 ± 1.54	19.2 ± 2.9
Food	Social	6.04 ± 2.07	8.03 ± 0.81	4.2 ± 0.47
Social	Food	0.72 ± 0.22	2.08 ± 0.21	0.96 ± 0.1
Social	Combined	2.12 ± 0.19	1.22 ± 0.28	0.97 ± 0.21
Social	Social	0.29 ± 0.05	1.68 ± 0.58	0.26 ± 0.05

Table 3

Condition A	Condition B	P-value of Comparison
Food reinforcement under food restriction	Social reinforcement under food restriction	<0.0001
Food reinforcement under social restriction	Social reinforcement under social restriction	0.046
Food reinforcement under combined restriction	Social reinforcement under combined restriction	<0.0001
Food reinforcement under food restriction	Food reinforcement under social restriction	0.0005
Food reinforcement under food restriction	Food reinforcement under combined restriction	<.0001
Food reinforcement under combined restriction	Food reinforcement under social restriction	<.0001

Table 4

Order	Deprivation Condition	Number of Sessions		
		Green	Purple	Orange
1	Combined	12	17	14
2	Social	10	11	8
3	Combined	26	16	9
4	Food	13	11	18
5	Combined	N/A	8	11