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Author(s)	Kawamori, Ai; Matsushima, Toshiya
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Title:

Subjective value of risky foods for individual domestic chicks: a hierarchical Bayesian model

Authors:

Ai Kawamori, Toshiya Matsushima^{CA}

Affiliation

Laboratory of Animal Behavior and Intelligence, Department of Biology

Faculty of Science, Hokkaido University

Kita 10, Nishi 8, Sapporo 060-0810, Japan

CA: e-mail: matusima@sci.hokudai.ac.jp

Abstract

For animals to decide which prey to attack, the gain and delay of the food item must be integrated in a value function. However, the subjective value is not obtained by expected profitability when it is accompanied by risk. To estimate the subjective value, we examined choices in a cross-shaped maze with two colored feeders in domestic chicks. When tested by a reversal in food amount or delay, chicks changed choices similarly in both conditions (experiment 1). We therefore examined risk sensitivity for amount and delay (experiment 2) by supplying one feeder with food of fixed profitability and the alternative feeder with high- or low-profitability food at equal probability. Profitability varied in amount (groups 1 and 2 at high and low variance) or in delay (group 3). To find the equilibrium, the amount (groups 1 and 2) or delay (group 3) of the food in the fixed feeder was adjusted in a total of 18 blocks. The Markov chain Monte Carlo method was applied to a hierarchical Bayesian model to estimate the subjective value. Chicks undervalued the variable feeder in group 1 and were indifferent in group 2, but overvalued the variable feeder in group 3 at a population level. Re-examination without the titration procedure (experiment 3) suggested that the subjective value was not absolute for each option. When the delay was varied, the variable option was often given a paradoxically high value depending on fixed alternative. Therefore, the basic assumption of the uniquely determined value function might be questioned.

Introduction

Because a food resource varies in nature, it is often impossible for foraging animals to know exactly *how much* and *when* (or *how proximately*) they would actually gain (Stephens 1981; Stephens and Krebs 1986). If repeatedly exposed to such a varying resource, foragers may learn the probability of occurrence of food, but the actual gain can be only determined stochastically. In studies on foraging behaviors, the stochastic nature of food due to resource variability is referred to as risk (see Kacelnik and Bateson 1996 for comprehensive review). Theoretical and empirical studies lead us to address the following two issues: (1) how are gain and time integrated in the value function (or utility function) for foraging decisions; and (2) whether and how the probability of occurrence of food is further integrated.

Empirical data are in favor of the idea that we should adopt a short-sighted value function (or utility function) such as the expectation of ratio $= G/T$, where G denotes the energy gain and T is the time spent acquiring the food (Bateson and Kacelnik 1996 in starlings; Stephens and Anderson 2001 in blue jays tested in concurrent choices). The results of studies on pigeons are in agreement with a value function defined as a hyperbolic function $f = A/(1 + kD)$ in which A denotes the amount of food, D is the delay until the food is reached, and k represents the discounting coefficient (Mazur 1984; see also Kalenscher and Pennartz 2008 for a recent comprehensive review on intertemporal decision-making). Similar results were obtained in chicks, and profitability ($f = e/h$; e denoting energy gain and h denoting total handling time) was assumed as the value function (Aoki *et al.* 2006; Matsushima 2008 for a review). Note that the handling time (h) included delay (D) and the time for consuming food, but the inter-trial interval was disregarded. In these studies, because the value function f is

convex to time t (as well as D), Jensen's inequality leads to risk proneness in variable delay, i.e.,

$$f((t_1+t_2)/2) < \{f(t_1)+f(t_2)\}/2 \quad (1)$$

for fixed mean $((t_1+t_2)/2)$ and the variable delay (t_1 or t_2 at equal probability).

If the value function f is linear to the amount (A or e), foragers must be risk-neutral for variability in amount. However, animals are often risk-averse for amount. In choices between a variable/large food and a fixed/small alternative, the fixed option is more frequently chosen, even when the expected amount is the same in these two options (Stephens and Paton 1986, Waser and McRobert 1998 in hummingbirds; Barnard and Brown 1985 in shrews; Reboresda and Kacelnik 1991 in starling). Therefore, the value function should be concave to the amount (A), i.e.,

$$f((A_1+A_2)/2) > \{f(A_1)+f(A_2)\}/2 \quad (2)$$

for a fixed mean $((A_1+A_2)/2)$ and the variable amount (A_1 or A_2 at equal probability).

Normative theory of risk-sensitive foraging (Stephens 1981) stresses the concavity of f to amount because a high possibility of starvation will disproportionately devalue food in small amounts. Examination of optimal choices with varying delay predicts a much more complex picture (McNamara and Houston 1987), and both risk aversion and proneness may arise as adoptive traits. Alternatively, risk sensitivity may be due to the stochastic nature of memory. By adopting a theoretical framework known as the scalar expectancy theory (SET, originally proposed by Gibbon 1977), Kacelnik and colleagues argued that delay and amount could be represented separately (Bateson and Kacelnik 1995, 1996; Kacelnik and Abreu 1998; Kacelnik and Brunner 2002), an idea that is not contradictory to the distinct neuronal representations of amount and delay in the chick striatum (Izawa *et al.* 2005). According to the SET-based hypothesis, both factors

(amount and delay) are sampled with the Gaussian noise that follows Weber's law, so that the variable factor will inevitably be undervalued at recall. An undervalued amount will lead to risk aversion, whereas an undervalued delay (or overvalued proximity) will lead to risk-prone choices (Reboreda and Kacelnik 1991).

In this study, we estimated the subjective value of a variable food option (variable in amount or delay) in individual chicks. We adopted profitability for the value function, so that effects of convexity to delay (formula (1)) were minimized. Consumption time was fixed at 4 s and handling time (h) was determined by delay without the confounding effects of amount. The behavioral titration procedure (Bateson and Kacelnik 1996) was adopted, and we examined whether two groups with different initial conditions converged. Data were analyzed by a hierarchical Bayesian model in order to directly estimate individual risk sensitivity in the form of probability distribution.

Methods

Animals

A total of 84 male domestic chicks (*Gallus domesticus*, White Leghorn strain) were used and 6-10 chicks were allocated to each group. Groups of 3 chicks were communally housed in transparent plastic cages (25 x 15 x 16 cm), which were thermo-controlled (30 °C) and illuminated by white light bulbs (12 h L: 12 h D, light period starting at 08:00). Hatchlings were obtained from a local commercial supplier (Hokuren poultry farm, Iwamizawa) on post-hatch day 1. On days 2 and 3, chicks were fed once a day with mash food (1.0 g and 2.0 g per chick, respectively). From day 4 until the end of experiments, chicks were fed with the same mash food (2.7 g per

chick) once a day after the behavioral tests were completed. Water was freely available. After the experiments, chicks were sacrificed by inhaling carbon dioxide. In order to avoid effects of preceding experiences, chicks were examined once and not reused in subsequent experiments.

In order to monitor the effects of restricted food supply, we measured the body weight every day before the main ration of the day (mash food) was supplied. Body weight steadily increased and reached 40.9 ± 0.43 g (mean $\pm$ s.e.m., $n = 84$) on day 10, which was *ca.* 70% of the body weight of freely fed chicks (58.8 ± 1.93 g; $n = 6$). In comparable studies, adult pigeons were generally maintained at 75-80% of free-feeding weights for a long period of time (see review by Kacelnik and Bateson 1996). However, at a considerable level of food restriction, chicks did not show any behavioral signs indicative of negative energetic budget, and behavioral abnormalities such as stereotyped pecking at non-food objects were not observed (Savory and Maros 1993). Therefore, we assumed that the animals were in a fair health, despite the energy budget being far from ideal.

Apparatus

A cross-shaped maze was equipped with a pair of start boxes (21-cm long, 12-cm wide) and another pair of feeder arms (Fig. 1A). Each of the feeder arms was composed of a runway (20-cm long, 12-cm wide), a mechanical sensor (a 13-cm long floor plate with a micro-switch), a food tray (a circular plastic dish, 6 cm in diameter), and a computer-controlled feeding machine. The sensor detected the point of time at which the chick reached the feeder and then triggered the computer (RCX, Lego Co.) to start serving millet food after a pre-programmed delay (ranging from 0 to 8 s). Grains of millet food were served one by one at a pre-programmed interval and the total

consumption time was adjusted to 4 s irrespective of the amount (Fig. 1B). The food trays and terminal walls were painted red or blue so that chicks associated food reward with color.

Figure 1 around here

Profitability

Profitability was calculated for each visit to a feeder as the number of millet grains per total handling time or sum of the delay and consumption time fixed at 4 s. A larger amount yields a proportionately high profitability, whereas a shorter delay yields a hyperbolically high profitability. Fig. 1C shows the scale by which a food reward of certain amount and delay is valued by profitability. Five grains of food delivered after a 2-s delay had a profitability of $5/(2 + 4) = 0.83$ grains/s. For a delay fixed at 2 s, profitability of 1-9 food grains was 0.17-1.50 grains/s. Similarly, when the amount was fixed at 5 grains, profitability of food grains at 8.0-0.0-s delay was 0.48-1.25 grains/s. Running time on the runway was short (<1 s in most cases) and was disregarded.

Procedures of behavioral studies

General Procedures After habituation to the apparatus on day 4, chicks were trained to associate colored feeders with food reward in forced-choice trials and then tested in binary choice trials (consecutively for 6 days from day 5 to day 10). Three blocks of behavioral studies were performed per day (thus 18 blocks in total) with inter-block intervals of 1-3 h. During the interval, groups of 3 chicks were communally housed in cages. On the other hand, training and test trials were accomplished individually in the

apparatus. Behaviors were examined in the daytime (9:00-16:00), and chicks usually gained *ca.* 1 g of millet food during these 3 blocks. Thereafter (at 18:00 or later), chicks were fed with limited amount of mash food as described above.

One block was composed of a series of training trials (8 forced-choice trials) followed by a separate series of test trials (10 binary choice trials) in which a chick was allowed to choose one of the two feeders. In both training and test trials, chicks gained an associated food reward. Inter-trial interval was set at > 30 s, and each chick was housed individually in a plastic cage during the interval. In the training trials, a chick was forced to visit one feeder to gain food, whereas the other feeder was occluded by an opaque screen placed on the runway (Fig.1A). One of the two opposing feeders was alternately used in the training series. Similarly, one of the two start boxes was pseudo-randomly chosen in a counterbalanced manner, so that chicks did not associate the turning direction with the consequently gained food reward. On the other hand, in the test trials, the screen on the runway was removed, and both feeders were available. We recorded the number of trials in which a chick chose one of the feeders.

Experiment 1: Reversal One of the two opposing feeders was assigned to high profitability and the other was assigned to low profitability during the first half of the experiment (blocks 1-9 on days 5-7) in a counter-balanced manner in each group. In order to examine chick responses to a change in profitability, we analyzed how the choice follows a reversal that was placed midway on day 8. The assignment was reversed in the latter half (blocks 10-18 on days 8-10) and the chick responses to the reversal were examined. Profitability was reversed either by changing the amount (1 or 9 grains, with equal delay of 2 s in group 1) or delay (0 or 8 s, with equal amount of 5 grains in group 2). We recorded the number of choices of the better feeder in binary

choice trials and examined whether these choices changed differently in groups 1 and 2.

Experiment 2: Titration In order to examine chick responses to risk, we adopted behavioral titration in 3 groups of chicks with different experimental conditions. In all groups, one feeder was assigned to a variable feeder and the other was assigned to a fixed feeder in a counterbalanced manner in each group. The variable feeder supplied high- or low-profitability food at equal probability ($p = 0.5$) in a manner unpredictable in each trial. The fixed feeder supplied food of intermediate profitability that was fixed in all trials in each block. We searched for equilibrium points at which the two feeders were equally chosen by gradually adjusting the profitability of the fixed feeder. If the equilibrium level of profitability matched its expected value of the variable feeder (kept at a constant value in this study; see below for details), we assumed that chicks were indifferent to risk. If it was lower (or higher) than the expected value, then chicks were assumed to be risk-averse (or risk-prone).

For behavioral titration, we adopted a procedure similar to that employed by Bateson and Kacelnik (1996) for starlings. During the 8 forced-choice trials of a block, each chick was rewarded by high-profitability food in 2 of the 4 forced trials to the variable feeder and was rewarded by low-profitability food in the other two trials. On the other hand, in all of the 4 forced trials to the fixed feeder, each chick was rewarded by identical food and its profitability was titrated based on the choices made in the preceding block. The titration followed 2 rules: (1) the profitability of the fixed feeder was incremented (or decremented) in the n -th block if the chick chose the fixed feeder in ≤ 4 trials (or ≥ 6 trials) out of the 10 test trials in the preceding $(n-1)$ -th block; and (2) the profitability was unchanged in the n -th block if the chick made equal choices (*i.e.*, choosing the variable feeder in 5 of the 10 test trials) in the $(n-1)$ -th block.

Steps of profitability of the fixed feeder are indicated on the scale shown in Fig. 1C. In groups 1 and 2, profitability was adjusted by changing the amount of food in 9 steps (from 1 grain to 9 grains in group 1) or 5 steps (from 3 to 7 grains in group 2). In group 3, profitability was adjusted by changing the delay in 9 steps (8.0, 5.6, 3.9, 2.8, 2.0, 1.3, 0.8, 0.3, and 0 s; see Fig. 1C), so that the steps were linearly spaced from profitability = 0.42 to 1.25 grains/s. Note that both groups 1 and 3 had 9 steps, and groups 2 and 3 had similar ranges of profitability. In all groups, the midpoint profitability of the fixed feeder was set at 0.83 grains/s, which was identical to the expected value of profitability of the variable feeder. In half of the chicks in each group, the profitability of the fixed feeder started from the highest step of the range (thus referred to as subgroup H). In the other half, the initial profitability was set at the lowest step (subgroup L), and we examined whether these two subgroups converged to an equilibrium point in the late blocks.

Chicks received nearly equal amounts of food from both feeders. The total number of grains obtained from the variable feeder was counted in each block (both forced- and free- choice trials), and the cumulative count was normalized by the sum of food gained from both feeders, thus yielding a gain ratio. The gain ratio was averaged over 18 blocks for each individual, and the individual data were merged for comparison among groups in the form of mean $\pm$ s.e.m.: 0.55 ± 0.04 (group 1, $n = 12$), 0.51 ± 0.03 (group 2, $n = 20$), and 0.50 ± 0.00 (group 3, $n = 20$).

Experiment 3: Re-examination of risk sensitivity to delay The effects of early blocks were examined in the choices of variable delay. The same procedure as that for group 3 of experiment 2 was used except that the delay of the fixed feeder was not adjusted. Titration was not performed, and the number of choices of the variable

feeder was recorded in two groups of chicks. From block #1 to #9, chicks of subgroup H (n = 10) were trained and tested in choices between a variable feeder (0 or 8 s delay at $p = 0.5$) and a fixed feeder with a delay = 0 s, whereas the delay of the fixed feeder was set at 8 s in subgroup L (n = 10). From block #10 to #18, the delay of the fixed feeder was set at 2 s in both subgroups and the choices were compared.

Statistical analyses

Statistical analysis using generalized linear mixed models (GLMMs) was used to assess the difference between two groups of chicks in experiments 1 and 3. We constructed two models to explain the behavioral data; one model assumed that the two groups of chicks differed, whereas the other model assumed that the two groups did not. The most likely values of the parameters involved (intercepts and coefficients) were estimated on the basis of the choice data using R (computer language developed for statistical computations, version 2.6.0) and the glmmML package in R (R Development Core Team 2005; <http://www.R-project.org>). Akaike's information criterion (AIC) was calculated as a sum of the deviance and the number of parameters for each model. A lower AIC value implied a better fit to the model.

As the response variable, we focused on the choice ratio, i.e., the proportion of trials in which the chick chose the better feeder. Because chicks were tested in binary choices, we assumed that the choice ratio followed a binominal distribution for the error structure with a choice probability = $Q(X)$ ($\in [0, 1]$), which was approximated by a logistic function (link function) as

$$Q(X) = 1 / (1 + \exp (-X)) \quad (3)$$

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

$$X = \beta_1 + \beta_2 * block + \beta_3 * factor + r_i \quad (4)$$

β_1 denotes bias at the population level.

block denotes the number of present blocks (an integer ranging from 1 to 9 or from 10 to 18), representing the cumulative number of experiences. β_2 indicates how the past experiences are integrated in choices in the present blocks.

factor (integer 0 or 1) denotes the group (or subgroup) of chicks. In one statistical model, *factor* was assigned to the groups: *factor* = 0 for group 1 and *factor* = 1 for group 2. In the alternative model, *factor* was disregarded and assigned to 0 in both groups. In other words, β_3 indicates the possible difference between the two groups.

r_i denotes random effects of individuals or noise that was not experimentally controlled.

The most likely values of β_1 , β_2 , and β_3 were computed on the basis of choice data using a freeware for statistical computation (R, version 2.6.0) on a PC. AICs for these two statistical models were compared.

In experiment 2, Bayesian approaches were adopted in order to estimate subjective values and other cognitive parameters, which could not be obtained by direct observation but derived from the behavioral data in an implicit manner. To analyze the behavioral data, we applied the Markov chain Monte Carlo (MCMC) method to compute the likely posterior distributions (McCarthy 2007). Random sampling was repeated toward a highly likely distribution of each parameter using a software developed specially for Bayesian estimation (WinBUGS 1.4.3; Lunn *et al.* 2000) linked to the R platform. The reproducibility of our MCMC simulation was assessed by calculating the Brooks-Gelman-Rubin statistic (R_{hat}), which must be < 1.2 for all

parameters (Kass *et al.* 1998).

The choice ratio $Q(X)$ was approximated by a logistic function of a linear predictor X . X was given for each individual (i) and block (b) as a weighed difference of values between the variable and fixed feeders. Our main goal was to compute the posterior probability density of VV_i (subjective Value of the Variable feeder in each individual) based on the choice data obtained from all of the blocks.

$$X_{b,i} = B_i + E_i * (VF_{b,i} - VV_i) \quad (5)$$

B_i denotes the innate bias consistently produced by each individual for the fixed feeder. Here, we assume unspecified factors other than profitability, such as preferences to the position or color of feeders or both. Preliminary data suggested no population-level bias, so that B_i is assumed to be obtained by Gaussian distribution with a mean = 0 at the population level. Hyperprior distribution of the variance of B_i is assumed to be gamma distribution with 0.01 for the shape parameter and 100 for the scale parameter (denoted as `dgamma (0.01, 0.01)` in R).

E_i represents the coefficient of how strongly the difference of values acts on choices. E_i was given by $\exp(\log_effect_i)$, thus it is non-negative; $\log_effect_i$ is assumed to be given by Gaussian distribution. Hyperprior distribution of the mean of $\log_effect_i$ is a Gaussian distribution defined with 0.0 for the mean and 100 for variance, i.e., `dnorm (0.0, 100)`. Hyperprior distribution of the variance of $\log_effect_i$ is `dgamma (0.01, 0.01)`.

$VF_{b,i}$ denotes the objective value of the fixed feeder. Because the fixed feeder gradually changes along blocks, we calculated $VF_{b,i}$ by averaging profitability over the past K_i blocks, where K_i is an implicitly given integer that follows

Poisson distribution for each individual. K_i thus gives a measure as to how far each chick refers to past blocks. Hyperprior distribution of the mean of K_i is `dgamma (0.01, 0.01)`.

VV_i denotes the subjective value of the variable feeder in terms of profitability.

We assumed that each individual has VV_i that is invariant along block (b).

VV_i is assumed to be given by Gaussian distribution for each group.

Hyperprior distribution of the mean of VV_i is `dnorm (0.0, 100)` and

hyperprior distribution of the variance of VV_i is `dgamma (0.01, 0.01)`.

A total of 6000 Monte Carlo iterations per chain (including 2000 burn-in iterations) were accomplished, and one out of every 10 steps was sampled from the remaining 4000 steps, thus yielding 400 samples per single calculation trial. The calculation was repeated 3 times, and a total of 1,200 samples were obtained for each individual. Of these samples, we calculated the median to represent each individual chick.

Results

Experiment 1: Responses to reversal in amount and delay

It has been shown that chicks flexibly change their choices when the associated amount is altered (Ichikawa *et al.* 2004), but response to altered delay was not examined previously. In the present study, responses to reversal were examined in two groups of chicks, i.e., group 1 for reversed profitability by amount and group 2 by delay of food reward. Fig. 2 shows the results in which the number of choices of better feeder (ranging from 0 to 10) was plotted against the number of blocks (from #1 to #18). Chicks in both groups gradually shifted their choices toward the better feeder both in

the early and late series of blocks.

AICs were compared separately in both the early (#1 to #9) and late (#10 to #18) blocks. In the early blocks, AIC with only the block factor (137.5) was smaller than that with the block + group factors (139.3) and that with only the group factor (304.0), suggesting that differences between groups should be disregarded. Also, in the late series of blocks, AIC with only the block factor (186.7) was smaller than that with the block + group factors (188.6) and that with only the group factor (780.2). Even though the profitability range was larger in group 1 than in group 2 (Fig. 1C), chicks responded similarly to reversal in amount and delay, thus validating experiment 2.

Figure 2 around here

Experiment 2: Responses to variability in amount and delay

Behavioral data The variable feeder served food of variable amount to groups 1 and 2 and food of variable delay to group 3. Fig. 3 shows the results in which the profitability of the fixed feeder was plotted against the block number. In group 1, the profitability of both subgroups H and L converged in a range below the expected value of 0.83 grains/s (particularly in blocks #15 to #18; Fig. 3A), suggesting that chicks were risk-averse for amount. A convergence of median values also occurred in group 2 (in blocks #8 to #18; Fig. 3B), but a high degree of variation among individuals (as indicated by long boxes and whiskers) made it vague. We therefore conclude that chicks of group 2 were neither risk-averse nor risk-prone at the population level. In group 3, sub-groups did not show convergent results (in blocks #9 to #18; Fig. 3C) and the inter-individual variation was large. It is notable that chicks in subgroup L showed

a paradoxically high profitability in late blocks (#12 to #18; profitability reaching the ceiling value of 1.25 grains/s), as a majority of chicks chose the variable feeder (delay = 0 or 8 s) even though the alternative fixed feeder supplied food with delay = 0 s. Risk sensitivity was thus inconclusive in group 3 as long as we focused on convergent points at the population level. We therefore set out to develop a hierarchical Bayesian model in order to perform comprehensive analyses of the data.

 Figures 3 and 4 around here

Estimation of cognitive parameters by a hierarchical Bayesian model Fig. 4 shows the distribution of estimated parameters in groups 1, 2, and 3; each symbol represents an individual chick. Subgroups L and H are separately shown for VV_i (subjective value; Fig. 4A), whereas they are merged for other parameters B_i , E_i , and K_i (B). The distribution of VV_i in 3 representative chicks (indicated by * in group 2) is shown in the right column of Fig. 4A. Because the MCMC samples estimate the probability distribution of VV_i , the probability $p(VV_i > 0.83)$ directly gives rise to the probability that the individual was risk-prone. Chicks with probability $p(VV_i > 0.83) > 0.95$ were thus classified as risk-prone and those with $p(VV_i > 0.83) < 0.05$ were classified as risk-averse.

In group 1, 2 chicks (subgroup L) and 5 chicks (H) were classified as risk-averse, but none of them were risk-prone. In group 2, chicks did not show consistent risk sensitivity at the population level, and both subgroups contained risk-prone and risk-averse chicks. In group 3, chicks were risk-prone at the population level because individual medians were distributed more frequently above the expected value of 0.83,

and the number of risk-prone chicks (5 chicks in subgroup L and 2 chicks in subgroup H) was higher than that in groups 2 (3 chicks in subgroup L and 1 in subgroup H).

For other parameters such as B_i , E_i , and K_i , distributions of individual medians strongly overlapped among groups 1, 2, and 3, suggesting that the model was appropriate in indicating VV_i as the key parameter for the differences among groups. Furthermore, K_i ranged high around 10-20, suggesting that chicks take considerable number of previous blocks into account. However, in one individual, K_i could not pass the criterion of ($R_{hat} < 1.2$) due to multiplicity of peaks (two) in posterior distribution, whereas all parameters successfully met the criterion in other individuals.

Experiment 3: Inconsistent risk sensitivity for variable delays

As no clearly convergent results were shown between subgroup of chicks in group 3 (experiment 2, Fig. 3C), we re-examined the risk sensitivity to delay without the titration procedure, and the results are shown in Fig. 5. In subgroup H, preference for the variable feeder was not found at the population level even after the delay of the fixed feeder was changed from 0 to 2 s. On the other hand, in subgroup L, the variable feeder was chosen much more frequently after the change from 8 to 2 s. AICs were calculated for the choice data in the late blocks #10-18 in which both subgroups were tested in the same condition. AIC with the subgroup factor (315.5) was smaller than AIC with block + subgroup factors (317.4) and AIC with the block factor (321.6), indicating a considerable difference between subgroups throughout the late blocks. A subjective value might not be uniquely given for the feeder with variable delay, or alternatively, chicks might not be able to evaluate the fixed feeder when the alternative feeder is variable. In this case, chicks in subgroup L might have greatly undervalued the fixed feeder with a long delay of 8 s in early blocks (#1-9) and not updated the

valuation in late blocks (#10-18).

Figure 5 around here

Discussion

The present study gives us a complex picture of risk sensitivity for amount and delay in domestic chicks. Without risks (experiment 1), chicks responded similarly to reversals in amount and delay (Fig. 2), suggesting that they can update the subjective value of the feeder after a change in profitability, regardless of whether the change was caused by an altered amount or delay. When the amount varied and the variance was large (group 1 in experiment 2), chicks consistently showed risk aversion (Fig. 3A). With a smaller variance in amount (group 2), consistent risk sensitivity was not found at the population level (Fig. 3B), and the subjective value of the risky feeder (V_i) varied widely among individuals (Fig. 4A). On the other hand, when the delay was varied (group 3 in experiment 2), chicks showed risk-prone choices at the population level compared with chicks in group 2 (Figs. 3C, 4A), although the variance of the variable feeder was almost the same (Fig. 1C). However, re-examination without the titration procedure (experiment 3) failed to show consistent risk proneness for delay (Fig. 5). We further discuss these results in view of the frameworks for integration of amount, delay, and risk in subjective values.

Risk-averse choices for variable amount; amount and risk may be integrated in a concave utility function

In inter-temporal choices, chicks are given binary options of a small/short delay

reward (SS) and a large/long delay reward (LL). By adjusting the delay of LL, an equilibrium point was found at which both SS and LL were equally chosen (Izawa *et al.* 2003, Aoki *et al.* 2006), in a manner compatible with the idea that chicks evaluate food by its profitability (Matsushima *et al.* 2008). However, risk-averse choices found in this study (group 1 but not group 2 in experiment 2) suggest that subjective value is not a linear function of amount but concave as in equation (2).

Risk aversion is often accounted for in terms of the daily energy budget rule (Stephens 1981). Yellow-eyed juncos when tested in a positive budget showed risk aversion for variable amounts (Caraco *et al.* 1980). When tested in a negative budget, juncos showed a risk-prone choice (Caraco *et al.* 1980, 1990) in accordance with the predictions of the budget rule. Similarly, adult pigeons maintained at 80% of the free-feeding weight (thus supposed to be in a negative budget) showed risk-prone choices for variable amount (Mazur 1984, 1986). Another study on pigeons showed risk aversion (Hamm and Shettleworth 1987), and reasons for this discrepancy have not been determined. Some factors other than the energy budget rule may be applied to large birds such as pigeons and chickens.

In the present study, we examined choices of growing chicks in restricted food supply, and the growth rate was maintained at a considerably low level (see Methods). It is possible that the budget was positive because the body weight steadily increased and the energy intake exceeded the daily requirement. Alternatively, we may argue for a negative budget because experiments were performed before the main ration of the day was supplied, and the body weight was *ca.* 70% of freely fed chicks of the same age. As in pigeons, it is possible that choices by large-body animals such as chickens (as well as juvenile chicks) cannot be explained by the budget rule. Risk sensitivity in

chicks must be re-examined in systematically controlled budget states at different developmental stages.

Conditional risk-prone choices for variable delay; delay and risk may not be integrated in an absolute utility function

In experiment 2, VV_i of group 3 chicks (estimated median values) were distributed in a range higher than those in group 2 (Fig. 4A), suggesting a tendency for chicks to be risk-prone with variable delay at the population level. This tendency is basically compatible with the general patterns found in a wide variety of animals (Kacelnik and Bateson 1996). However, half of subgroup L chicks showed paradoxically high preference for the variable feeder in late blocks; note that the median was fixed at a ceiling value of 1.25 in blocks #12-18 (Fig. 3C). These chicks chose the variable feeder (delay = 0 or 8 s) more frequently, even when the alternative fixed feeder supplied food at delay = 0 s.

The inconsistent results for subgroups L and H were reproduced in experiment 3 (Fig. 5), indicating that the subjective value of the variable feeder was not uniquely given but was conditional and dependent on early experiences. Most probably, the variable feeder was given a different subjective value depending on the alternative option (fixed feeder). When the fixed feeder was poor in terms of long delay (8 s in blocks #1-9 in subgroup L), the subjective value of the variable feeder was set extremely high even in late blocks (#10-18). At present, we are unable to explain the high value in either mechanistic or functional terms.

The conditional nature of the subjective value of the risky feeder violates the assumptions of absolute and independent value assignment for each option such as

expected utility (Stephens and Krebs 1986). Instead, choices may be based on a comparative value that is given in a context-specific manner (Shafir 1994, intransitivity in honeybees; Hurly and Oseen 1999, inconsistent choices in trinary choices from those in binary choices studied in hummingbirds). Our inability to give a unique estimate of the subjective value may also indicate that chicks do not value food by an integrated utility function when the option varies in delay.

Aspects of the risk-sensitive choice may be explained as non-adaptive traits. As cited in the Introduction, Kacelnik and his colleagues intensively studied the risk-sensitive choices of starlings in a series of quantitatively controlled studies and found that starlings are clearly risk-prone in delay and slightly risk-averse in amount. Based on the scalar expectancy theory of Gibbon (1977), they argued that the pattern of risk sensitivity could arise by constraint of information processing in which the recalled amount and time are inevitably accompanied by errors (Reboreda and Kacelnik 1991, Kacelnik and Bateson 1996). Basically, a similar pattern was found in domestic chicks and this similarity could be due to common constraints on cognitive processes rather than convergent evolution due to common selection pressure.

We may argue that the tendency of risk proneness in delay may be an adaptive behavior against scroungers because chicks generally forage in a group. In social foraging, animals can gain food by adopting the strategy of either producer or scrounger (Koops and Giraldeau 1996). A producer does not always gain the food that it finds because other group members, scroungers, may rush to intercept the food resource. The risk-prone choices for delay could be explained as an adaptive trait in this context of social foraging. If a producer chooses the risky food of varying delay, the producer may deter the attention of scroungers and thus reduce the probability of interception

because the scrounger must intercept at the precise time the food is found. To test this hypothesis, we will have to examine the rate of successful interception when the food reward varies in delay in the domestic chicks. Further comparisons of risk sensitivity among related species with and without social foraging could also give us further insight.

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Figure legends

Fig. 1 (A) Top view of the experimental apparatus: a cross-shaped maze equipped with two feeder arms and two start boxes. In forced-choice training trials, one of the feeder arms is occluded. In free-choice test trials, both feeders are available. (B) Timetable of a trial. The screen is removed to allow the chick to approach the feeder (start). After a short period of running, the chick arrives at the mechanical sensor. After a pre-programmed delay (ranging from 0 to 8 s), the feeder serves millet grains one by one at equal intervals. Consumption time is fixed at 4 s. (C) Relationship between profitability (grains/s), amount (grains), and delay (s) in this study. In experiment 1, the profitability of feeders is changed by amount (1 or 9 grains in group 1) or delay (8.0 or 0.0 s in group 2). In experiments 2 and 3, the profitability of the variable feeder is changed by amount or delay on a trial basis with $p = 0.5$.

Fig. 2 Similar responses to reversal in food amount and delay (experiment 1). Number of choices of the better feeder (i.e., feeder of a higher profitability) is plotted against the number of blocks. Short horizontal bars indicate the medians of groups 1 and 2, each containing 6 chicks. Boxes denote the 25-75% range and whiskers denote the min-max range. For AICs, see text.

Fig. 3 Distinct responses to risk in food amount and delay (experiment 2). Profitability of the fixed feeder is plotted against number of blocks in group 1 (A), group 2 (B), and group 3 (C). Each group has two subgroups composed of equal numbers of chicks ($n = 6$ or 10) in which the profitability of the un-risky feeder of the

first block is set at the bottom (open columns with black median bars) or at the top (filled columns with white median bars) of the range. Subgroups L and H are shown by open and filled columns, respectively.

Fig. 4 Estimation of parameters in individual chicks using hierarchical Bayesian models. Results of MCMC computations based on linear predictor model are shown. Each symbol denotes median of samples obtained for each individual. (A) Subjective value of variable feeder (VV_i). Individual data in subgroups L and H in groups 1, 2, and 3 are compared. Samples obtained from 3 representative chicks (indicated by *) are shown in the right column; the ordinate denotes the probability density in arbitrary units and the abscissa represents profitability (grains/s). (B) Bias (B_i), effect of value difference (E_i) and the number of blocks included for the objective value of the fixed feeder (K_i) are estimated. Individual data in groups 1, 2, and 3 are compared, and the subgroups are merged. For details of the Bayesian analysis, see text.

Fig. 5 Inconsistency found in the risk-prone choices for variable delay (experiment 3). Numbers of choices of the variable feeder (0 s or 8 s delay at $p = 0.5$; amount is fixed at 5 grains) in the two groups are compared. In early blocks (#1 to #9), delay of the fixed feeder is set at either 0 s (group 1) or 8 s (group 2). In late blocks (#10 to #18), it is set at 2 s in both groups. Short horizontal bars indicate the medians of subgroups H and L each containing 10 chicks. Boxes denote the 25-75% range and whiskers denote the min-max range. For AICs, see text.

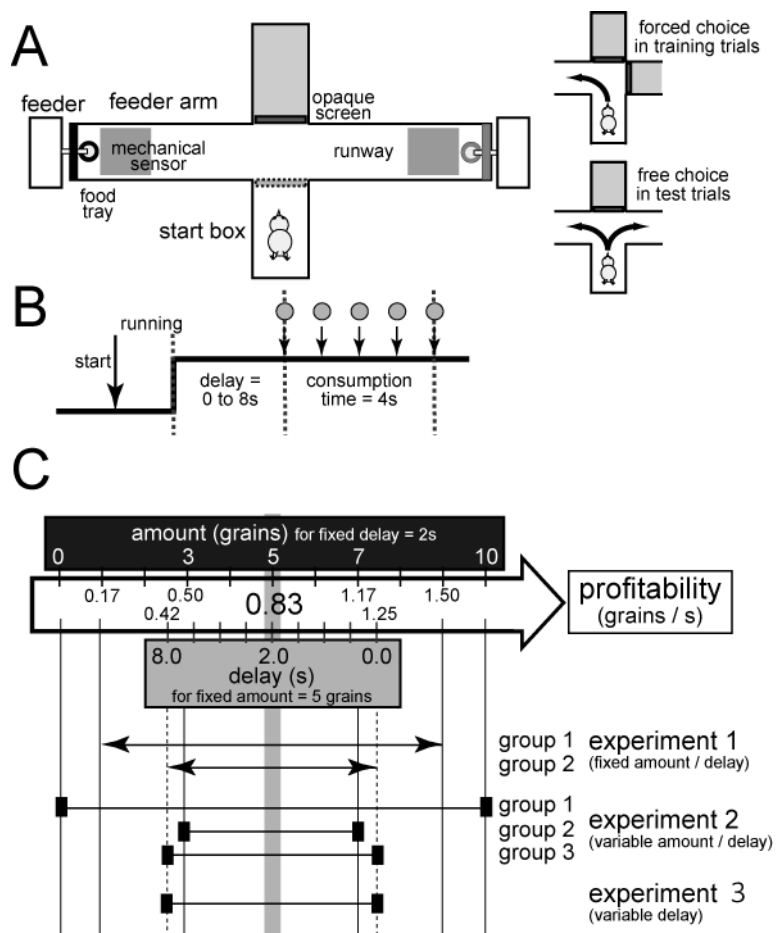


Fig. 1

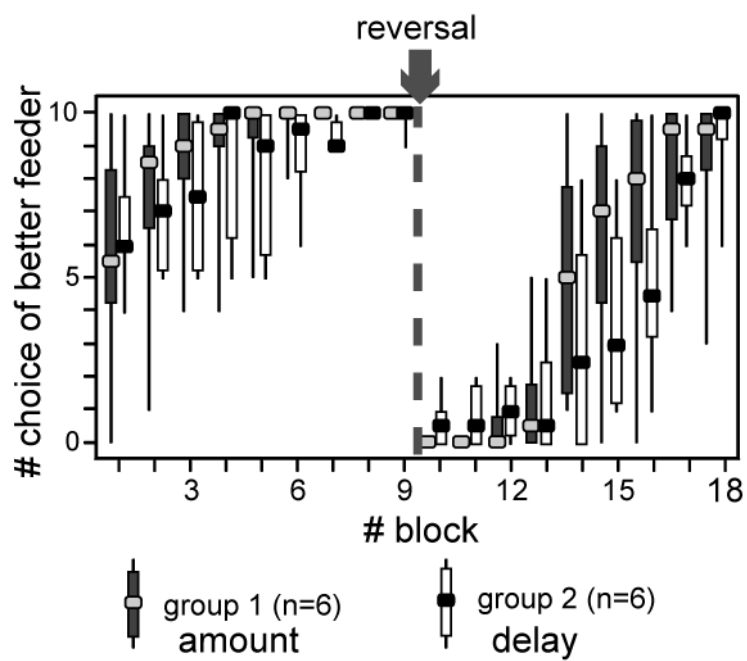


Fig. 2

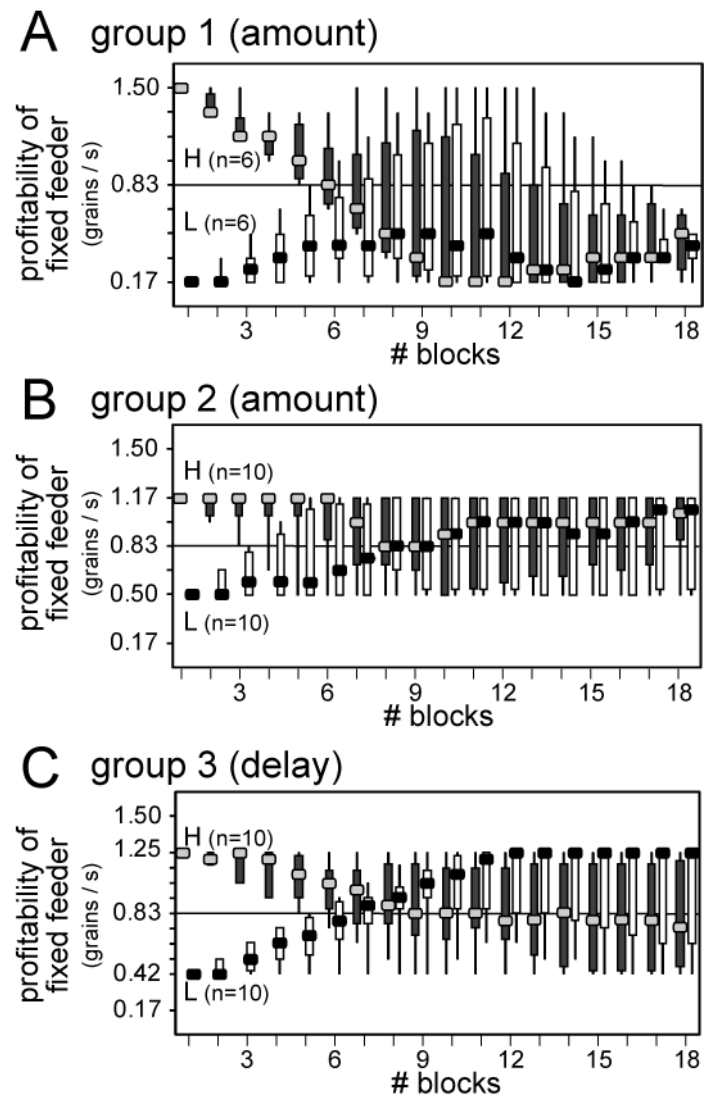


Fig. 3

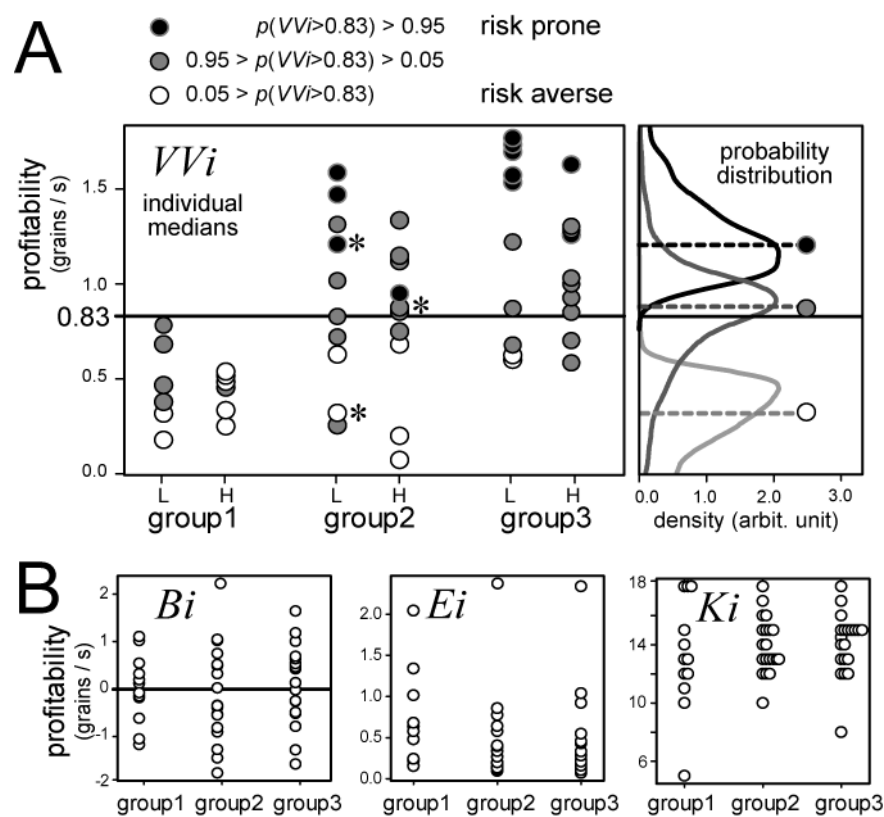


Fig. 4

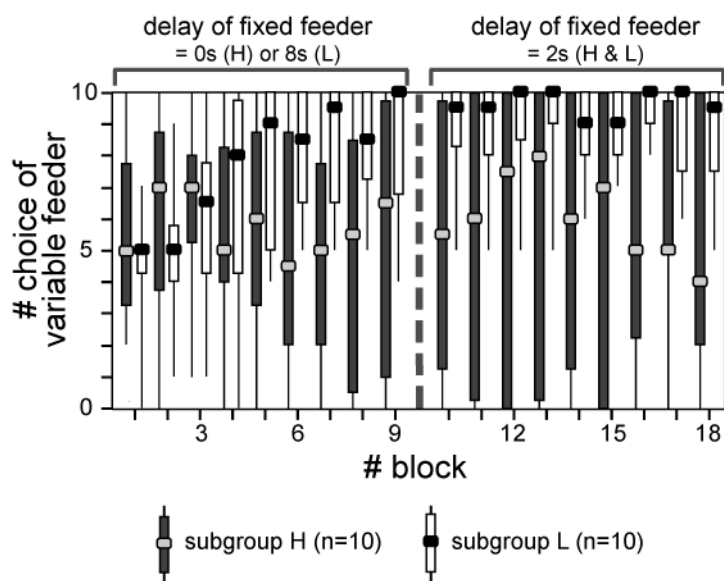


Fig. 5