



Title	Food variance and temporal discounting in socially foraging chicks
Author(s)	Mizuyama, Ryo; Uno, Leo; Matsushima, Toshiya
Citation	Animal behaviour, 120, 143-151 https://doi.org/10.1016/j.anbehav.2016.07.032
Issue Date	2016-10
Doc URL	http://hdl.handle.net/2115/71570
Rights	This manuscript version is made available under the CC-BY-NC-ND 4.0 license http://creativecommons.org/licenses/by-nc-nd/4.0/
Rights(URL)	https://creativecommons.org/licenses/by-nc-nd/4.0/
Type	article (author version)
File Information	Food variance and temporal discounting in socially foraging chicks.pdf



[Instructions for use](#)

Food variance and temporal discounting in socially foraging chicks

Ryo Mizuyama^{a†}, Leo Uno^{a†}, Toshiya Matsushima^{b*}

^a Graduate School of Life Science, Hokkaido University, Sapporo, Japan

^b Department of Biology, Faculty of Science, Hokkaido University, Sapporo, Japan

Received 11 March 2016

Initial acceptance 25 April 2016

Final acceptance 7 July 2016

MS number 16-00216

† Both authors contributed equally.

*Correspondence: T. Matsushima, Department of Biology, Faculty of Science,
Hokkaido University, N10-W8, Kita-ku, Sapporo, Hokkaido 060-0810, Japan.

E-mail address: matusima@sci.hokudai.ac.jp

Previous studies have shown that domestic chicks, *Gallus gallus domesticus*, trained in a competitive foraging condition would subsequently develop a high degree of impulsiveness in an intertemporal choice paradigm. Competition inevitably causes variance in the amount of food that the foragers gain. However, it is not known whether the food variance is causally linked with the impulsiveness. In experiment 1, we compared four groups of chicks trained in combinations of two social conditions (pseudocompetition or isolated) and two food conditions (variable or constant food).

The food variance was introduced by varying the number of grains in each trial according to a binomial distribution. The subject chick was separated from the

コメント [AT1]: Author: 'variant' means 'different'. I think you mean 'variable'.

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

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

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

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

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

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

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

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

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

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

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

constant amount).

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

METHODS

Subjects

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

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

<H2>Ethical note

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

<H2>Sequence and profitability of trials

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

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

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

<H2>Apparatus

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

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

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

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

<H2>Variable food and constant food conditions

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

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

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

<H2>Behavioural training and test procedures

<H3>Experiment 1

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

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

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

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

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

<H3>Experiment 2

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

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

<H2>Statistical analysis

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

<H1>RESULTS

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

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

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

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

<H1>DISCUSSION

<H2>Development of choice impulsiveness

コメント [AT2]: Author: the figure legend, not the text, should describe the figure.

コメント [AT3]:

コメント [AT4]: Author: keep subheadings to about 6-8 words to fit the column width of the journal.

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

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

been assumed to be a concave function of the amount ([Kacelnik & El Mouden, 2013](#)).

Further systematic investigations are thus necessary regarding the effects of variance on amount-based choices.

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

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

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

<H2>Collection risk hypothesis and risk-sensitive choices

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

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

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

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

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

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

<H2>Conditional and contextual modulation of foraging behaviours

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

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

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

Acknowledgments

We are grateful to colleagues in the subdepartment of Behavioural Neurobiology in the Biology Department, Hokkaido University, particularly for Makoto Mizunami, Dr Masayo Soma and Dr Kazuhiro Wada. Critical comments by Dr Taiki Takahashi (Department of Behavioural Sciences, Faculty of Letters, Hokkaido University) were particularly valuable. It is also acknowledged that the apparatuses used in this study were manufactured with the technical aids of the skilled engineer, Mr Yasutaka Sasaki in the machine laboratory of the Faculty of Science. We also express our sincere gratitude to the anonymous referees for their valuable and encouraging comments. T.M. conceived the study. T.M. and R.M. designed the experiments. T.M. and L.U. developed the experimental apparatus and computer programs. R.M. and L.U. conducted the experiments and analysed the data. T.M. wrote the manuscript. All authors have approved the manuscript for publication. T.M. was funded by the Japan Society for the Promotion of Science (JSPS, Kakenhi; Grant-in-Aid for Scientific Research (B) #25291071 and Grant-in-Aid for Challenging Exploratory Research #26650114). The authors declare no competing interests.

457

458 **REFERENCES**

- 459 Abeyesinghe, S.M., Nicol, C.J., Hartnell, S.J., & Wathes, C.M. (2005). Can domestic
460 fowl, *Gallus gallus domesticus*, show self-control? *Animal Behaviour*, 70, 1-11.
461 (doi: 10.1016/j.anbehav.2004.10.011)
- 462 Ainslie, G. (1974). Impulse control in pigeons. *Journal of Experimental Analysis of*
463 *Behavior*, 21, 485-489. (doi: 10.1901/jeab.1974.21-485)
- 464 Ainslie, G. (1975). Specious reward: a behavioral theory of impulsiveness and impulse
465 control. *Psychological Bulletin*, 82, 463-496. (doi: 10.1037/h0076860)
- 466 Amita, H., Kawamori, A., & Matsushima, T. (2010). Social influences of competition on
467 impulsive choices in domestic chicks. *Biological Letters*, 6, 183-186. (doi:
468 10.1098/rsbl.2009.0748)
- 469 Amita, H., & Matsushima, T. (2011). Instantaneous and cumulative influences of
470 competition on impulsive choices in domestic chicks. *Frontier in Neuroscience*, 5,
471 article 101. (doi: 10.3389/fnins.2011.00101)
- 472 Amita, H., & Matsushima, T. (2014). Competitor suppresses neuronal representation of
473 food reward in nucleus accumbens / medial striatum of domestic chicks.
474 *Behavioural Brain Research*, 268, 139-149. (doi: 10.1016/j.bbr.2014.04.004)
- 475 Aoki, N., Csillag, A., & Matsushima, T. (2006). Localized lesions of arcopallium
476 intermedium of the lateral forebrain caused a handling-cost aversion in the
477 domestic chick performing a binary choice task. *European Journal of*
478 *Neuroscience*, 24, 2314-2326. (doi: 10.1111/j.1460-9568.2006.05090.x)
- 479 Aoki, N., Suzuki, R., Izawa, E.-I., Csillag, A., & Matsushima, T. (2006). Localized
480 lesions of the ventral striatum, but not the arcopallium, enhanced impulsiveness in

the choice based on anticipated spatial proximity of food rewards. *Behavioural Brain Research*, 168: 1-12. (doi: 10.1016/j.bbr.2005.10.002)

Benson, K.E., & Stephens, D.W. (1996). Interruptions, tradeoffs, and temporal discounting. *American Zoologist*, 36, 506-517. (doi: 10.1093/icb/36.4.506)

Barnard, C.J., & Sibly, R.M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29, 543-550. (doi: 10.1016/S0003-3472(81)80117-0)

Charnov, E.L. (1976). Optimal foraging: attack strategy of a mantid. *The American Naturalist*, 110, 141-151. (doi: 10.1086/283054)

Giraldeau, L.-A., & Lefebvre, L. (1986). Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Animal Behaviour*, 34, 797-803. (doi: 10.1016/S0003-3472(86)80064-1)

Giraldeau, L.-A., Hogan, J.A., & Clinchy, M.J. (1990). The payoffs to producing and scrounging: What happens when patches are divisible? *Ethology*, 85, 132-146. (doi: 10.1111/j.1439-0310.1990.tb00393.x)

Giraldeau, L.-A., Soos, C., & Beauchamp, G. (1994). A test of the producer-scrounger foraging game in captive flocks of spice finches, *Lonchura punctulata*. *Behavioral Ecology and Sociobiology*, 34, 251-256. (doi: 10.1007/BF00183475)

Giraldeau, L.-A., & Caraco, T. (2000). *Social Foraging Theory*. Princeton, NJ: Princeton University Press.

Giraldeau, L.-A., & Dubois, F. (2008). Social foraging and the study of exploitative behaviour. *Advances in the Study of Behaviour*, 38, 59-104. (doi: 10.1016/S0065-3454(08)00002-8)

Grissom, R.J. (1994). Probability of the superior outcome of one treatment over another.

505 *Journal of Applied Psychology*, 79, 314-316. (doi: 10.1037//0021-9010.79.2.314)

506 Herrnstein, R.J. (1997). *The matching law*. Cambridge, MA: Harvard University Press.

507 Herrnstein, R.J., & Mazur, J.E. (1987). Making up of our minds: a new model of

508 economic behavior. *The Sciences*, Nov./Dec., 40-47.

509 Izawa, E.-I., Zachar, G., Yanagihara, S., & Matsushima, T. (2003). Localized lesion of

510 caudal part of lobus parolfactorius caused impulsive choice in the domestic chick:

511 evolutionarily conserved function of ventral striatum. *Journal of Neuroscience*, 23,

512 1984-1902.

513 Izawa, E.-I., Aoki, N., & Matsushima, T. (2005). Neural correlates of the proximity and

514 quantity of anticipated food rewards in the ventral striatum. *European Journal of*

515 *Neuroscience*, 22, 1502-1512. (doi: 10.1111/j.1460-9568.2005.04311.x)

516 Kalenscher, T., Windmann, S., Diekamp, B., Rose, J., Güntürkün, O., & Colombo, M.

517 (2005). Single units in the pigeon brain integrate reward amount and

518 time-to-reward in an impulsive choice task. *Current Biology*, 15, 594-602. (doi:

519 10.1016/j.cub.2005.02.052)

520 Kalenscher, T., & Pennartz, C.M.A. (2008). Is a bird in the hand worth two in the

521 future? The neuroeconomics of intertemporal decision-making. *Progress in*

522 *Neurobiology*, 84, 284-315. (doi:10.1016/j.pneurobio.2007.11.004)

523 Kacelnik A., & Bateson, M. (1996). Risky theories – the effects of variance on foraging

524 decisions. *American Zoologist*, 36, 402-434. (doi: 10.1093/icb/36.4.402)

525 Kacelnik, A., & El Mouden, C. (2013). Triumphs and trials of the risk paradigm.

526 *Animal Behaviour*, 86, 1117-1129. (doi: 10.1016/j.anbehav.2013.09.034)

527 Kawamori, A., & Matsushima, T. (2010). Subjective value of risky foods for individual

528 domestic chicks: a hierarchical Bayesian model. *Animal Cognition*, 13, 431-441.

(doi: 10.1007/s10071-009-0293-1)

Matsushima, T., Kawamori, A., & Bem-Sojka T. (2008). Neuro-economics in chicks: Foraging choices based on amount, delay and cost. *Brain Research Bulletin*, 76, 245-252. (doi: 10.1016/j.brainresbull.2008.02.007)

Mazur, J.E. (2002). *Learning and memory* (5th edition). Upper Saddle River, NJ: Prentice Hall.

McNamara, J.M., & Houston, A.I. (1987). A general framework for understanding the effects of variability and interruption on foraging behavior. *Acta Bioltheoretica*, 36, 3-22. (doi: 10.1007/BF00159228)

Mottley, K., & Giraldeau, L.-A. (2000). Experimental evidence that group foragers can converge on predicted producer-scrouter equilibria. *Animal Behaviour*, 60, 341-350. (doi: doi:10.1006/anbe.2000.1474)

Ogura, Y., Izumi, T., Yoshioka, M., & Matsushima, T. (2015). Dissociation of the neural substrates of foraging efforts and its social facilitation in the domestic chick. *Behavioural Brain Research*, 294, 162-176. (doi: 10.1016/j.bbr.2015.07.052)

Ogura, Y., & Matsushima, T. (2011). Social facilitation revisited: increase in foraging efforts and synchronization of running in domestic chicks. *Frontier in Neuroscience*, 5, 91. (doi: 10.3389/fnins.2011.00091)

Shafir, S., Reich, T., Tsur, E., Erev, I., & Lotem, A. (2008). Perceptual accuracy and conflicting effects of certainty on risk-taking behaviour. *Nature*, 453, 917-920. (doi: 10.1038/nature06841).

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B*, 367, 2767-2772. (doi: 10.1098/rstb.2012.0216)

553 Sozou, P.D. (1998). On hyperbolic discounting and uncertain hazard rates. *Proceedings*
554 *of the Royal Society London B*, 265, 2015-2020. (doi: 10.1098/rspb.1998.0534)
555 Stephens, D.W., Krebs, J.R. (1986). *Foraging theory*. Princeton, NJ: Princeton
556 University Press.
557 Takahashi, T., Ikeda, K., & Hasegawa, T. (2007). A hyperbolic decay of subjective
558 probability of obtaining delayed rewards. *Behavioral and Brain Functions*, 3, 52.
559 (doi: 10.1186/1744-9081-3-52)

560

561 Appendix

562

コメント [AT5]: Fig. A1

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

	Cue period	Postchoice	Mechanical	Handling	Intertrial	Amount	Profitability	Profitability
	(A)	delay (B)	lag (C)	time (D)	interval (E)	(X)	X/(B+C+D)	X/(A+B+C+D+E)
	(s)	(s)	(s)	(s)	(s)	(mg)	(mg/s)	(mg/s)
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

FIGURE LEGENDS

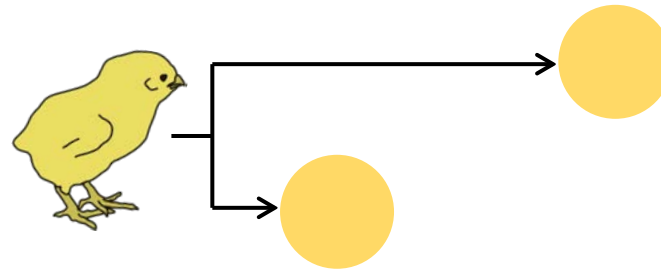
Figure 1. Intertemporal choice paradigm in the context of social foraging. See text for explanations.

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

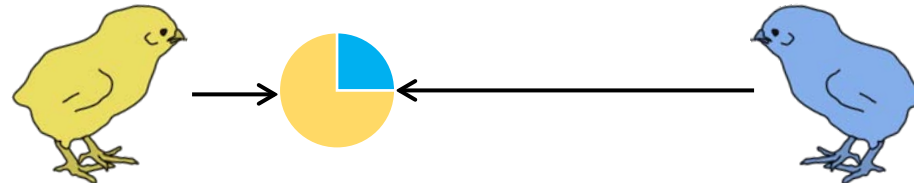
Figure 3. Results of (a, b) experiment 1 and (c) experiment 2. We compared the number of LL choices between the different groups. Circles denote individuals, and horizontal bars represent the median of the group. The number of individuals in each group is indicated by *N*. Different letters above each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

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

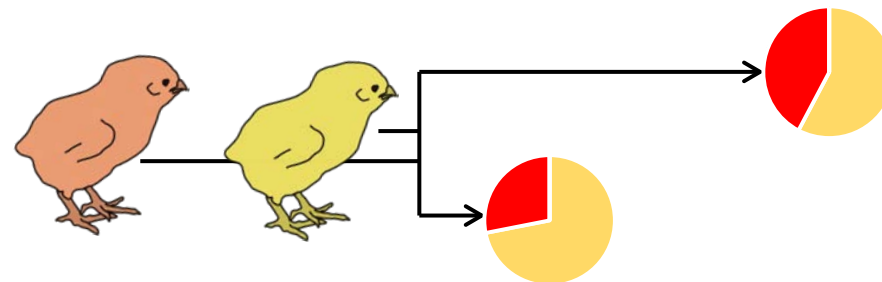
(a) One forager expects the same amount irrespective of the distance.



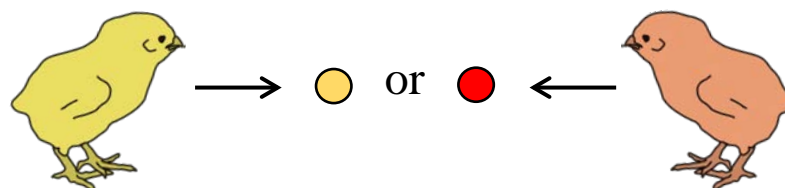
(b) Competing foragers share food depending on the distance.



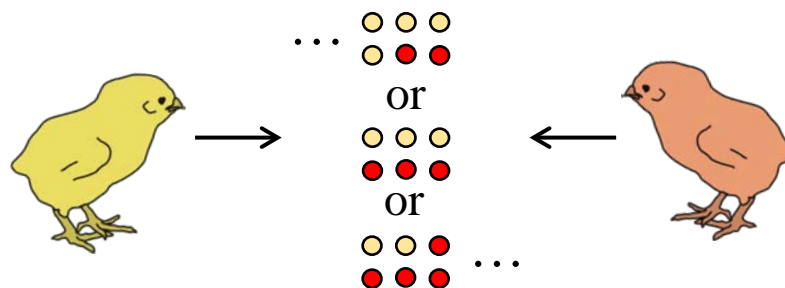
(c) Producer gains more from the proximate food than the delayed alternative.



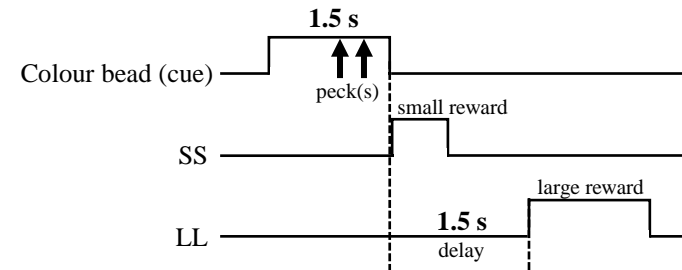
(d) Unshareable food item yields a high degree of variance.



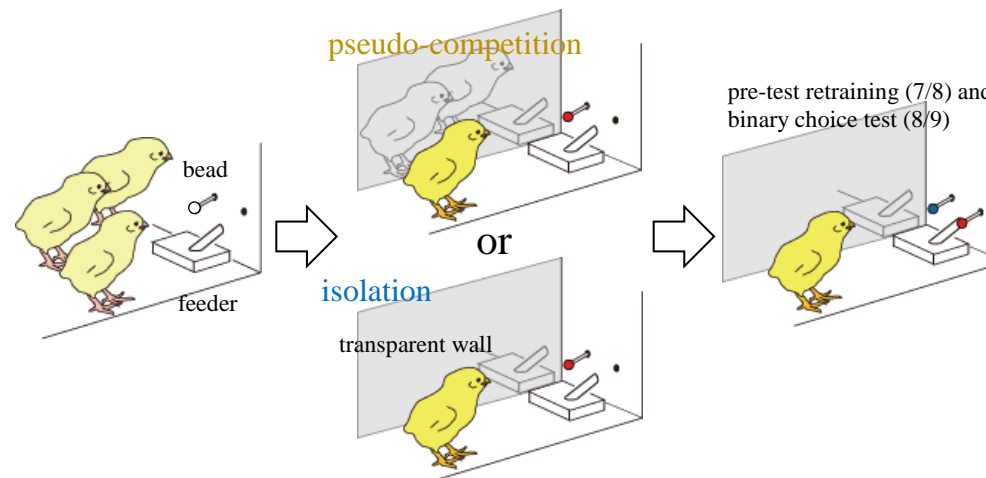
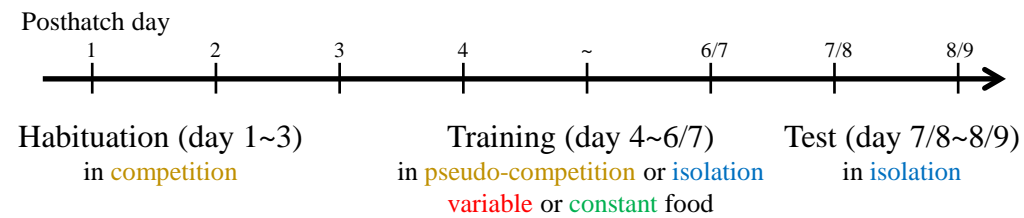
(e) Patch of shareable food items yields a low degree of variance.



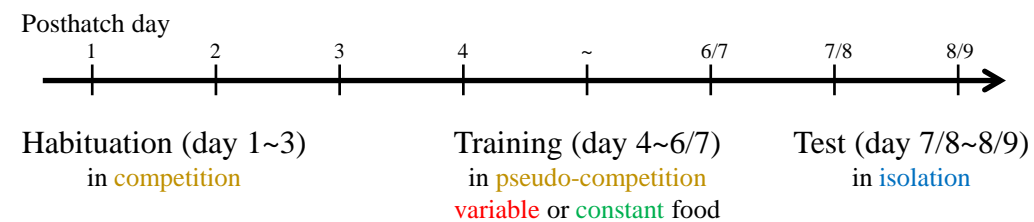
(a)



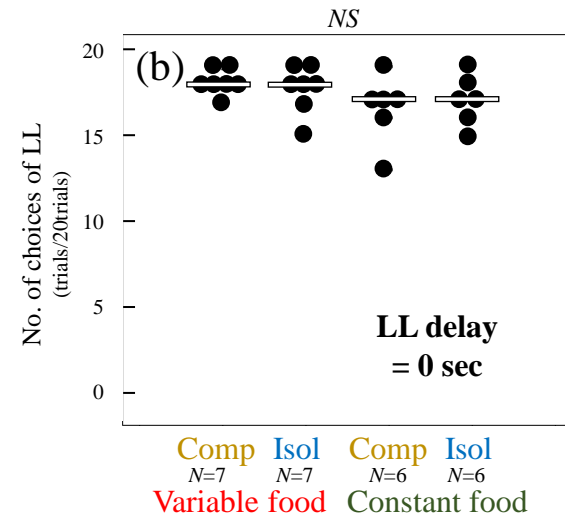
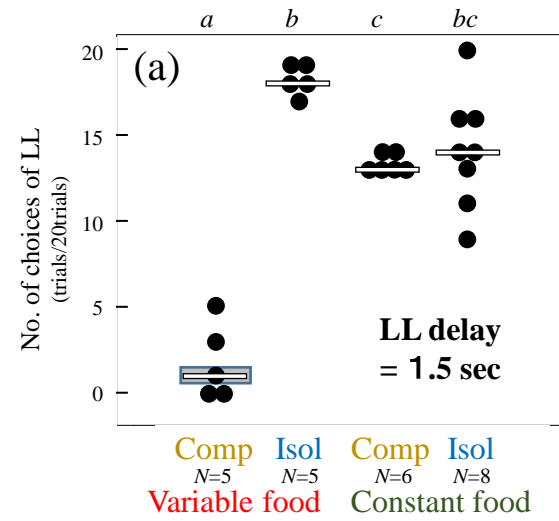
(b) Experiment 1



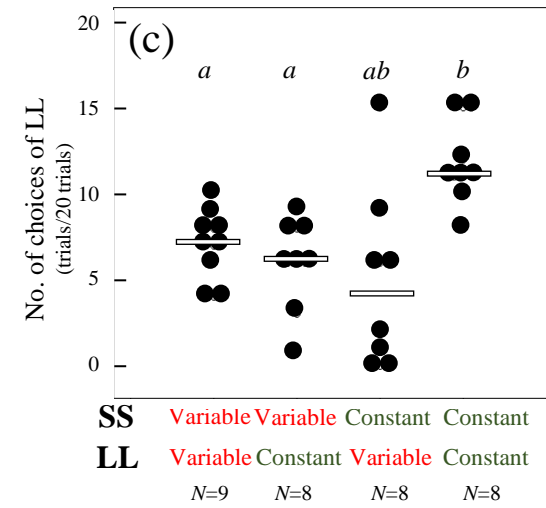
(c) Experiment 2



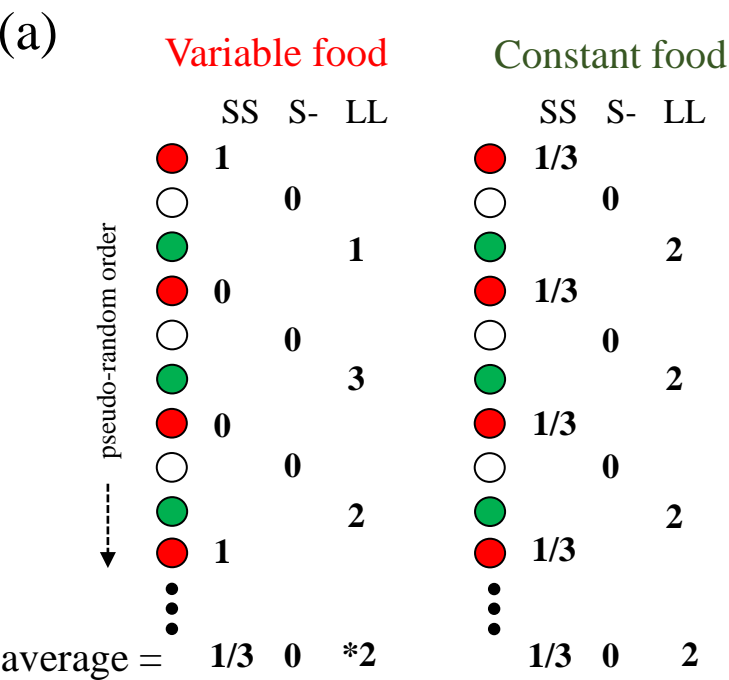
Experiment 1



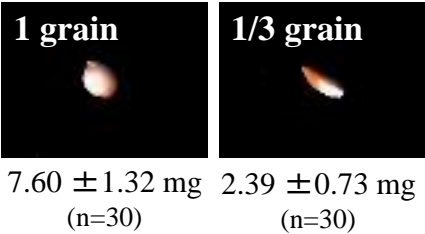
Experiment 2



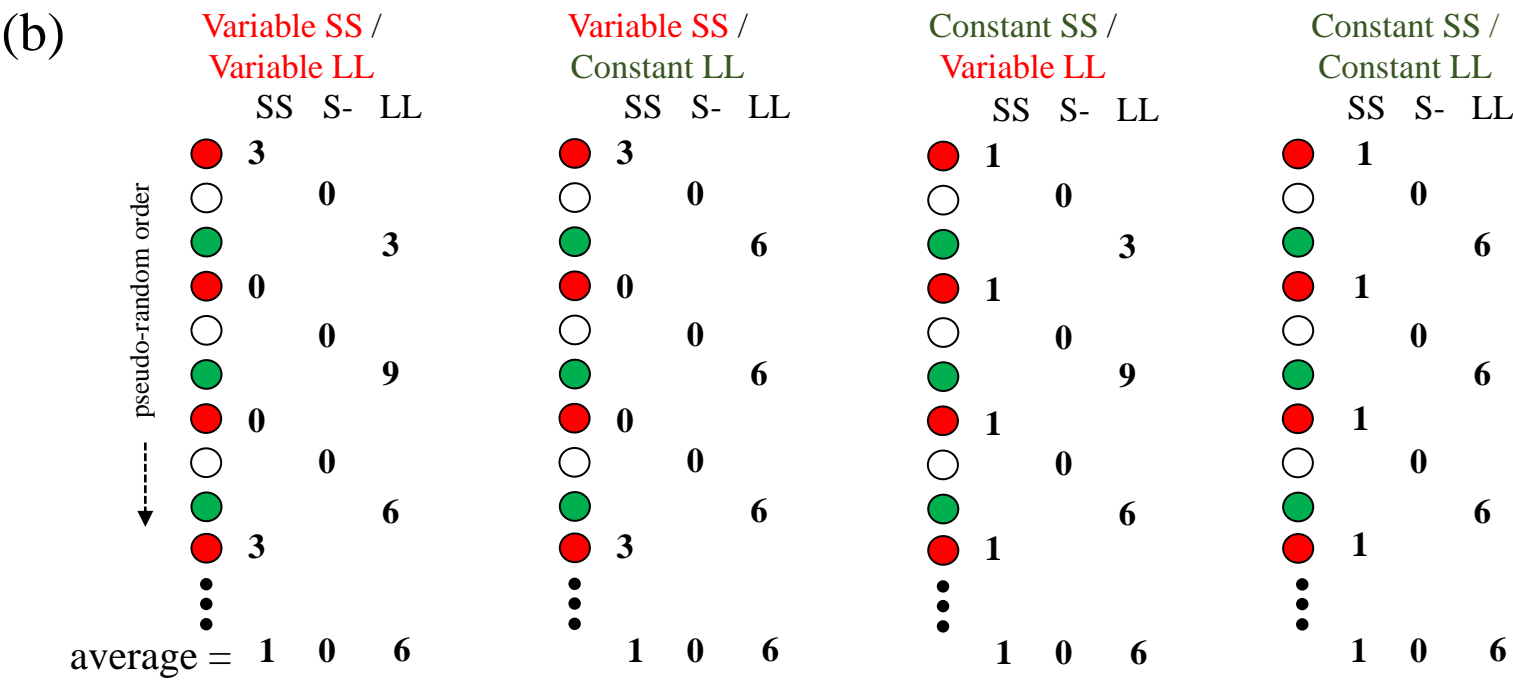
Experiment 1



	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



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