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1 Title:

2 **Four eyes match better than two: sharing of precise patch-use time among socially**
3 **foraging domestic chicks**

4

5 Running title:

6 **Matching and social foraging**

7

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27 ***Keywords***

28 collective intelligence; ideal free distribution; matching behaviour; social facilitation;
29 social foraging

30

31 ***Highlights***

32 ● Domestic chicks were tested in a task that mimicked patch-use behaviour.

33 ● Pairing or perceived competition by mirror facilitated the running effort.

34 ● Pairing, but not the mirror, led to precise matching of patch-use time.

35 ● Patch-use time was shared by the pair and stored as a lasting preference.

36

37

38 **Abstract**

39

40 To examine how resource competition contributes to patch-use behaviour, we examined
41 domestic chicks foraging in an I-shaped maze equipped with two terminal feeders. In a
42 variable interval schedule, one feeder supplied grains three times more frequently than the
43 other, and the sides were reversed midway through the experiment. The maze was
44 partitioned into two lanes by a transparent wall, so that chicks fictitiously competed without
45 actual interference. Stay time at feeders was compared among three groups. The “single”
46 group contained control chicks; the “pair” group comprised the pairs of chicks tested in the
47 fictitious competition; “mirror” included single chicks accompanied by their respective
48 mirror images. Both “pair” and “mirror” chicks showed facilitated running. In terms of the
49 patch-use ratio, “pair” chicks showed precise matching at approximately 3:1 with
50 significant mutual dependence, whereas “single” and “mirror” chicks showed a comparable
51 under-matching. The facilitated running increased visits to feeders, but failed to predict the
52 patch-use ratio of the subject. At the reversal, quick switching occurred similarly in all
53 groups, but the “pair” chicks revealed a stronger memory-based matching. Perceived
54 competition therefore contributes to precise matching and lasting memory of the better
55 feeder, in a manner dissociated from socially facilitated food search.

56

57 **1. Introduction**

58

59 The term “matching law” was coined after an intensive series of psychological studies
60 on choice behaviours, starting with the pioneering works of Skinner, Herrnstein and
61 colleagues (for historical reviews, see monographs by Davison and McCarthy, 1988, and
62 Herrnstein, 1997). In early studies (Herrnstein, 1961), subjects (pigeons) were tested using
63 an operant chamber equipped with two response keys as options, in which they responded
64 in a manner proportionate to the corresponding relative reinforcement. In a simple function
65 linking reinforcement rate and response intensity, the matching law provides a
66 generalizable empirical and theoretical framework about how animals (including humans)
67 make choices among options of different values (such as food items or patches). Herrnstein
68 argued that matching behaviour is a product of the melioration process, in which individual
69 subjects always switch to an alternative option if its reinforcement rate is higher (Herrnstein
70 and Prelec, 1991). Because melioration gives a reasonable account for the dynamic process
71 of value update, and because this process could give rise to optimal behaviours in highly
72 uncertain environments, the matching law has attracted particular attention in recent
73 developments of reinforcement learning theories (Sutton and Barto, 1998; Sakai and Fukai,
74 2008) and neuroeconomics (Platt and Glimcher, 1999; Sugrue et al., 2004; Mobbs et al.,
75 2013).

76 A comparable idea, known as ideal free distribution (IFD), has been proposed in
77 ecological studies of population density. Fretwell and Lucas (1969) formulated
78 geographical distribution of population density in terms of habitat selection. They assumed
79 that animals select one of several possible habitats based on its relative advantages (such as
80 food supply), but increased density in one habitat inevitably decreases its suitability. If
81 animals make *ideal* selections in a manner *free* of moving cost, individual melioration will
82 lead to a stable equilibrium, at which the population density will be proportionate to the
83 suitability of each habitat. In contrast to the psychological framework of matching law, the
84 IFD assumes competitive interactions as a critical factor.

85 More recent studies on social foraging behaviours suggest an alternative game-
86 theoretical view of resource competition, where different foraging tactics co-exist in a
87 foraging flock (Giraldeau et al., 1990). When food items are sharable (kleptoparasitism),
88 two beneficial tactics may appear, namely producer and scrounger (see Giraldeau and
89 Caraco, 2000 for a comprehensive review). Due to frequency dependence, both tactics
90 would subsequently attain the same level of individual fitness as a stable equilibrium. In
91 addition to personal information acquired individually, scrounging individuals would gain
92 information about the location and suitability of habitats from producing companions
93 (Giraldeau and Beauchamp, 1999; Danchin et al., 2004). Individual foragers may
94 concurrently search for food and join a group of foragers (information sharing), or they
95 might adopt an exclusive tactic at a time (producer-scrounger game). In both cases,
96 however, inadvertent sharing of information on food resources could contribute to an
97 economically optimal decision.

98 These considerations led us to ask the following questions, is precise matching
99 achieved solely through melioration of personal information in individuals, or does social
100 grouping contribute to matching behaviour? In case of the latter, is food patch information
101 shared among the competing individuals? We addressed these questions using domestic
102 chicks as subjects. Chicks adjust their foraging decisions according to their social
103 conditions. For example, choice impulsiveness (in terms of a stronger temporal
104 discounting) is conditionally enhanced by competition (Amita et al., 2010, Amita and
105 Matsushima, 2011, 2014), if and only if accompanied by food risk (Mizuyama et al., 2016).
106 Foraging effort is also socially facilitated in patch-use behaviour, and paired chicks run
107 significantly more than single foragers even without interference of food resource (Ogura
108 and Matsushima, 2011, Ogura et al., 2015, Xin et al., 2017). However, the functional role
109 of the social facilitation remains unclear. Facilitated running could make chicks visit
110 feeders more frequently, leading to a higher chance of finding food and more precise
111 matching, even without active information sharing among the foraging chicks. Otherwise,
112 competing chicks may learn about food availability in patches directly by observing the
113 behaviour of companions.

114 In the present study, we compared patch-use behaviour between groups under single
115 and paired conditions. Feeders at both ends of a maze supplied millet grains without any
116 predictive cues, so that information on food availability would be critical. To study the
117 behaviour in static conditions, the food supply rate at the feeders was biased at a fixed ratio
118 of 3:1 between the feeders. To examine dynamic behavioural changes, the bias was
119 reversed midway through the experiment, and we examined how quickly chicks switched
120 patch-use time. If competition (or perceived pseudo-competition, to speak more strictly) is
121 critical, then the pair chicks would show more precise matching and quicker switch to the
122 reversal than the single chicks. However, as argued above, differences between the two
123 groups could be ascribed to improved personal information through facilitated running. We
124 therefore added a “mirror” group, in which single chicks were accompanied by their mirror
125 image along the lane. The preliminary experiment revealed facilitated running in both of
126 the mirror and pair groups. However, if information sharing is critical, then mirror chicks
127 would show less precise matching than the pair chicks, as they would not learn about food
128 availability from the mirror image.

129

130 **2. Materials and methods**

131

132 *2.1. Subjects*

133 Male domestic chicks (*Gallus gallus domesticus*) were purchased on post-hatch day 1
134 (D1) from a local supplier (Iwamura Poultry Ltd. /Hokkaido Central Poultry Ltd., Yubari,
135 Japan). Chicks were communally housed in transparent plastic cages (15 × 28 × 12 cm;
136 kept at ca. 30°C) with a 12:12-h light:dark cycle with lights on at 08:00. Chicks received
137 millet grains and chick mash, with the amount adjusted daily such that body weight
138 increased by ~5% per day, and that the chicks actively consumed food in tests. Water was
139 freely available.

140

141 *2.2. Ethical Note*

142 We did not perform any invasive treatments or stressful handling of the chicks during
143 the experiments. When a chick emitted distress calls in the experimental apparatus, we
144 stopped the experiment. We thus discarded data from 4 out of 64 chicks, and the present
145 results were based on the remaining 60 chicks. The experiments were conducted under the
146 guidelines and approval (#11-0042) of the Committee on Animal Experiments of Hokkaido
147 University. The guidelines are based on the national regulations for animal welfare in Japan
148 (Law for Humane Treatment and Management of Animals; after a partial amendment No.
149 68, 2005). After the experiments, chicks were euthanized using carbon dioxide.

150

151 2.3. *Apparatus*

152 An I-shaped maze was partitioned into two parallel lanes ($12 \times 88 \times 40$ cm, Fig. 1b,
153 Ogura and Matsushima, 2011) by a transparent Plexiglas or mirror partition, and each lane
154 accommodated one chick at a time, except during habituation. Each of the terminal walls
155 (one red, one yellow) held a pair of food trays, with one tray in each lane. We used a micro-
156 robot (Mindstorms RCX, LEGO, Denmark) to deliver millet grains simultaneously to each
157 of the paired trays. Although no actual food interference occurred, the chicks in the
158 partitioned lanes experienced fictitious interference over the delivered food. Food delivery
159 in the opposite patches was not linked, but independently controlled. Four 60-W light bulbs
160 illuminated the maze, and chicks were video-recorded via a camera on the ceiling (DCR-
161 SR65, Sony, Japan). This provided an aerial view of the running trajectories, which were
162 traced offline using Move-Tr/2D 7.0 (Library Co., Japan).

163

164 2.4. *Procedures*

165 Chicks were habituated to the maze in daily sessions on post-hatch day 6 to day 7 (D6–
166 7, Fig. 1a). A pair of chicks was introduced to a lane with starter food (180 grains). After
167 the food was consumed, the feeders were turned on to deliver millet according to the
168 variable interval (VI) schedule. The delivery interval varied uniformly in 10–20 s with a
169 mean of 15 s (VI15). Two grains of millet were delivered at a time, and the paired chicks

170 received a total of 240 grains in ~16 min. After the delivered food was consumed, the
171 chicks remained in the maze for an additional 2-min ‘no food (after feeding)’ period.

172 On D8–11, chicks were randomly allocated to one of three groups (Fig. 1b): ‘single’
173 (n=18), ‘pair’ (n=24), and ‘mirror’ (n=18). In the single group, chicks were individually
174 tested in one lane. In the pair group, randomly chosen pairs of chicks were tested in the
175 partitioned lanes. Chicks equally gained 1 grain per chick per delivery, and actual
176 interference did not occur. In the mirror group, chicks were individually tested in one lane,
177 and the Plexiglas partition was replaced with a mirror. Biased food delivery started as soon
178 as the chicks were introduced to the maze. One feeder (e.g. yellow) supplied grains on a
179 VI10 schedule (range = 6.7–13.3 s, mean = 10 s) and the other (red) supplied grains on a
180 VI30 schedule (range = 20–40 s, mean = 30 s). Colour allocation was randomized among
181 individuals. After the food delivery period, chicks were left in the maze for an additional 2-
182 min ‘no food (after feeding)’ period. On D12–15, the feeding rate schedules were reversed
183 between the two feeders. Behaviour was also recorded during a 2-min ‘no food (before
184 feeding)’ period.

185

186 2.5. *Statistical Analysis of Data*

187 We obtained the running distances and patch-use ratios from the recorded trajectories.
188 Running distance was calculated as the cumulative distance the subject ran during the 16-
189 min feeding period. Patch-use ratio was calculated as the proportion of the time during
190 which the subject stayed close (< 10 cm) to the VI10 feeder on D8–11, divided by the total
191 stay time at both feeders. We conducted statistical tests using a two-way ANOVA with
192 repeated measures and Holm’s multiple comparisons test using R software (version 3.1.3,
193 Windows version). Significance was set at $P = 0.05$.

194 In the pair chicks, the behaviours of individuals are supposed to be mutually dependent.
195 To estimate the effects of the companion’s patch-use behaviour on the focal subject, we
196 conducted multiple regression analysis as follows:

$$197 \quad Y = \beta_0 + \beta_1 \times X_1 + \beta_2 \times X_2 + r_i,$$

198 where Y is the response variable or the patch-use ratio of subject, β_0 is the intercept, and β_1
199 is the coefficient of the patch-use ratio of the companion chick ($=X_1$). β_2 is the coefficient
200 of the day ($=X_2$; numeric variables 1–4 were assigned), and r_i is the random intercept for
201 each individual. By the same token, we estimated the effects of the companion's running
202 distance on the subject's running distance. Furthermore, we estimated the effects of the
203 subject's running distance on the subject's patch-use ratio. For these analyses, we used R
204 (version 3.2.4) with lmerTest (version 2.0-30; Kuznetsova et al., 2016) and lme4 (version
205 1.1-12; Bates et al., 2016) libraries (see Appendix for further information on the statistics).

206

207 **3. Results**

208

209 During the feeding period, chicks actively shuttled between the two feeders. Figure 1c
210 show the representative trajectories of the three groups on D11 (left) and D12 (right). A
211 high degree of synchrony appeared among chicks in the pair group. In the pair group
212 (middle), the synchrony index (as measured by the proportion of time when the two chicks
213 were found on the same side of the maze) gradually increased from ~0.8 (D8) to 0.9 (D11)
214 (pre-reversal, Fig. 2f), with a significant effect of day (one-way ANOVA; $F_{33}^3 = 13.29$,
215 $P < 0.0001$). After the feeder reversal, the effect of the day was weaker but remained
216 significant ($F_{33}^3 = 3.364$, $P < 0.05$). On the first day of the post-reversal period (D12),
217 chicks in all three groups quickly switched their patch-use ratio, staying at the VI10 patch
218 longer than the alternative VI30 patch (Fig. 2b–c).

219 Social facilitation of the running distance was found in both the pair and mirror groups
220 (Fig. 2a), both before and after the reversal. On D8–11 (pre-reversal), we found a
221 significant effect of group ($F_{57}^2 = 11.36$, $P < 0.0002$), day ($F_{158.07}^{2.77} = 93.27$, $P < 0.0001$),
222 and interaction ($F_{158.07}^{5.55} = 9.010$, $P < 0.0001$). Multiple comparisons revealed significant
223 difference between the single vs. pair groups and single vs. mirror groups, but not between
224 the pair vs. mirror groups. On D12–15 (post-reversal), we found a significant effect of
225 group ($F_{57}^2 = 26.49$, $P < 0.0001$) and day ($F_{142.06}^{2.49} = 8.966$, $P < 0.0002$), but not
226 interaction ($F_{142.06}^{4.98} = 0.6555$, $P > 0.05$). A significant difference was found between the

227 single vs. pair groups and single vs. mirror groups, but not between the pair vs. mirror
228 groups. For detailed statistical data, see Appendix Tables 1.1.1 to 1.2.2.

229 Precise matching occurred only in the pair group, and chicks in both the single and the
230 mirror groups showed under-matching (Fig. 2b). On D8–11, the ratio differed among the
231 three groups of chicks, and we found a significant effect of group ($F_{57}^2 = 11.11$, $P <$
232 0.0002), but not day ($F_{131.45}^{2.31} = 2.665$, $P > 0.05$) or interaction ($F_{131.45}^{4.61} = 1.016$, $P >$
233 0.05). On D12–15, a significant effect of interaction ($F_{159.55}^{5.6} = 3.243$, $P < 0.01$) was
234 found, but not group ($F_{57}^2 = 2.304$, $P > 0.05$) or day ($F_{159.55}^{2.8} = 2.543$, $P > 0.05$; see
235 Appendix Tables 2.1.1 to 2.2.3). The pairing contributed to precise matching (Fig. 2b), but
236 the facilitated running distance in the mirror group (Fig. 2a) did not.

237 We also examined how chicks switched their patch-use ratio during the 16 min of the
238 first post-reversal day (D12, during feeding), and found that chicks in all three groups
239 changed the patch-use ratio quickly within the first 2-min bin (Fig. 2c). ANOVA revealed
240 no significant effect of group ($F_{57}^2 = 0.6398$, $P > 0.05$), whereas effect of the 2-min bins
241 was highly significant ($F_{258.32}^{4.53} = 31.26$, $P < 0.0001$); however, the interaction (groups \times
242 2-min-bins) was not significant ($F_{258.32}^{9.06} = 0.1884$, $P > 0.05$; see Appendix Table 5). Pair
243 chicks switched as quickly as the single and the mirror chicks did, suggesting that
244 perceived competition does not contribute to switching responses to the reversal.

245 Between the paired chicks, we found a strong inter-dependence in their patch-use
246 behaviour, such that a subject's patch-use ratio was highly predictable by the companion's.
247 However, the running distance of the subject failed to predict that subject's patch-use ratio.
248 Regression analyses were performed on the patch-use ratio data of 24 subjects (12 pairs)
249 repeated for the 4 days before the reversal (Appendix Tables 3.1.1 and 3.1.2). The
250 estimated coefficient of the companion's patch-use ratio was positive and significant
251 ($P < 0.01$), whereas the negative coefficient of the focal subject's running distance was not
252 ($P = 0.138 > 0.05$); increased running tended to reduce the subject's patch-use ratio.
253 Almost identical results were obtained on the 4 days after the reversal (Tables 3.2.1 and
254 3.2.2). Significant mutual dependence was found also in the running distance (Appendix
255 Tables 4.1 and 4.2), both for the pre-reversal and the post-reversal data, in which the

256 positive estimated coefficients of the companion running distance were highly significant
257 ($P < 0.0001$). Taken together, the findings indicate that it is improbable to assume that the
258 precise matching found in the pair chicks was due to the socially facilitated running.

259 On D12 and afterwards, chicks started running as soon as they were introduced to the
260 maze, even before food delivery was turned on. The patch-use ratio during the ‘no food
261 (before feeding)’ period could thus represent the memory-based valuation of the patches
262 (Fig. 2d). Significant effects occurred in group ($F_{55}^2 = 4.160, P < 0.05$) and day ($F_{146.08}^{2.66} =$
263 $27.49, P < 0.0001$), and the interaction ($F_{146.08}^{5.31} = 3.052, P < 0.02$) was also significant.
264 On D12 and D13, we observed significant differences between the pair vs. single and pair
265 vs. mirror groups, but not between the single vs. mirror groups (Appendix Tables 6.1 to
266 6.4); no significant inter-group differences appeared on D14 or D15.

267 Chicks continued running for a few minutes more after the food delivery was turned
268 off. The patch-use behaviour after feeding (Fig. 2e) followed that observed during feeding
269 (Fig. 2b). On D8–11, we observed a significant effect of group ($F_{57}^2 = 6.008, P < 0.005$)
270 and day ($F_{156.19}^{2.74} = 3.625, P < 0.02$), but not interaction ($F_{156.19}^{5.48} = 1.398, P > 0.05$; see
271 Appendix Tables 7.1.1 and 7.1.2). On D12–15, a significant effect occurred in day
272 ($F_{128.93}^{2.26} = 4.466, P < 0.02$), but not in group ($F_{57}^2 = 0.2863, P > 0.05$) or interaction
273 ($F_{128.93}^{4.52} = 1.784, P > 0.05$; see Appendix Table 7.2).

274

275 **4. Discussion**

276

277 *4.1. Information sharing and matching behaviour in socially foraging chicks*

278 The results of the present study stress the importance of social foraging for sharing of
279 food patch information and precise matching. Individual melioration may yield under-
280 matching, as shown by the single chicks. The competitive interaction (even without actual
281 interference of food resource) could lead to a precise patch-use ratio, and hence to optimal
282 allocation of time according to food availability. With precise matching, the risk of death
283 by starvation would be efficiently minimized in nature. The present results correspond also
284 with a theoretical study (Seth 2002) in which simulated groups of foragers developed

285 matching as an adaptive trait, only if there is considerable interference competition for food
286 resources. However, it remains unknown whether the shared information and the precise
287 matching are causally linked.

288 Socially facilitated running distance (Ogura and Matsushima, 2011) does not
289 contribute to the matching *per se*, because (i) the mirror group chicks showed socially
290 facilitated running, but not precise matching (Fig. 2a–b), and (ii) the running distance failed
291 to predict the patch-use ratio of the focal subjects in the pair group. Socially foraging chicks
292 may therefore interact in two distinct ways. Chicks stay with their companion’s stay at the
293 food patch, and they run with their companion’s run in the travel between patches. But,
294 these actions (i.e. staying and running) are not causally associated.

295 Careful consideration is needed for the precise matching found in the pair chicks,
296 because the pair chicks could simply have a higher patch-use ratio than the single chicks
297 through mutual inter-dependence. If so, groups composed of three or more individuals
298 might even show over-matching, or a disproportionately higher stay time at the more
299 beneficial feeder. Alternatively, we may assume that the precise matching occurred because
300 the paired chicks were accompanied by familiar cage-mates, whereas chicks of the mirror
301 group were accompanied by own image that is probably not familiar. It has actually been
302 shown that domestic chicks can recognize familiar companions and strangers (Vallortigara
303 and Andrew 1994). However the social facilitation of running occurs irrespective of
304 whether the companion chick was the cage-mate or not (Ogura and Matsushima,
305 unpublished observation; also see Hayashi et al. 2001 for the Japanese quail chicks and
306 isolation-induced distress calls). It remains an open question whether the matching also
307 depends on the individual familiarity, though it does not seem to be highly plausible.
308 Furthermore, we must stress that the data for pair chicks were composed of 12 independent
309 sets of experiments in 24 chicks, whereas each of the single and mirror groups comprised 18
310 independent individuals. Although the unbalanced experimental design was indispensable
311 in the present study, an independent line of empirical support may be needed.

312

313 *4.2. Social effects of switching in response to feeder reversal*

314 Chicks quickly switched with the feeder reversal in all groups (Fig. 2c), suggesting that
315 individual melioration of personal information is sufficient, and the social condition is not
316 critical particularly in this dynamic situation where the better feeder is reversed. The quick
317 switching behaviour found in this study is somewhat contradictory to the difficulty of
318 extinction found in the operant pecking responses (Ichikawa et al., 2004; Wen and
319 Matsushima, 2016), which may depend more on the chicks' lasting reference memory of
320 the food reward. Contrary to our initial expectation, memory-based behaviour ("before
321 feeding (no food)", Fig. 2d) revealed perseverated patch-use behaviour in the pair groups,
322 particularly on D13. Most probably, the interactions between the paired chicks during the 4
323 days before the reversal (D8-11) had a lasting effect on the feeder preference (or
324 memorized values of feeders) in the post-reversal tests; see below for further discussion.
325 The significant effect of the day in the post-reversal patch-use ratio (D12-15; Fig. 2b) may
326 also be accounted for by the enhanced memory in the pair chicks.

327

328 4.3. *Social enhancement of the lasting patch memory*

329 The pair group chicks showed an enhanced memory of the better feeder (Fig. 2d)
330 compared with the single and mirror group chicks. It is unclear if the memory formation
331 was enhanced during pre-reversal D8–11, or if memory retrieval (or dependence on the
332 memorized preference) was enhanced during post-reversal D13, or both occurred. To
333 address to the latter possibility, chicks must be tested in the single condition on post-
334 reversal D13. Alternatively, to address to the former possibility, chicks must receive a mild
335 depletion of mesolimbic dopaminergic projections in the pre-reversal D8–11, as this
336 treatment selectively interferes with memory formation without affecting social facilitation
337 (Ogura et al., 2015).

338 What functional role does the social enhancement of memory have in group foraging
339 animals such as chicks? Development of inter-individual variance might be considered,
340 rather than the learning itself. In a recent study on socially foraging house sparrows
341 (Belmaker et al., 2012; Ilan et al., 2013), stochastic chance events such as "beginner's luck"
342 could lead group members to differentiate their foraging preference based on memory,

343 giving rise to the skill pool effect (Giraldeau, 1984). Different social contexts may lead
344 chicks to develop differentiated behavioural traits with respect to impulsiveness (Amita et
345 al., 2010) and/or risk sensitivity (Kawamori and Matsushima, 2010, 2012). A longitudinal
346 study would help to elucidate chicks' social foraging behaviours.

347

348 *4.4. Multiple factors for the control of patch-use behaviours*

349 Taking all of the above into account, we can assume that several factors determine
350 patch-use behaviour, namely (1) the immediate reinforcement rate (individual melioration),
351 (2) the patch-use behaviours of companions (shared information), and (3) lasting memory
352 of the food patches (memorized values). In a static situation where the reinforcement bias is
353 fixed (such as in the 4 days before the reversal), the shared information is critical for the
354 precise allocation of patch-use time and for the memorized value. In a more dynamic
355 situation, where the reinforcement bias changes, the factor of immediate individual
356 melioration may predominate. The distinctly context-dependent controls of patch-use
357 behaviour found in this study may be compatible with recent neuroscience studies (Kim,
358 Ghazizadeh and Hikosaka, 2015 in monkeys; Wen and Matsushima, 2016 in chicks), where
359 the findings suggest that the mesolimbic system conveys both updated and sustained values
360 even at single neuron level. It is noteworthy that the avian "association cortices" of the
361 forebrain (Aoki et al., 2003 in chicks; Browning et al., 2011, Koenen et al., 2013 in
362 pigeons) multiply code the reward outcomes in a manner comparable with mammalian
363 counterparts (Apps et al., 2016 in humans). Further neuro-psychological studies are
364 required to elucidate the underlying brain mechanisms of social modification in patch-use
365 behaviour.

366

367 *4.5. Do chicks play the producer-scrounger game?*

368 What function does the information sharing play in foraging animals? Naturally, IFD
369 may be more reliably achieved through social foraging (Giraldeau and Beauchamp, 1999;
370 Danchin et al., 2004). But, it is premature to conclude that chicks behave according to the
371 producer-scrounger game for several reasons. First, chicks showed no clear phenotypic

372 behavioural differentiation, such as the head-position reported in nutmeg mannikins
373 (Coolen et al., 2001; Wu and Giraldeau, 2004). Second, a high proportion of joining
374 occurred as assumed from the high level of synchrony index (0.8–0.9; Fig. 2f).

375 Synchrony is however context-dependent. When pair chicks strongly interfered with
376 one another over the food (Ogura and Matsushima, 2011), the index gradually decreased
377 from ~0.8 to ~0.6 during 7 consecutive days of the experiment; because of relatively large
378 finder's share, chicks may have adopted scrounger tactics gradually less frequently. In the
379 present study, on the other hand, use of scrounger tactics may have been the primary option,
380 because the competition was fictitious and chicks always secured food. If chicks competed
381 food, they might adopt scrounger tactics less frequently, such that information sharing on
382 the patch-use ratio would be reduced. Further experimental manipulation of the conflict
383 condition is warranted.

384

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519

520 **Figure legends**

521 **Figure 1.** (a) Procedures of behavioural tests on post-hatch days 6–15. (b) Schematic
522 illustration of I-shaped maze with two lanes partitioned by a Plexiglas wall, and two
523 terminal food patches along the yellow and the red wall, each composed of two food trays.
524 Three groups of chicks were examined in ‘single’, ‘pair’, and ‘mirror’ conditions. (c)
525 Representative trajectories. The y-axis indicates the position along the maze (Yellow: top
526 and Red: bottom), and the x-axis is the time. Arrowheads denote the timing of food
527 delivery, and horizontal rods indicate the stay time for each visit. Horizontal black lines
528 indicate the midpoint of the maze.

529

530 **Figure 2.** (a) Averaged running distance (y-axis) plotted against the post-hatch day; days
531 8–11 for the pre-reversal tests, and days 12–15 for the post-reversal tests. (b–e) Patch-use
532 ratio at the more profitable feeder in the pre-reversal test (y-axis) plotted against the post-
533 hatch day; during the 16-min feeding period (b), the ‘no food (before feeding)’ period (d),
534 and ‘no food (after feeding)’ period (e). In (c), the ratio on the first post-reversal day 12
535 was plotted against the 2-min bins. Dashed horizontal lines indicate 0.75 (3:1) and 0.25
536 (1:3). (f) Synchrony index between the paired chicks plotted against the day. Mean \pm SEM.

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