

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



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ABSTRACT

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

1. Introduction

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

uncertain environments, the matching law has attracted particular attention in recent developments of reinforcement learning theories (Sutton and Barto, 1998; Sakai and Fukai, 2008) and neuroeconomics (Platt and Glimcher, 1999; Sugrue et al., 2004; Mobbs et al., 2013).

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

More recent studies on social foraging behaviours suggest an alternative game-theoretical view of resource competition, where different foraging tactics co-exist in a foraging flock (Giraldeau et al., 1990). When food items are sharable (kleptoparasitism), two beneficial

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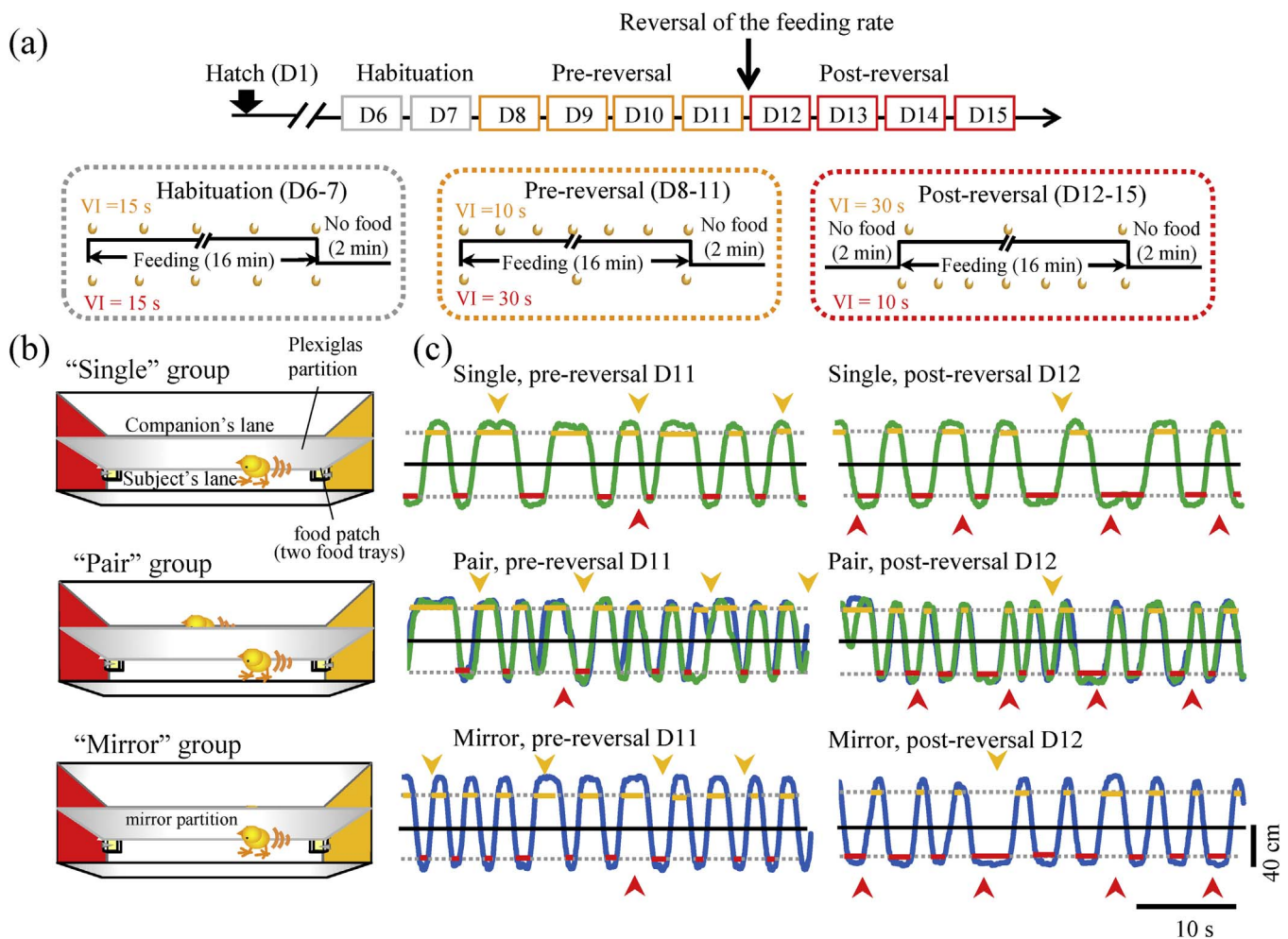


Fig. 1. (a) Procedures of behavioural tests on post-hatch days 6–15. (b) Schematic illustration of I-shaped maze with two lanes partitioned by a Plexiglas wall, and two terminal food patches along the yellow and the red wall, each composed of two food trays. Three groups of chicks were examined in 'single',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

tactics may appear, namely producer and scrounger (see [Giraldeau and Caraco, 2000](#) for a comprehensive review). Due to frequency dependence, both tactics would subsequently attain the same level of individual fitness as a stable equilibrium. In addition to personal information acquired individually, scrounging individuals would gain information about the location and suitability of habitats from producing companions ([Giraldeau and Beauchamp, 1999](#); [Danchin et al., 2004](#)). Individual foragers may concurrently search for food and join a group of foragers (information sharing), or they might adopt an exclusive tactic at a time (producer-scrounger game). In both cases, however, inadvertent sharing of information on food resources could contribute to an economically optimal decision.

These considerations led us to ask the following questions, is precise matching achieved solely through melioration of personal information in individuals, or does social grouping contribute to matching behaviour? In case of the latter, is food patch information shared among the competing individuals? We addressed these questions using domestic chicks as subjects. Chicks adjust their foraging decisions according to their social conditions. For example, choice impulsiveness (in terms of a stronger temporal discounting) is conditionally enhanced by competition ([Amita et al., 2010](#); [Amita and Matsushima, 2011, 2014](#)), if and only if accompanied by food risk ([Mizuyama et al., 2016](#)). Foraging effort is also socially facilitated in patch-use behaviour, and paired chicks run significantly more than single foragers even without interference of food resource ([Ogura and Matsushima, 2011](#); [Ogura et al.,](#)

[2015](#); [Xin et al., 2017](#)). However, the functional role of the social facilitation remains unclear. Facilitated running could make chicks visit feeders more frequently, leading to a higher chance of finding food and more precise matching, even without active information sharing among the foraging chicks. Otherwise, competing chicks may learn about food availability in patches directly by observing the behaviour of companions.

In the present study, we compared patch-use behaviour between groups under single and paired conditions. Feeders at both ends of a maze supplied millet grains without any predictive cues, so that information on food availability would be critical. To study the behaviour in static conditions, the food supply rate at the feeders was biased at a fixed ratio of 3:1 between the feeders. To examine dynamic behavioural changes, the bias was reversed midway through the experiment, and we examined how quickly chicks switched patch-use time. If competition (or perceived pseudo-competition, to speak more strictly) is critical, then the pair chicks would show more precise matching and quicker switch to the reversal than the single chicks. However, as argued above, differences between the two groups could be ascribed to improved personal information through facilitated running. We therefore added a "mirror" group, in which single chicks were accompanied by their mirror image along the lane. The preliminary experiment revealed facilitated running in both of the mirror and pair groups. However, if information sharing is critical, then mirror chicks would show less precise matching than the pair chicks, as they

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