Title:

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

Running title:

Matching and social foraging

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Keywords

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Highlights

- Domestic chicks were tested in a task that mimicked patch-use behaviour.
- Pairing or perceived competition by mirror facilitated the running effort.
- Pairing, but not the mirror, led to precise matching of patch-use time.
- Patch-use time was shared by the pair and stored as a lasting preference.

Abstract

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

1. Introduction

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

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

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

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

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

2. Materials and methods

2.1. Subjects

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

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 × 88 × 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

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

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

2.5. Statistical Analysis of Data

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

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

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

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

3. Results

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

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

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

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

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

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

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

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

Chicks continued running for a few minutes more after the food delivery was turned off. The patch-use behaviour after feeding (Fig. 2e) followed that observed during feeding (Fig. 2b). On D8–11, we observed a significant effect of group ($F_{57}^{2} = 6.008$, $P < 0.005$) 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 Appendix Tables 7.1.1 and 7.1.2). On D12–15, a significant effect occurred in day ($F_{128.93}^{2.26} = 4{,}466$, $P < 0.02$), but not in group ($F_{57}^{2} = 0.2863$, $P > 0.05$) or interaction ($F_{128.93}^{4.52} = 1.784$, $P > 0.05$; see Appendix Table 7.2).

4. Discussion

4.1. Information sharing and matching behaviour in socially foraging chicks

The results of the present study stress the importance of social foraging for sharing of food patch information and precise matching. Individual melioration may yield under-matching, as shown by the single chicks. The competitive interaction (even without actual interference of food resource) could lead to a precise patch-use ratio, and hence to optimal allocation of time according to food availability. With precise matching, the risk of death by starvation would be efficiently minimized in nature. The present results correspond also 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 comprised18
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*

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

4.3. Social enhancement of the lasting patch memory

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

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

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

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

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

4.5. Do chicks play the producer-scrounger game?

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

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

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

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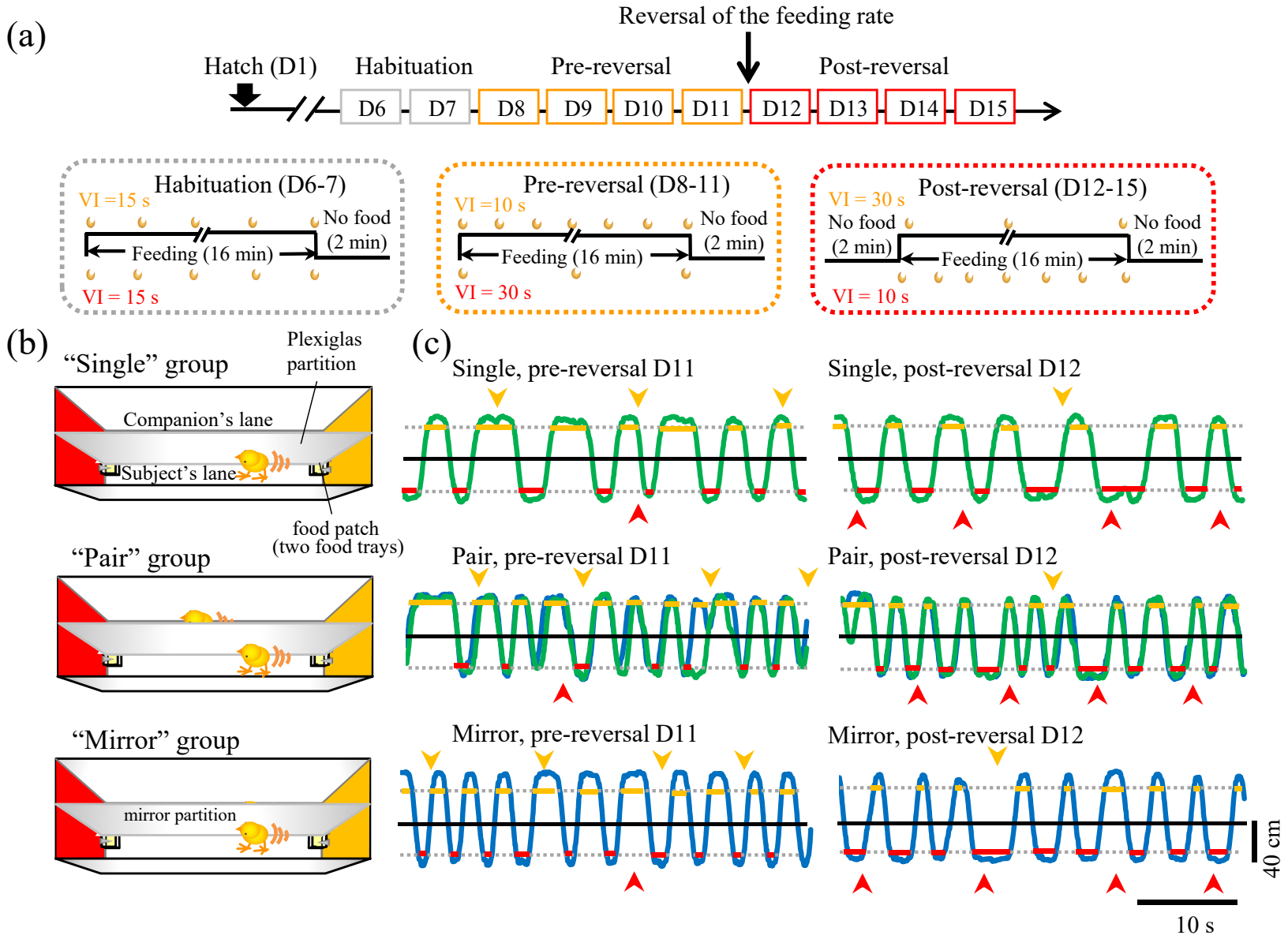
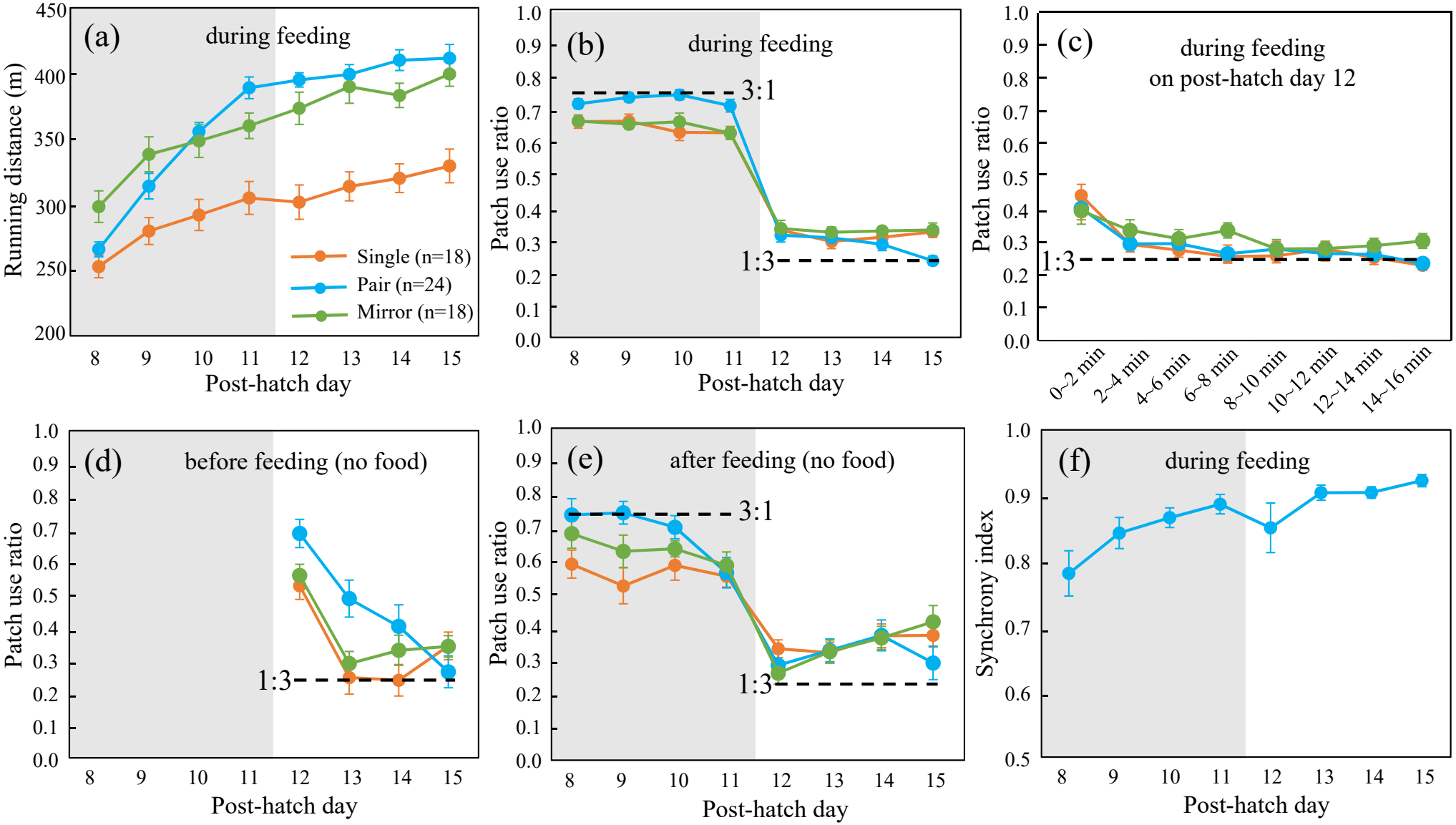
Figure legends

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

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


(a)
Reversal of the feeding rate
Hatch (D1)
Habituation
Pre-reversal
Post-reversal
D6
D7
D8
D9
D10
D11
D12
D13
D14
D15
Habituation (D6-7)
VI =15 s
No food
(2 min)
Feeding (16 min)
VI = 15 s
Pre-reversal (D8-11)
VI =10 s
No food
(2 min)
Feeding (16 min)
VI = 30 s
Post-reversal (D12-15)
VI = 30 s
No food
(2 min)
No food
(2 min)
Feeding (16 min)
VI = 10 s
(b)
"Single" group
Plexiglas
partition
Companion's lane
Subject's lane
food patch
(two food trays)
"Pair" group
"Mirror" group
mirror partition
(c)
Single, pre-reversal D11
Single, post-reversal D12
Pair, pre-reversal D11
Pair, post-reversal D12
Mirror, pre-reversal D11
Mirror, post-reversal D12
40 cm
10 s


(a)
during feeding
Running distance (m)
Post-hatch day
Single (n=18)
Pair (n=24)
Mirror (n=18)
(b)
during feeding
Patch use ratio
3:1
1:3
Post-hatch day
(c)
during feeding
on post-hatch day 12
Patch use ratio
1:3
0~2 min
2~4 min
4~6 min
6~8 min
8~10 min
10~12 min
12~14 min
14~16 min
(d)
before feeding (no food)
Patch use ratio
1:3
Post-hatch day
(e)
after feeding (no food)
Patch use ratio
3:1
1:3
Post-hatch day
(f)
during feeding
Synchrony index
Post-hatch day