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Title

**Social influences of competition on impulsive choices in domestic chicks**

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Running titles

**Influences of competition on impulsiveness**

Summary

Domestic chicks were trained to peck at colored beads to gain delayed food reward and were tested in binary choices between a large/long-delay option (***LL***, 6 grains after a delay of 0 - 3 sec) and a small/short-delay alternative (***SS***, 1 grain after a delay of 0 sec). In experiment 1, chicks that were trained in groups of three individuals for 3 days showed fewer choices of ***LL*** in the test than did those trained in isolation, suggesting that competition caused impulsive choice. Collection risk did not explain the social influences since the longer delay was not accompanied by a higher probability of interruption. In experiment 2, in order to identify the critical factor, we tested the effects of perceived competition (coincident feeding without interruption) and scrounging (gaining food without pecking bead) separately. Food amount varied according to a binominal distribution around the expected mean (2 grains for ***LL*** and 1/3 grain for ***SS***) and delays were fixed at 1.5 sec (***LL***) and 0 sec (***SS***). The perceived competition primarily contributed to the facilitated impulsive choice, whereas the scrounging had a secondary effect. Coincident foraging during competition is thought to play a critical role.

**Keywords:** temporal discounting, choice, risk, social foraging

## INTRODUCTION

Animals often choose an immediate small reward even though a delayed alternative option yields a larger gain (Kalenscher & Pennarts 2008, Matsushima *et al.* 2008). Since this behavioral trait clearly characterizes impulsiveness measured in terms of a high temporal discounting, relevant neural and developmental factors have been intensively studied in animals and humans (Cardinal 2006, Tripp & Wickens 2008). It has been suggested that the reward is discounted because when there is a delay there is a higher risk of being interrupted and consequently losing the reward ("collection risk" hypothesis; McNamara &Houston 1987, Benson & Stephens 1996, Sozou 1998). Interception of food items by competitive foragers is thought to be a major cause of the interruption. Although this argument is intuitively simple and plausible, the link between competition and impulsiveness has not been empirically supported. A recent behavioral study in jays (Henly *et al.* 2008) failed to support the collection risk hypothesis, but the interruption was an experimental incorporated termination of the task and was not caused by competitive foragers. It is, however, not so easy to study the effects of competition because competitive foraging can give rise to a complex set of factors, including (1) *risk* due to the increased variability of food amount that each individual actually gains and (2) *noise* (or decreased perceptual accuracy) due to the increased variability. For example, in competition, the amount of gained food would inevitably vary in every occasion. Foragers may thus under-value the larger alternative when it is delayed because of the increased *risk*. Otherwise, a delay causes an increase in *noise* and the larger alternative is wrongly judged as being smaller. Alternatively, competition could affect choices through (3) increased chance to gain food without attentive foraging (*scrounging*) and (4) presence of coincidently foraging individuals

(*perceived competition*). Here we present behavioral evidence that competitive foraging facilitates impulsive choice through *perceived competition*.

## 1. MATERIAL AND METHODS

### (a) Animals

The present study is based on data obtained from 82 successfully trained male domestic chicks (*Gallus domesticus*, white leghorns). New hatchlings (post-hatch day 1) purchased from a local supplier were housed in transparent plastic cages (15 x 28 x 12 cm) that were thermo-controlled at *ca.* 30°C under illumination (12L: 12D, light period starting at 08:00). On day 2 to 4, each chick was fed with 1 to 3 g of food per day (mixture of millet and chick mash food). On day 5 and afterwards, each chick gained 0.5-1.0 g of millet during experiments and was then fed with 4 g of ration once in the evening. Water was freely available. Chicks grew steadily, maintaining *ca*. 80% of the freely feeding body weight. Body weight did not significantly differ between competitive and non-competitive groups. After the end of experiments, chicks were sacrificed by carbon dioxide. Experiments were conducted under guidelines and approval of the Committee of Animal Experiments of Hokkaido University. The guidelines are based on the national regulations for animal welfare in Japan (Law for the Humane Treatment and Management of Animals; after a partial amendment No.68, 2005).

### (b) Behavioral procedures

**Experiment 1** A blue bead was associated with a large/long-delay option (***LL***, 6 grains delivered after a delay of 0.0, 1.5 or 3.0 sec) and a red bead was associated with a small/short-delay alternative(***SS***, 1 grain after a delay of 0.0 sec). A white bead was

used as a non-rewarding bead (***S–***). For details see the supplementary materials. Chicks were trained for 3 days from post-hatch day 5 to 7 either in isolation (no competition) or in a group of three individuals (competition) (Fig. 1A). On day 8, chicks in both groups were trained in isolation. Chicks were trained in one block of training per day, consisting of 72 pseudo-randomly arranged trials with inter-trial intervals of 15-20 sec: 18 trials with ***LL***/***S–***, 18 trials with ***SS***/***S–***and 36 trials with ***S–*** /***S–***. Nine chicks were used for each of the six conditions, and we discarded the individuals if they failed to be trained to peck the rewarding beads. On day 9, in order to examine lasting effects of competition on choices, chicks were individually tested in 20 trials with ***LL*** and ***SS***. Test trials were randomly intermixed with 10 ***LL***/***LL*** and 10 ***SS***/***SS*** trials and 40 ***S–*** /***S–*** trials. Side of presentation was counter-balanced among trials in each block. Most-likely-fitting curves were obtained by assuming a logistic model and a linear predictor. To statistically access the difference among groups, a generalized linear mixed model (GLMM; Bolker *et al.* 2009) with AICs (Akaike's Information Criteria) was adopted. See supplementary material for details.

**Experiment 2** Chicks were trained and tested according to the same timetable and color assignment as in experiment 1. To separate the factors (*risk*, *noise*, *scrounging* and *perceived competition*), we modified the experimental apparatus as shown in Fig. 2A. We assumed that each chick has an equal chance to get each grain in the competition condition, and set the amount to vary at every trial according to a binominal distribution in all of the four groups ($n$=12 each) (Fig. 2B). As in experiment 1, we discarded chicks that were not successfully trained. For ***SS***, 1 grain was supplied in 18 trials and no food was supplied in the remaining 36 trials, so that the mean was 1/3 grain in 54 trials. These 54 trials were randomly assigned to 3 blocks of

training on post-hatch day 5-7. For ***LL***, similarly, 0-6 grains were supplied and the mean was set at 2 grains in 54 trials. On day 8 (training in isolation) and day 9 (test), 1 grain and 6 grains were given for ***SS*** and ***LL***, respectively.

To determine the contributions of two other factors (*perceived competition* (*pc*) and *scrounging* (*sc*)), we compared choices of four groups arranged in a 2x2 factorial design (Fig. 2B). In the two groups (*none* and *pc*), chicks were trained without (*none*) or with (*pc*) companion chicks placed in the left partition. The pair of companion chicks was supplied with 3 grains of millet at the time when the food was given to the subject. In the other two groups (*sc* and *pc*+*sc*), besides the training block given to *none* and *pc*, two additional blocks of scrounging as a companion chick was given.

## 2. RESULTS

Competition facilitated impulsive choices (experiment 1, Fig. 1B). Contextual facilitation was disregarded since the chicks were tested singly. With a delay of 0 sec, chicks in both groups similarly chose ***LL*** over ***SS***, suggesting that they made choices based on associated food amount. With a delay of 3 sec, chicks showed proximity-based choices of ***SS*** over ***LL*** in both groups. With a delay of 1.5 sec, on the other hand, the no-competition chicks tended to choose ***LL*** more frequently than the competition chicks, suggesting that impulsiveness was selectively enhanced. AICs were calculated for models including competition (156.2), delay to ***LL*** (125.9), and an additive model containing both variables (113.3), indicating that the competitive foraging modified choices.

Perceived competition caused the facilitation as the primary factor (experiment 2, Fig. 2B). The factors (*risk* and *noise*) due to variable amount *per se* failed to decrease

the number of choices of ***LL*** (*none* group) compared with the data shown in Fig. 1A at a delay of 1.5 sec;;; needs statistical tests. Perceived competition (*pc*), on the other hand, caused much fewer choices of ***LL*** in both groups (*pc* and *pc*+*sc*). Scrounging without perceived competition (*sc*) also caused impulsiveness. AICs calculated for the two factors (*pc* and *fr*) were 117.2 (null model), 99.8 (*pc* model), 117.1 (*fr* model) and 96.8 (*pc* and *fr* model), indicating that the perceived competition contributed to facilitation as the primary factor. On the other hand, the free riding contributed to facilitation to a lesser degree. The effects of free riding might have been caused by the perceived competition that the chicks experienced in the free-riding trials.

## 3. DISCUSSION

The "collection risk" hypothesis does not explain the observed influences of competition on impulsive choices, because the interruption occurred after the end of the delay period in the present experiments. The results of experiment 1 therefore suggest that some other factor is involved in the choices based on food proximity. On the other hand, the associated food amount was not affected, since the choices of ***LL*** were similar in both of the competition and no competition groups for the delay to ***LL*** = 0 sec (Fig. 1B).

The variability in food amount (therefore *risk* and *noise*) *per se* failed to facilitate impulsiveness (Fig. 2C). Actually, in the training, the *none* group of chicks often failed to reliably peck at the bead associated with ***SS***, suggesting that the low and variable profitability of the ***SS*** food led to a low subjective value. This is in agreement with our recent finding that chicks are risk-averse to variable amount, particularly when the risky option includes non-rewarding trials (Kawamori and Matsushima submitted).

Alternatively, the impulsiveness could be due to a higher level of perceptual *noise*, similar to that reported in risk-taking behaviors (Shafir *et al.* 2008). However, this hypothesis does not explain the observed difference between *none* and *pc* in experiment 2.

Of possible factors involved, we examined the effects of *free riding* and *perceived competition* separately. In the *pc* and *pc+fr* groups, on the other hand, chicks were successfully trained to peck at the ***SS*** bead, suggesting that the *perceived competition* increased the subjective value of ***SS***, the immediate food. In this study, we did not know whether the subjective value of ***LL*** was decreased. Other behavioral measures linked to the rate of temporal discounting must be searched for.

This study provides, to the best of our knowledge, the first empirical evidence of the lasting effect of social foraging (for reviews see Galef & Giraldeau 2001) on economical decision making (Kalenscher & Pennarts 2008). In the context of social learning, it is often argued that *what* and *where* to forage (and even *how* to forage) are transmitted in terms of response facilitation and local enhancement (Hoppitt & Laland 2008). In this study, however, we did not dissociate these possible processes for facilitation. Does the perceived competition facilitate impulsiveness even when the two feeders are placed at a distance? What happens if free food is given to the competitors not coincidentally with the subject? Cognitive processing underlying the effects of perceived competition on foraging decisions remain to be specified.

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***Figure legends***

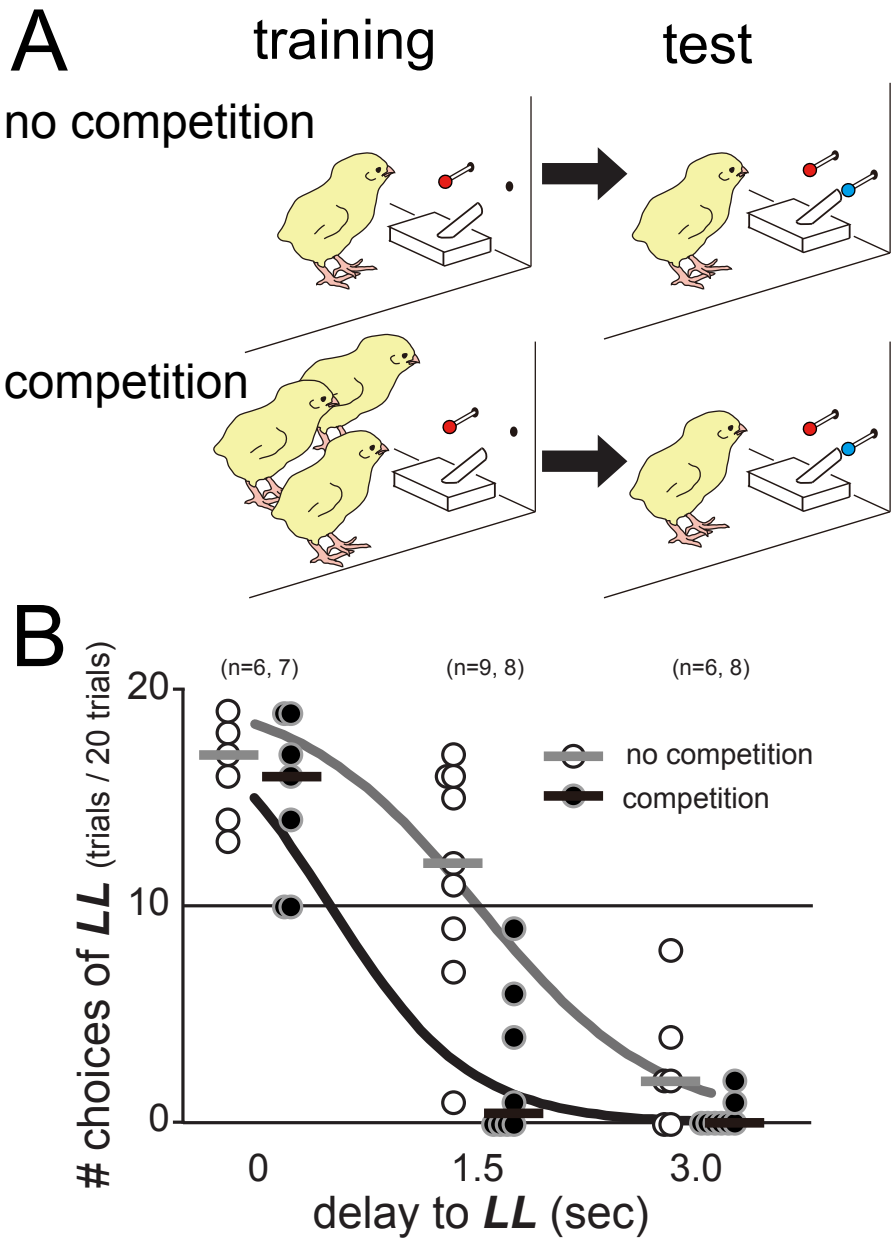
Figure 1. When trained competitively, chicks showed fewer choices of large/long delay reward (***LL***) over small/short-delay reward (***SS***).

(A) Experimental configuration of two groups of chicks, no competition and competition. (B) Number of choices of ***LL*** was plotted against delay of ***LL*** (0, 1.5 or 3 sec) in six groups of chicks. Open and filled circles denote no competition and competition individuals, and short horizontal bars indicate the median in each group. Most-likely-fitting curves are shown separately for each group. See text for AICs.

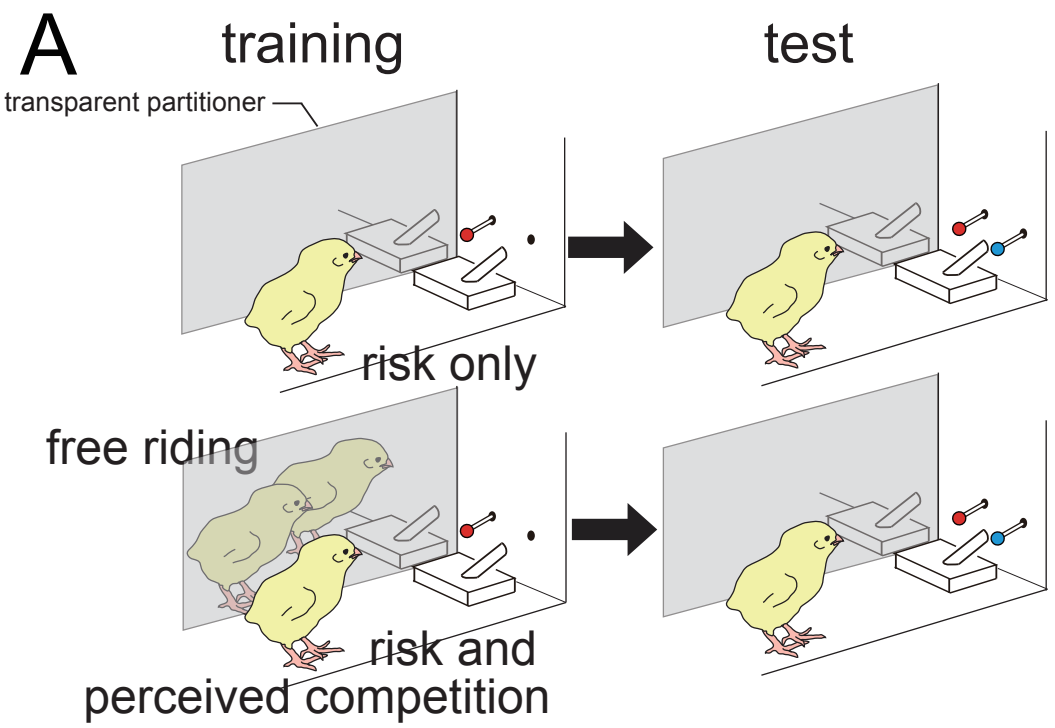
Figure 2. Perceived competition facilitated impulsiveness without actual interruption.

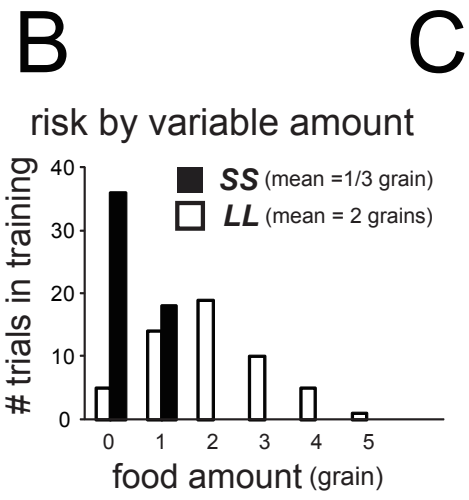
(A) Experimental configuration of four groups of chicks, *none* (risk only), *pc* (risk and perceived competition, *pc*), *sc* (*risk* and two additional blocks of scrounging, *sc*) and *pc*+*sc* (*risk* combined with *pc* plus two blocks of *sc*). (B) Risk was experimentally introduced in terms of variable amount of food in each trial. Three training blocks consisted of a total of 54 ***SS*** trials and 54 ***LL*** trials, in which the rewarding bead was simultaneously presented with an ***S–*** bead. Food amount was varied according to

binominal distributions that were arranged to yield mean = 1/3 grain (***SS***) and 2 grains (***LL***), respectively. (C) Numbers of choices of ***LL*** were compared among four groups of chicks. Single symbols denote individual chicks, and horizontal bars indicate the median. See text for AICs.

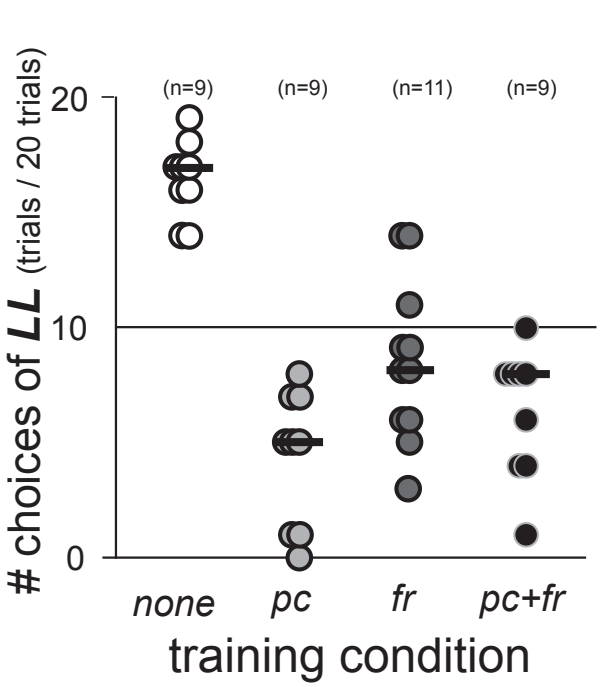

A
training
test
no competition
competition
B
(n=6, 7)
(n=9, 8)
(n=6, 8)
20
10
0
# choices of LL (trials / 20 trials)
no competition
competition
0
1.5
3.0
delay to LL (sec)

Amita_fig_1




*none*: risk only > test
*pc* : risk & pc > test
*fr* : risk only + fr + fr > test
*pc+fr*: risk & pc + fr + fr > test

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**Supplementary materials on statistical analysis using GLMM**

In both Experiments 1 and 2, we focused on the number of choices of ***LL*** as the response variable. Since chicks were tested in binary choices, we assumed that the choice ratio followed a binominal distribution with a choice probability = $Q(X)$ ($\in [0, 1]$), which was approximated by a logistic function as

$$Q(X) = 1 / (1 + \exp(-X)) \qquad (1)$$

in which a linear predictor $X$ was given as a weighed sum of the following explanatory variables.

$$\text{Experiment 1:} \quad X = \beta_1 + \beta_2 * delay + \beta_3 * comp + r_i \qquad (2)$$

$$\text{Experiment 2:} \quad X = \beta'_1 + \beta'_2 * pc + \beta'_3 * fr + r'_i \qquad (3)$$

$\beta_1$ and $\beta'_1$ denote bias at the population level.

*delay* (0.0, 1.5 and 3.0) denotes the delay to ***LL***. $\beta_2$ indicates how the delay contributes to the choices.

*comp* (integer 0 or 1) denotes the competition. In one statistic model, different *comp* values were assigned to the groups: *comp* = 0 for the no competition group and *comp* =1 for the competition group. In an alternative model, *comp* was disregarded and assigned to 0 in both groups. $\beta_3$ indicates how the competition contributes to the choices.

*pc* (integer 0 or 1) denotes the *perceived competition*. $\beta'_2$ indicate how the *perceived competition* contributes to the choices.

*fr* (integer 0 or 1) denotes *free riding*. $\beta'_3$ indicate how the *free riding* contributes to the choices.

Four models were compared: null model (*pc* = 0 and *fr* =0), pc model (*pc* =1 and *fr* =0), fr model (*pc* = 0 and *fr* =1) and pc & fr model (*pc* =1 and *fr* =1).

$r_i$ and $r'_i$ denote the random effect for each individual ($i$), or noise that was not experimentally controlled.

The most likely values of $\beta_1$, $\beta_2$, $\beta_3$ and $r_i$ (or, $\beta'_1$, $\beta'_2$, $\beta'_3$ and $r'_i$) were computed on the basis of the choice data by using R (version 2.6.0) on a PC (McCarthy 2007). AICs were given as a sum of the deviance and the number of parameters, and they were compared among models.

**Supplementary materials on the apparatus**

We used an operant chamber for recording behaviors in the inter-temporal choice paradigm. A thermo-controlled box (21x 19 x 25 cm, maintained at *ca.* 27-30°C and illuminated by light bulbs) was used (see Aoki *et al.* 2006). One of the surrounding walls was equipped with a pair of holes placed side by side (separated by 3 cm and placed 4 cm above floor level), through which one or two colored beads (white, green, blue or red) were presented for 1 sec (Fig. 1A). Upon pecking at a bead associated with reward, millet food was supplied to the central food tray on the floor (placed between the two holes) after a programmed delay. Colored beads were assigned to reward options: small/short-delay food (***SS*** delivered after a constant lag $\Delta = 0.2$ sec) and large/long-delay food (***LL*** delivered after *delay* + $\Delta$). We observed the behaviors through a video camera placed above the feeder without being seen by the subject chick. In experiment 2, the chamber was divided into two partitions by a transparent Plexiglas. A subject was trained and tested in the right partition, and a pair of free-riding companion chicks gained food in the left partition. Two partitions were equipped with a pair of feeders separated by 3 cm. Through the partitioner, the subject chick and the companion chicks could see each other. The beads and the food trays were also visible.

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