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1 **Food variance and temporal discounting in socially foraging chicks**

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16 Previous studies have shown that domestic chicks, *Gallus gallus domesticus*, trained in

17 a competitive foraging condition would subsequently develop a high degree of

18 impulsiveness in an intertemporal choice paradigm. Competition inevitably causes

19 variance in the amount of food that the foragers gain. However, it is not known whether

20 the food variance is causally linked with the impulsiveness. In experiment 1, we

21 compared four groups of chicks trained in combinations of two social conditions

22 (pseudocompetition or isolated) and two food conditions (variable or constant food).

23 The food variance was introduced by varying the number of grains in each trial

24 according to a binomial distribution. The subject chick was separated from the

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25 competitors by a transparent wall, and no actual interference occurred. Chicks were
26 subsequently tested in binary choices between a small reward after a short delay (SS)
27 and a large reward after a long delay (LL) in an isolated and constant food condition. If
28 chicks had been trained under the pseudocompetition and variable food, they chose LL
29 significantly less frequently than the other three groups. The effect disappeared when
30 the LL delay was omitted, suggesting that chicks accurately memorized the food amount.
31 The food variance is thus a necessary condition for the stronger temporal discounting.
32 Otherwise, the observed effect could be ascribed to a paradoxical risk proneness
33 associated with the variable option. In experiment 2, we compared four groups of chicks
34 in which food amount varied either in SS or LL, or both. The subsequent binary choice
35 tests revealed that the chicks chose SS irrespective of whether SS or LL had varied.
36 These results cannot be explained in terms of a greater risk-prone choice of the variable
37 option. Coincidence of perceived competition and food variance, at least in one option,
38 is sufficient for chicks to develop choice impulsiveness.

39

40 **Keywords:** competition, domestic chicks, impulsive choice, probability discounting,
41 risk sensitivity, social foraging behaviour, temporal discounting

42

43 Animals (including humans) often choose an immediate reward over a larger
44 alternative that is available after a delay. According to a widely accepted psychological
45 framework of choice behaviour (Mazur, 2002), preference for an immediate option can
46 be explained in terms of temporal discounting of subjective value (Ainslie, 1974, 1975).
47 The degree of discounting is measured in an intertemporal choice paradigm, in which a
48 small/immediate option and a large/delayed alternative are simultaneously presented for

49 the subject to choose one. If the slope of the discounting function is sufficiently steep,
50 the immediate reward will have a higher value than the larger discounted alternative,
51 particularly in the short period before the immediate reward is gained. The subject will
52 thus choose the small option. Because the smaller rewards reduce the overall payoff in
53 the long run, choosing the immediate reward appears to contradict optimization theory
54 (Herrnstein and Mazur, 1987; also see Herrnstein, 1997).

55 In studies of foraging behaviour (Stephens & Krebs, 1986), however, animals are
56 assumed to have a limited knowledge of food resources. Encounters with prey items
57 will therefore follow a Poisson process. Under this constraint, theoretically, foragers
58 construct an optimal diet menu uniquely based on the profitability of each prey item
59 (Charnov, 1976). Here, profitability (e/h) is given as the ratio of the energetic gain (e)
60 divided by the total handling time (h). Foragers are thus assumed to discount prey items
61 according to a hyperbolic function of time. Empirical evidence is generally in favour of
62 the hyperbolic discounting theory (Kalenscher, Windmann, Diekamo, Rose, Güntürkün
63 & Colombo, 2005; Kalenscher & Pennarts 2008). However, behavioural data are not in
64 favour of the zero-one rule, one of the major predictions of the diet menu model. Instead,
65 the choice ratio follows the relative value of the profitability of the food reward in
66 domestic chicks, *Gallus gallus domesticus* (Izawa, Zachar, Yanagihara & Matsushima,
67 2003; Aoki, Csillag & Matsushima, 2006; Matsushima, Kawamori & Ben-Sojka, 2008),
68 as would be expected from Herrnstein's matching rule (Herrnstein, 1997) in which
69 response rate is given by the relative reinforcement rate. Also note that the self-control
70 choice is reported to be highly context-dependent in domestic fowl (Abeyesinghe, Nicol,
71 Hartnell and Wathes, 2005).

72 In nature, animals do not always forage individually. They can gain food also by

73 scrounging prey items from producers, i.e. other individuals that search and find food
74 for themselves. Intensive theoretical and empirical studies of social foraging behaviour
75 have enabled us to characterize this producer–scrounger game (Barnard & Sibly, 1981;
76 Giraldeau & Lefebvre, 1986; Giraldeau, Soos & Beauchamp, 1994; Mottley &
77 Giraldeau, 2000; also see the monograph by Giraldeau & Caraco, 2000). Briefly,
78 producers and scroungers will inevitably reach a stable Nash equilibrium, at which point
79 both player types will yield comparable suboptimal payoffs. However, switchable
80 players would benefit by flexibly changing the producer/scrounger roles in a
81 frequency-dependent manner.

82 The behaviour of chicks can also be described using the game-theoretical situation
83 of social foraging behaviour (Fig. 1). If a chick has no competition for food, the same
84 amount of food will be expected irrespective of the distance between the chick and the
85 food (Fig. 1a). As the profitability of the distant food is lower, the chicks will choose the
86 more proximate food (Matsushima, Kawamori & Ben-Sojka, 2008). Actually, they show
87 spatial discounting in a manner similar to the temporal discounting (Aoki, Suzuki,
88 Izawa, Csillag & Matsushima, 2006). On the other hand, when two chicks compete over
89 a food item (Fig. 1b), the chick located closer to the food source (yellow) will gain more
90 than the other chick (blue). If this sharing rule generally holds, a different payoff is
91 expected in the producer–scrounger situation (Fig. 1c). Here, the producer chick
92 (yellow) searches for and finds the food item, and the other chick (red) scrounges. As
93 the producer is closer to the food, she will enjoy the finder’s share (Giraldeau & Caraco
94 2000; Giraldeau & Dubois 2008) and gain more than the scrounger, as would be
95 assumed in most cases of scramble kleptoparasitism. Furthermore, the producer’s share
96 will be higher in the proximate food option than in the remote alternative, if the ratio of

97 the individual distance to food determines the finder's share. The impulsive producers
98 may thus gain a fitness advantage in the competitive condition.

99 However, the share of the finding producer is known to depend on a variety of
100 factors such as social status of the foragers and the richness of the food patch (Giraldeau
101 & Caraco, 2000). Divisibility of food patches is known to be particularly important in
102 social foraging of relatively nonaggressive birds such as finches (Giraldeau, Hogan &
103 Clinchy, 1990). If the food item is not shareable (such as a single grain), the probability
104 of not gaining food will be high (Fig. 1d) as would be the case in aggressive
105 kleptoparasitism. Conversely, if the food consists of shareable pieces (such as multiple
106 grains) and thus is simultaneously exploited by competing foragers, the ratio of the
107 variance to the expected gain (or the coefficient of variation) will be low (Fig. 1e). The
108 consequence of social foraging therefore also depends on how the food can be shared.

109 The ability to adjust temporal discounting according to foraging conditions (such as
110 density of the competitive foragers and variance in the food resource available) would
111 therefore be highly adaptive. Such adjustments may rely on two factors: the presence of
112 scroungers and the variance of food gain. As predicted, chicks trained in competitive
113 conditions develop a high degree of choice impulsiveness; when trained in a
114 pseudocompetitive situation in which scrounging is mimicked, chicks tend to choose a
115 small and short-delay option (SS) more frequently than a large and long-delay
116 alternative (LL) in a subsequent choice test (Amita, Kawamori & Matsushima, 2010).
117 However, whether the food variance associated with social foraging is necessary for the
118 development of choice impulsiveness has not been examined. We addressed this issue in
119 experiment 1 by comparing four groups of chicks trained in a 2×2 block design, i.e.
120 social condition (pseudocompetition or isolated) and food condition (variable or

121 constant amount).

122 Conditioned impulsiveness may arise from stronger temporal discounting for both
123 SS and LL options. Alternatively, the apparent impulsiveness might be caused by the
124 risk sensitivity of chicks. Animals generally avoid variable food, and thus are ‘risk
125 averse’ (Kacelnik & Bateson, 1996). Chicks also show risk aversion when the amount
126 of food varies, but they are paradoxically prone to risk when the delay to the food varies
127 instead (Kawamori & Matsushima, 2010; for a theoretical account, see Kacelnik & El
128 Mouden 2013). Food variance may influence SS and LL choices in a different manner,
129 leading to biased choices towards SS options. If that is the case, the effect of variable SS
130 options should therefore be different from that of variable LL options. In experiment 2,
131 we addressed this possibility by comparing four groups of chicks trained according to a
132 2 × 2 block designed with SS (variable or constant food) and LL (variable or constant
133 food).

134

135 <H1>METHODS

136 <H2>Subjects

137 We purchased newly hatched male domestic chicks (White Leghorn strain) from
138 local suppliers (Iwamura Poultry Ltd./Hokkaido Central Poultry Ltd., Yubari, Japan).
139 The chicks were housed in groups of three in transparent plastic cages (15 × 28 cm and
140 12 cm high) illuminated by white LED lamps (12:12 h light:dark with the light period
141 starting at 0900 hours) in a room at a controlled temperature (ca. 28 °C). As a daily diet,
142 the chicks received a mixture of millet grains and mash food, and the amount of food
143 was adjusted so that the chicks (1) actively consumed food during the behavioural
144 experiments, and (2) steadily increased in body weight by 5–10% per day. If not stated

145 otherwise, food was provided once a day after the behavioural experiments. To avoid
146 competition for food, individual chicks were isolated during feeding.

147 <H2>*Ethical note*

148 We did not perform any invasive treatments or stressful handling during the course
149 of the experiments. If a chick produced distress calls while in the experimental
150 apparatus, we immediately stopped the experiment and discarded it. We thus excluded
151 nine of the 128 chicks used in this study. Of the remaining chicks, 12 were excluded
152 because they stopped operant pecking and/or consuming food in the experimental
153 apparatus. In addition, another set of 29 chicks did not reach the criteria during pretest
154 retraining (see below). Behavioural data were obtained from the remaining 78 chicks,
155 and the other ca. 50 chicks served as companions. The experiments were conducted
156 according to the guidelines and approval of the Committee of Animal Experiments at
157 Hokkaido University. The guidelines are based on the national regulations for animal
158 welfare in Japan (Law of Humane Treatment and Management of Animals, after partial
159 amendment No.68, 2005). After the experiments, the chicks were euthanized using
160 carbon dioxide.

161 <H2>*Sequence and profitability of trials*

162 The sequence of a single trial is shown schematically in Fig. 2a, and the presumed
163 profitability of options are summarized in Table 1. When the subject chick pecked at a
164 rewarding bead once or more during the initial cue period (fixed at 1.5 s), the associated
165 grain of millet (food) was delivered to the feeder after a programmed delay (0 s for SS,
166 or small and short-latency option; 1.5 s for LL, or large and long-latency option) plus a
167 brief mechanical lag (ca. 0.29 s in average). Chicks usually took 0.25–0.5 s to peck and
168 ingest one grain. The total handling time of the rewarding trials was therefore 0.25–0.5 s

169 (for 1 grain = 7.60 mg in SS) and 1.5–3.0 s (for six grains = 45.6 mg in LL). If the
170 profitability of a single trial (Table. 1) is given as $X/(B+C+D)$, it is presumed to be 9.5–
171 13.8 mg/s (LL) and 9.6–14.1 mg/s (SS), so that the two trial types were comparable.
172 This fits well with empirical data (Izawa, Zachar, Yanagihara, & Matsushima, 2003;
173 Amita, Kawamori & Matsushima, 2010), in which the choice of SS or LL was balanced
174 according to the 1.5–2.0 s delay assigned to the LL option.

175 The intertrial interval (ITI) ranged from 15 to 20 s irrespective of the preceding trial
176 type. When we included the ITIs, the profitability of the LL trials could be expressed as
177 $X/(A+B+C+D+E) = 1.6\text{--}2.3$ mg/s, which is ca. five times larger than that of the SS
178 trials (0.35–0.45 mg/s). As argued previously (Matsushima, Kawamori & Bem-Sojka,
179 2008), including the ITIs in the profitability calculation does not appropriately account
180 for the decision made by the chick. The actual total duration of the trials, calculated
181 after the experiments, was 15.8–17.8 s. This was in the range of the scheduled
182 timetable.

183 <H2>Apparatus

184 We used a thermocontrolled box (21 × 19 cm and 25 cm high, illuminated by light
185 bulbs and maintained at ca. 27–30 °C) to record chick behaviours in the intertemporal
186 choice paradigm. During training and tests, the box was separated into two chambers
187 via a transparent partition, one accommodating the subject chick and the other
188 containing the companion chicks (Fig. 2b, d). Chicks were trained either in isolation or
189 in pseudocompetition. In the latter condition, competitive social foraging was
190 fictitiously reproduced without actual interference among chicks. The subject received a
191 controlled amount of food, which was never scrounged by the companions. At the same
192 time, the subject did not have a chance to scrounge the food delivered to the companion

193 side. In this manner, the subject perceived the competitive social condition without
194 actual loss or gain of the food. In the present study, we thus separated the social factor
195 and the food factor. We also stress that the pseudocompetition caused a similar
196 impulsiveness in preceding studies (Amita, Kawamori & Matsushima, 2010).

197 The chamber containing the subject chick was equipped with a pair of holes (3 cm
198 apart and 4 cm above the floor) and a feeder below the holes. The companion chamber
199 had a feeder located immediately beside the partition. Through the holes in the chamber
200 wall, we presented one or two beads (white, red, green or transparent plastic) for a fixed
201 period of time (1.5 s). Colour assignment for SS, LL and S- (nonrewarding) options was
202 counterbalanced within each group of chicks. The side of the holes used for presentation
203 was also counterbalanced within each individual chick.

204 In the pseudocompetition condition, the companion chicks received two grains of
205 millet whenever the subject chick received food. We observed the chicks' behaviour
206 through a one-way mirror, without being seen by the chicks. In trials in the test phase,
207 two beads of either different colours or the same colour were presented simultaneously.
208 See below for detailed training and testing procedures.

209 **<H2>Variable food and constant food conditions**

210 To precisely control food distribution, millet grains were passed through a sieve so
211 that the weight of each grain was around 7.60 ± 1.32 mg (mean \pm SD, $N=30$). In
212 experiment 1, we also passed smaller grains through a sieve and kept grains that
213 weighed 2.39 ± 0.73 mg, ca. one-third of a regular grain.

214 We trained each subject chick in one of the two conditions, i.e. variable and
215 constant amount of food. For a schematic illustration of the food condition, see
216 Appendix Fig. A1. The amount of delivered food was adjusted so as to ensure that the

217 average gain was identical between the two conditions. In the variable condition, the
218 food amount varied pseudorandomly from trial to trial. For the SS option (associated
219 with red in the case shown here), one (experiment 1) or three grains of millet
220 (experiment 2) were delivered in one of three trials, so that the average amount was
221 one-third (experiment 1) or one grain (experiment 2). Similarly, for the LL option
222 (associated with green), the food amount varied according to the binomial distribution
223 with a mean of two grains (range 0–6, average = two grains; experiment 1) or six grains
224 (range 0–18, average = six grains; experiment 2). For the S- option, no food was
225 delivered, irrespective of the subject's response. Conversely, in the constant condition,
226 the amount of delivered food was fixed. In experiment 1, we delivered a one-third-size
227 grain for the SS option and two grains of ordinary weight for the LL option. In
228 experiment 2, we delivered one and six ordinary grains for the SS and LL options,
229 respectively. The trials were arranged in a pseudorandom order.

230 <H2>*Behavioural training and test procedures*

231 <H3>*Experiment 1*

232 The schedule included three phases (Fig. 2b): a habituation phase on posthatch days
233 1–3, training phase on days 4–6/7 and test phase (pretest retraining and test) on days
234 7/8–8/9. In the habituation phase, chicks were habituated to the chamber in groups of
235 three (i.e. in competition). On day 1, chicks received food (grains of millet) in the
236 chamber without any cue beads. On days 2 and 3, the chicks received autoshaping in 30
237 trials per day, in which they learned to peck at a transparent bead to gain millet grains
238 (two grains for three chicks) without a delay.

239 In the training phase on day 4 and afterwards, the chicks were trained in one block
240 per day either in isolation or pseudocompetition. One training block consisted of 72

241 pseudorandomly arranged trials: 18 trials with the SS option, 18 trials with the LL
242 option and 36 trials with the S- option. Groups of chicks were prepared in a 2×2 block
243 design for the social (pseudocompetition or isolated) and food (variable or constant)
244 conditions. In the first set of four groups, the delay of the LL option was fixed at 1.5 s.
245 In the second set, we omitted the delay and examined whether the variable condition
246 itself impaired the choices based on the food amount; chicks thus gained food without a
247 delay in both the LL and SS trials. The food amounts for each condition are shown in
248 the inset table in Fig. A1a.

249 In the pretest retraining on day 7/8, all of the trained chicks were exposed to the
250 isolated and constant food conditions. The chicks received binary choice trials in which
251 they chose between a rewarding option (SS or LL) and a nonrewarding S- option (18
252 trials with SS/S-, 18 trials with LL/S-). The trial order was pseudorandom with 36 trials
253 with S-/S-. Those chicks that reached a criterion (choice of the rewarding option in 15
254 or more trials for both the SS and LL options) were accepted for testing on the
255 following day. Note that the food amount was set at one grain for SS and six grains for
256 LL options.

257 On day 8/9, the chicks were tested in the isolated condition. The chicks were
258 exposed to binary choice trials between the SS and LL options (20 trials). These trials
259 were presented pseudorandomly together with trials with identical pairs (10 trials with
260 SS/SS, 10 trials with LL/LL and 40 trials with S-/S-). Chicks received the designated
261 amount of food (one and six grains for the SS and LL options, respectively), except for
262 in intertemporal SS/LL trials, in which no food was delivered irrespective of the chick's
263 responses.

264 **<H3>Experiment 2**

265 The procedures in experiment 2 were essentially identical to those in experiment 1,
266 except that all four groups of chicks were trained in pseudocompetition. The schedule
267 (Fig. 2c) comprised three phases: a habituation phase on posthatch days 1–3, a training
268 phase on days 4–6/7 and a test phase (pretest retraining and test) on days 7/8–8/9. To
269 examine the influence of different food conditions, we compared four groups of chicks
270 trained in different combinations of variable and constant food conditions for the SS and
271 LL options, namely, Variable SS/Variable LL, Variable SS/Constant LL, Constant
272 SS/Variable LL and Constant SS/Constant LL. The average amounts of food (one and
273 six grains for the SS and LL options, respectively) in the training phase were matched to
274 those in the test phase. See Fig. A1b for a schematic illustration.

275 In the pretest retraining period on day 7/8, chicks in all groups were exposed to the
276 isolated and constant food conditions. Those chicks that reached a criterion (choice of
277 the rewarding option in 15 or more trials for both the SS and LL options) were accepted
278 for testing on the following day. On day 8/9, as in experiment 1, chicks from the four
279 groups were individually tested with binary choice trials randomly mixed with trials
280 with identical pairs.

281 <H2>*Statistical analysis*

282 The behavioural data were analysed with nonparametric methods (Kruskal–Wallis
283 test with Steel–Dwass test, Wilcoxon signed-rank test) using R (version 3.1.3, Windows
284 version, The R Foundation for Statistical Computing, Vienna, Austria,
285 <http://www.r-project.org>). The significance level was set at $P = 0.05$. When necessary,
286 the effect size was estimated by Grissom’s probability of priority (Grissom, 1994).

287

288 <H1>RESULTS

289 <H2>Experiment 1: **Effects of variable food and pseudo-competition**

290 The number of LL choices differed significantly between the four groups (Fig. 3a;
291 Kruskal–Wallis test: $\chi^2_3 = 16.92, P < 0.001$). Post hoc Steel–Dwass tests revealed a
292 significant difference between the ‘Competition’ × ‘Variable’ group versus each of the
293 other three groups. Notably, the number of LL choices was not significantly different
294 between the two groups trained in the ‘Constant’ food condition (‘Competition’ ×
295 ‘Constant’ versus ‘Isolated’ × ‘Constant’). In the second set of four groups trained
296 without a delay in the LL option (Fig. 3b), chicks consistently chose LL, and we found
297 no significant differences between these groups (Kruskal–Wallis test: $\chi^2_3 = 5.111, P$
298 > 0.05).

299 <H2>Experiment 2: **Effects of partial introduction of variable food**

300 The number of LL choices differed significantly between the four groups (Fig. 3c;
301 Kruskal–Wallis test: $\chi^2_3 = 14.45, P < 0.005$). The Steel–Dwass test revealed
302 statistically significant differences between the ‘SS Variable’ × ‘LL Variable’ versus the
303 ‘SS Constant’ × ‘LL Constant’ conditions and between the ‘SS Variable’ × ‘LL Constant’
304 versus the ‘SS Constant’ × ‘LL Constant’ conditions ($P < 0.05$). In contrast, we did not
305 find any significant differences among any two of the three groups: the ‘SS Variable’ ×
306 ‘LL Variable,’ the ‘SS Variable’ × ‘LL Constant,’ or the ‘SS Constant’ × ‘LL Variable.’
307 We found a suggestive difference between the ‘SS Constant’ × ‘LL Variable’ and the ‘SS
308 Constant’ × ‘LL Constant’ conditions ($P = 0.054$) with a considerable effect size $\hat{p}_s =$
309 0.875 (as estimated by Grissom’s probability of superiority).

310

311 <H1>DISCUSSION

312 <H2>Development of choice impulsiveness

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313 Chicks trained in a condition in which competitive social foraging was mimicked
314 subsequently developed choice impulsiveness. In these chicks, the temporal discounting
315 of the delayed food option (LL) was stronger than that presumed by the
316 profitability-based valuation of food items (Charnov, 1976; Stephens & Krebs, 1986;
317 Matsushima, Kawamori & Ben-Sojka, 2008). As has been argued (Amita, Kawamori &
318 Matsushima, 2010) and schematically illustrated above (Fig. 1c), this apparent
319 impulsiveness could be an adaptive trait in the context of social foraging. A producing
320 forager, if accompanied by a scrounger, would expect more from an immediate option.
321 However, the effect of social foraging appears to be conditional rather than contextual,
322 because pseudocompetition does not instantaneously change their choices (Amita &
323 Matsushima, 2011). In the present study, we focused on another aspect of competition
324 over food: the variance in the food amount.

325 The results of experiment 1 (Fig. 3a) indicate that food variance is necessary for the
326 development of impulsiveness in chicks, whereas pseudocompetition alone failed to
327 cause an effect. Furthermore, we observed no difference between groups when the LL
328 delay was omitted (Fig. 3b). Neither the variable food nor the pseudocompetition
329 severely reduced the subjective value of the large food option, as would be inferred
330 from the scores in the subsequent test. This lack of the competition effect is not in
331 concert with our previous finding that the pseudocompetition contextually reduced the
332 cue responses in the ventral striatum (Amita & Matsushima, 2014). The observed
333 neuronal suppression may be responsible for acute effects such as the shortening of the
334 operant peck latencies in competition (Amita & Matsushima, 2011), other than the
335 lasting conditional effects examined in the present study. The lack of clear consequences
336 of variance is also counterintuitive, since the reinforcement value of food has generally

337 been assumed to be a concave function of the amount (Kacelnik & El Mouden, 2013).
338 Further systematic investigations are thus necessary regarding the effects of variance on
339 amount-based choices.

340 Careful consideration is needed of the finding that the chicks chose LL more than
341 SS in the control conditions (i.e. without the coincident competition and food variance,
342 Fig. 3a, c), even though we presumed that LL matched SS in profitability ($(X/(B+C+D))$,
343 Table 1). We may therefore argue that the control chicks developed self-control choices
344 to some extent. On the other hand, the choices may fit those expected from the
345 alternative measure of profitability ($(X/(A+B+C+D+E))$). If this is the case, the intertrial
346 intervals must be considered and the choices based on the proximate profitability need
347 to be amended. Other factors may also be taken into account. One is the number of
348 pecks required to consume one grain of food (κ), which is strongly influenced by
349 substrate and shape of the feeder (Aoki, Csillag & Matsushima, 2006). Another factor is
350 the mechanical lag associated with the SS delay, to which the intertemporal choice score
351 is highly sensitive (Matsushima, Kawamori, Bem-Sojka, 2008). In the present study, we
352 did not quantify κ and lag during the experiments.

353 Perceptual noises may be considered as cognitive processes underlying the
354 development of impulsiveness. It has been reported in honeybees and humans that
355 choices are sensitive to how certain the subject is about the reward distributions (Shafir,
356 Reich, Tsur, Erev & Lotem, 2008). In the present study, similarly, due to the increased
357 uncertainty, the subject chicks turned out to be paradoxically risk-prone, thus choosing
358 SS over LL more frequently. Another possibility, although not contradicting that
359 described above, is that the chicks failed to accurately associate the food amount with
360 the length of the delay in this specific condition. When pseudocompetition, food

361 variance and delay to the LL reward coincided, the subject chicks would be unable to
362 perceive the associated food amount, and subsequently they chose immediate options
363 solely on the associated proximity. Single-unit recording experiment from freely
364 behaving chicks (Izawa, Aoki & Matsushima, 2005) actually revealed distinct
365 populations of striatal neurons, one specifically coding for the proximity and another for
366 the amount of the anticipated reward. Below, we further discuss the issues of risk
367 sensitivity in reference to the present results.

368

369 <H2>*Collection risk hypothesis and risk-sensitive choices*

370 Our results may be consistent with the ‘collection risk’ hypothesis of temporal
371 discounting (McNamara & Houston, 1987; Benson & Stephens, 1996; Sozou, 1998), in
372 which delayed reward is discounted because it has a higher risk of being interrupted and
373 lost. Here, temporal discounting is attributed to the associated uncertainty, or the higher
374 probability of not gaining the delayed reward. Subjects avoid the risk (the cause), and
375 hence the delay (the consequence). This idea has been challenged by empirical studies
376 in humans (Takahashi, Ikeda & Hasegawa, 2007), where subjective probability and
377 delay discounting were carefully examined. In these studies, subjective probability
378 actually decayed when the delay increased, but it was not correlated with the degree of
379 temporal discounting. The authors argued that other parameters (such as pure time
380 preferences) should be considered.

381 In the present study, however, a longer delay for the LL option was not associated
382 with a higher risk. We assumed a binominal distribution of the food amount, as we
383 postulated that the chicks had an equal chance to get each grain. This assumption led to
384 a lower coefficient of variance in the LL option (six grains; Fig. 1e) compared with the

385 SS option (one grain; Fig. 1d). In terms of the probability of not gaining any food, the
386 immediate SS option ($P = 0.66$) was higher than the delayed LL option ($P = 0.13$).
387 Paradoxically, however, the chicks chose the SS option more frequently in the
388 ‘Competition’ × ‘Variable’ group, despite the higher coefficient of variance and the
389 higher probability of not gaining food.

390 The observed risk proneness with the variable delay may have caused the
391 apparently paradoxical choice of the SS option. As has been reported ([Kawamori &](#)
392 [Matsushima, 2010](#)), chicks show a preference for options that vary in delay (or
393 proximity; for general arguments, see reviews by [Kacelnik & Bateson, 1996](#); [Kacelnik](#)
394 [& El Mouden, 2013](#)). In the present study, the variable SS option gave rise to one grain
395 (or three grains) delivered immediately, or led to no reward. However, the chicks might
396 have behaved as if the delay varied instead, and thus showed a preference for the SS
397 option. We do not suppose that this is a plausible explanation, as such risk proneness is
398 not distinct in chicks ([Kawamori & Matsushima, 2010](#)).

399 In this respect, the results of experiment 2 are intriguing, as we found that the
400 variable food had similar effects on the SS and LL choices (Fig. 3c). The food variance
401 in either option was sufficient for the impulsive choices to develop. In the group ‘SS
402 Variable’ × ‘LL Constant,’ chicks chose SS more frequently than chicks in the ‘SS
403 Constant’ × ‘LL Constant’ group. The variable food amount associated with the SS
404 option made this option more valuable. We therefore cannot accept the idea that the
405 observed increase in temporal discounting is due to the higher probability of not gaining
406 food. In this sense, the present results do not empirically support the ‘collection risk’
407 hypothesis. This hypothesis must be reconstructed, taking the conditions affecting social
408 foraging into account.

409 Alternatively, the chicks might not evaluate each option based on the associated
410 variance in food amount. We may instead assume that each individual had a unique rate
411 of temporal discounting as a single scalar value, and the rate was applied equally to both
412 SS and LL irrespective of which of these options was variable. It is also possible that the
413 variable food was linked to the specific food patches, and each of the feeders had a
414 unique rate of temporal discounting. As a future study, we should examine whether each
415 chick shows a unique level of choice impulsiveness consistently for different feeders (or
416 different patches of food) located at a distance.

417

418 <H2>*Conditional and contextual modulation of foraging behaviours*

419 The present results were consistent with a previous report that choice impulsiveness
420 is conditionally modulated by preceding competition over food ([Amita & Matsushima,](#)
421 [2011](#)). As reported previously, this impulsiveness is not contextually modulated by the
422 competition at tests. However, evidence regarding whether conditioned impulsiveness
423 truly contributes to the survival of animals foraging in nature is not yet available.
424 Additionally, whether chicks adaptively change their level of impulsiveness in response
425 to modulations in the degree of social competition over food, such as the number of
426 competitors and uncertainty regarding food resources, is unclear. Functional links to
427 other aspects of individual personality (such as boldness, neophobia and other
428 exploratory tendencies; [Sih & Del Giudice, 2012](#)) could also be the topic of future
429 exploration.

430 Contextual modulation by foraging companions may contribute to individual fitness
431 in socially foraging animals. In chicks, the presence of a coincidentally foraging
432 conspecific shortens the operant peck latency ([Amita & Matsushima, 2011](#)). The

433 competitor further facilitates foraging efforts such as running and pecking activities
434 (Ogura & Matsushima, 2011; Ogura, Izumi, Yoshioka & Matsushima, 2015). As a
435 possible mechanism, pseudocompetition has been found to acutely suppress the firing
436 rate of medial striatum neurons (Amita & Matsushima, 2014), although the functional
437 link to contextual changes in behaviour remains unknown. The underlying
438 neurocognitive processes of the producer–scrounger game (Giraldeau & Caraco, 2000)
439 appear to involve a complex set of conditional and contextual modulations of foraging
440 decision mechanisms.

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457

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560

561 Appendix

562

コメント [AT5]: Fig. A1

563 **Table 1** Presumed profitability of LL, SS and S- options

	Cue period (A) (s)	Postchoice delay (B) (s)	Mechanical lag (C) (s)	Handling time (D) (s)	Intertrial interval (E) (s)	Amount (X) (mg)	Profitability X/(B+C+D) (mg/s)	Profitability X/(A+B+C+D+E)
LL	1.5	1.5	0.29	1.5~3.0	15~20	45.6 (6 grains)	9.5~13.8	1.6~2.3
SS	1.5	0	0.29	0.25~0.5	15~20	7.6 (1 grain)	9.6~14.1	0.35~0.45
S-	1.5	-	-	0	15~20	0	0	0

564

565 **FIGURE LEGENDS**

566

567 **Figure 1.** Intertemporal choice paradigm in the context of social foraging. See text for
568 explanations.

569

570 **Figure 2.** Experimental design and procedure. (a) Schema of single trials for the SS and
571 LL options. (b, c) Procedure of experiments 1 and 2. Schedules along posthatch days
572 (above) and schematic illustration of the training and test condition (below).

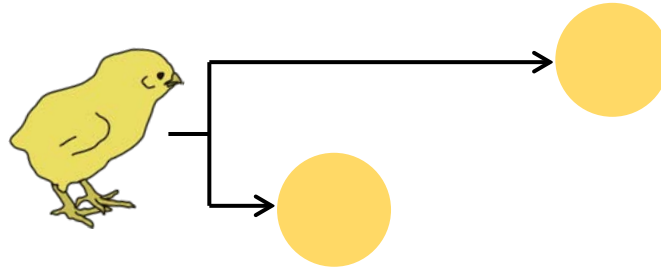
573

574 **Figure 3.** Results of (a, b) experiment 1 and (c) experiment 2. We compared the number
575 of LL choices between the different groups. Circles denote individuals, and horizontal
576 bars represent the median of the group. The number of individuals in each group is
577 indicated by *N*. Different letters above each graph denote statistically significant
578 differences ($P < 0.05$) revealed by multiple comparisons.

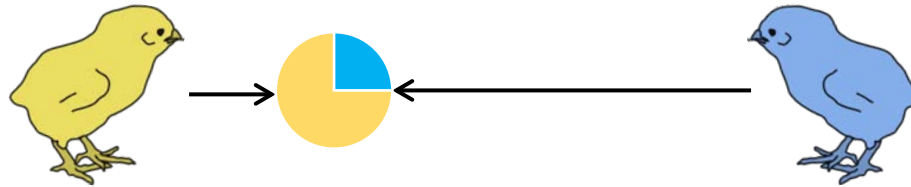
579

580 **Figure A1.** Details of the experimental procedures. (a) Schematic illustration of training
581 trials in experiment 1. In the variable food condition, the amount of food varied between
582 trials. In the constant food condition, by using smaller grains shown in photos below,
583 the average gain per trial was adjusted to be the same as the variable condition. The
584 expected amount of food gain is summarized in the inset table. (b) Training trials in
585 experiment 2. The four groups of chicks received different patterns of food variance.
586 Note that the average amount of food per trial was maintained identical throughout the
587 training (day 4 ~6/7), the pretest retraining (day 7/8) and the tests (8/9).

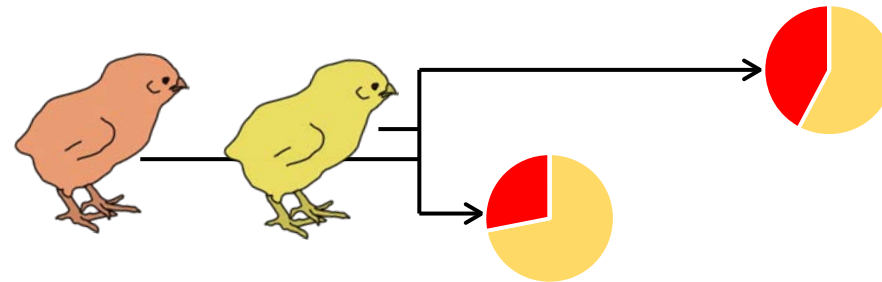
(a) One forager expects the same amount irrespective of the distance.



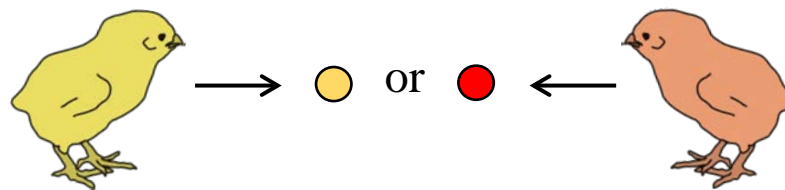
(b) Competing foragers share food depending on the distance.



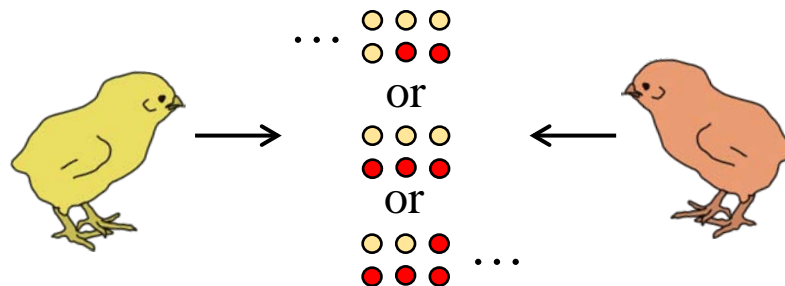
(c) Producer gains more from the proximate food than the delayed alternative.

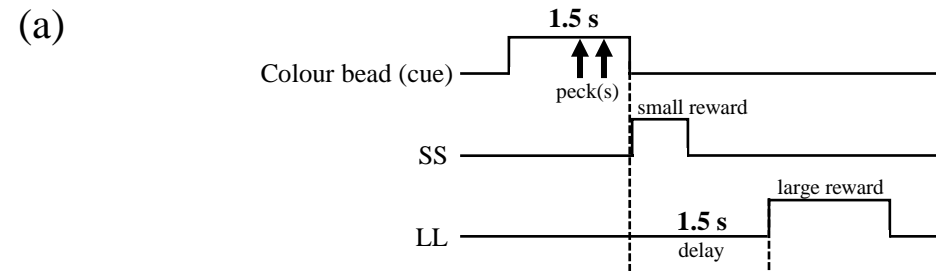


(d) Unshareable food item yields a high degree of variance.

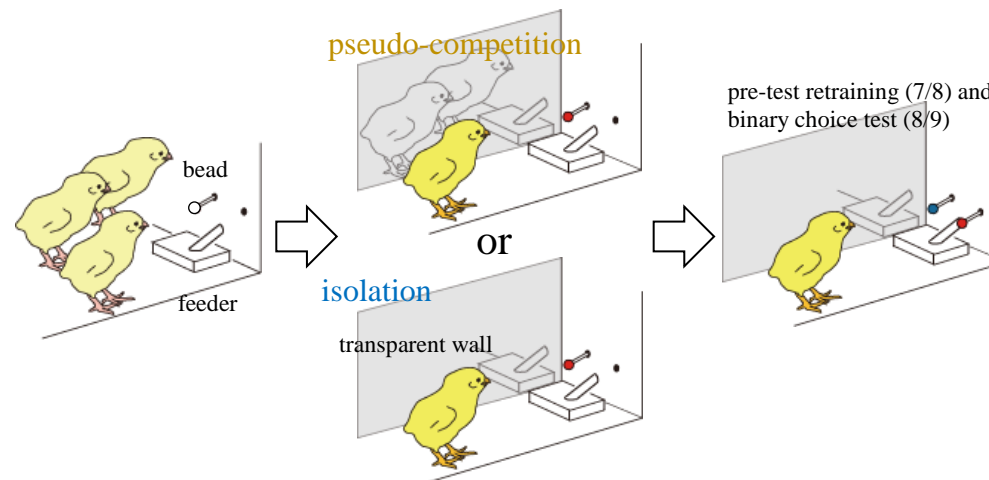
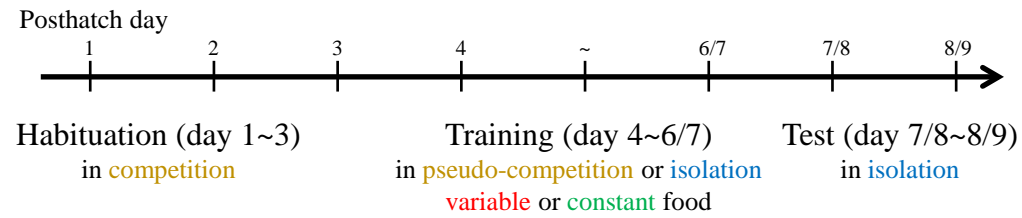


(e) Patch of shareable food items yields a low degree of variance.

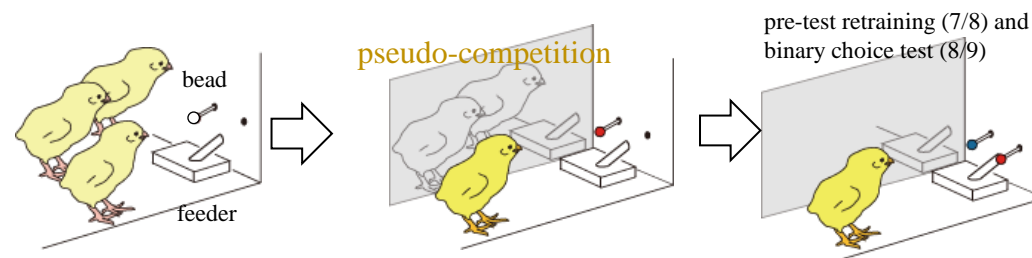
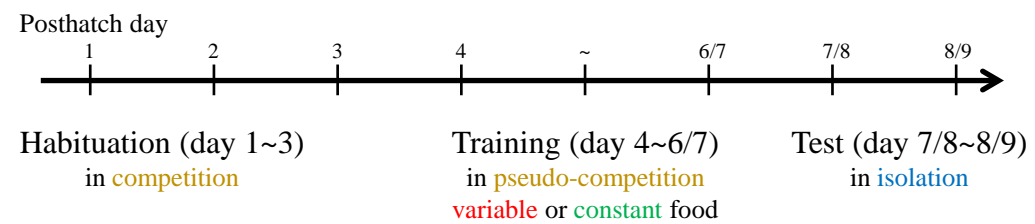




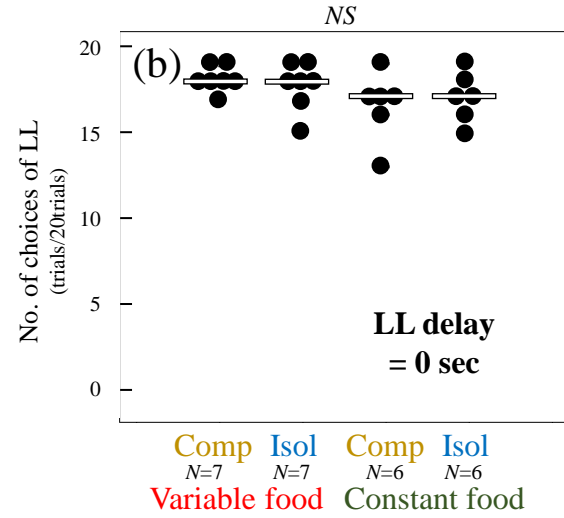
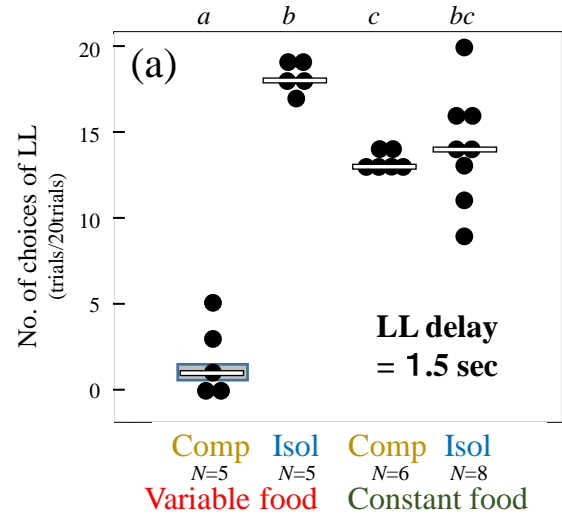
(b) Experiment 1



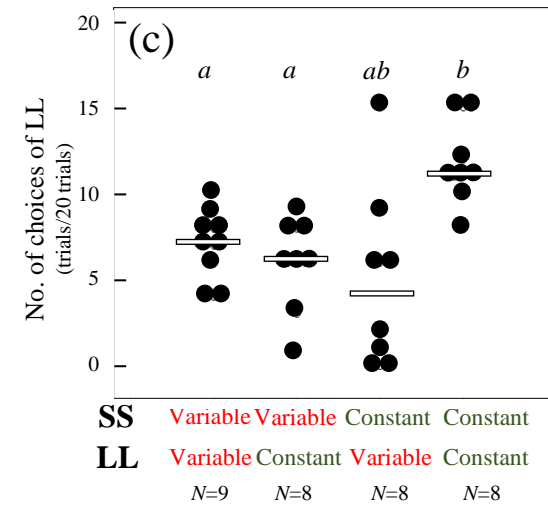
(c) Experiment 2



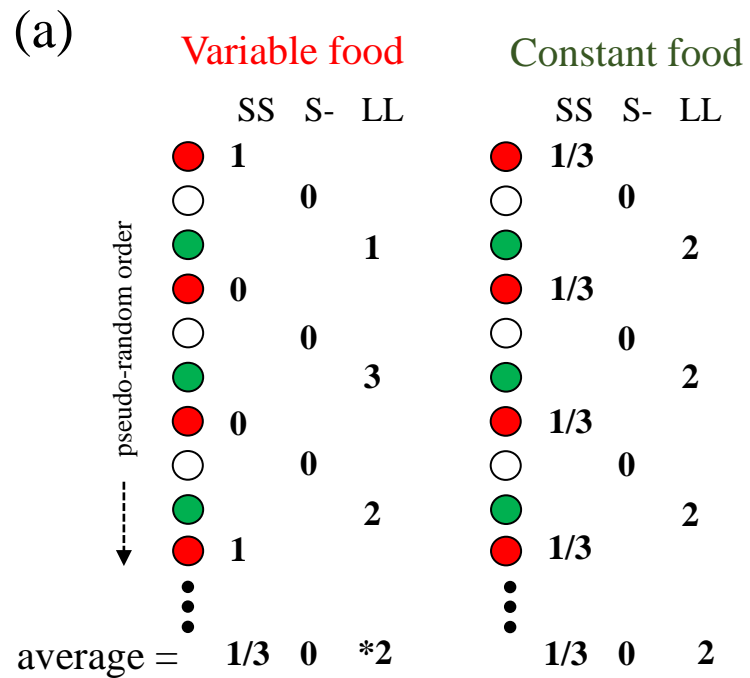
Experiment 1



Experiment 2



Experiment 1

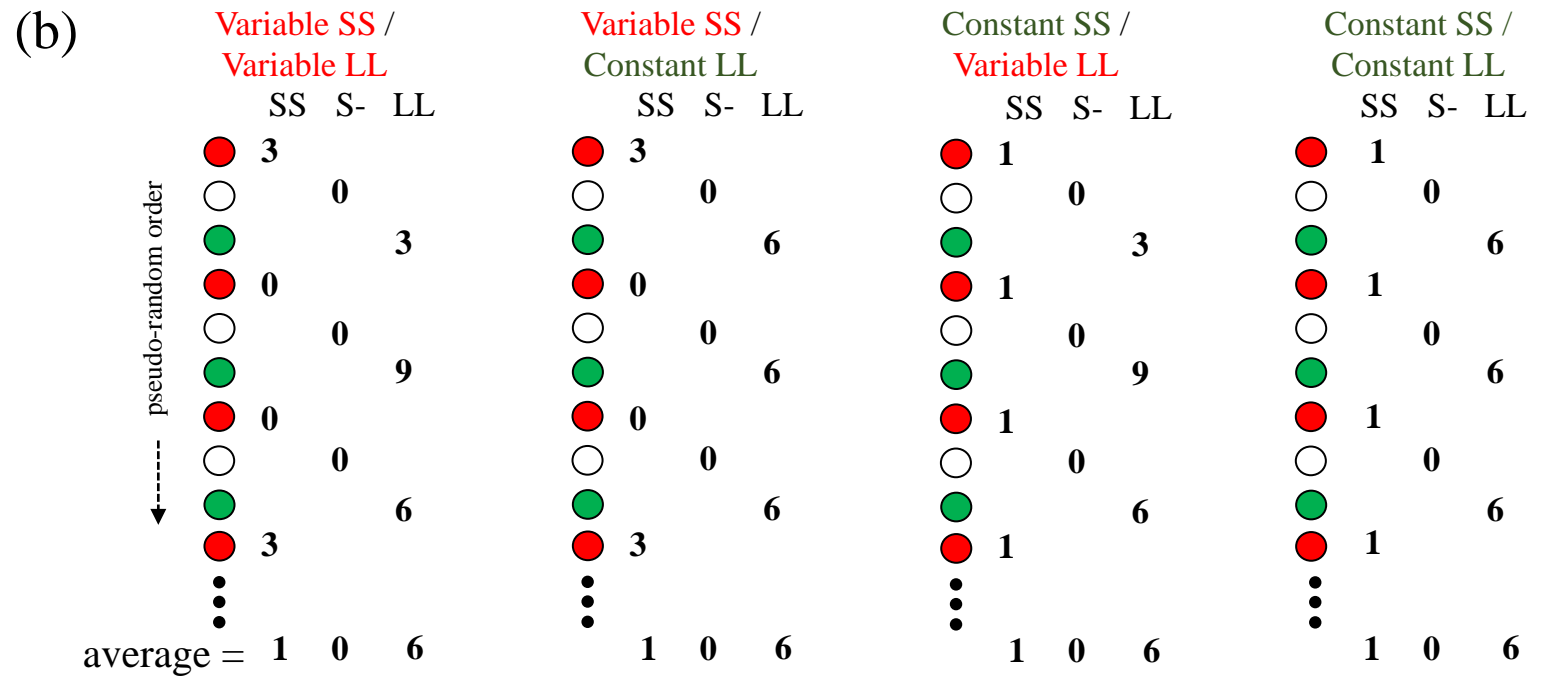


	Day 4	~	Day 6/7	Day 7/8	Day 8/9
LL	*2	*2	*2	6 (const)	6 (const) or 0 [#]
SS	1/3	1/3	1/3	1 (const)	1 (const) or 0 [#]
S-	0	0	0	0	0



7.60 ± 1.32 mg (n=30) 2.39 ± 0.73 mg (n=30)

Experiment 2



	Day 4	~	Day 6/7	Day 7/8	Day 8/9
LL	6	6	6	6 (const)	6 (const) or 0 [#]
SS	1	1	1	1 (const)	1 (const) or 0 [#]
S-	0	0	0	0	0