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ORIGINAL ARTICLE

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Use of public information when foraging: effects of time available to sample foods

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Abstract It has been proposed that use of socially acquired information by animals should increase as the time available for individual resource sampling decreases. We gave Norway rat "observers" either 2 or 5 h day^{-1} to sample four foods. Three of these foods were relatively palatable, but protein-poor; the fourth was relatively unpalatable, but protein-rich. We found that observer rats that for 2 h day^{-1} both sampled foods and interacted with demonstrators eating only the protein-rich food ate more of the protein-rich food than did observers that sampled for 2 h day^{-1} but had no opportunity to interact with demonstrators. On the other hand, observer rats that could sample foods for 5 h day^{-1} ate equal amounts of protein-rich food whether they interacted with a demonstrator fed protein-rich food or not. Subsequent analyses showed that the time available to observers to sample foods, rather than the opportunity to interact with demonstrators determined whether such interaction influenced observers' food choices. The results are consistent with the hypothesis that animals increase their use of public information in response to temporal constraints on opportunities for resource sampling.

Key words Social learning · Temporal constraints · Public information · Rats

Introduction

Boyd and Richerson (1988) suggested that in situations where it is difficult to acquire information by individual trial-and-error learning, dependence on individual learning should decrease, and use of social learning should increase. Giraldeau (1997, p. 68) similarly concluded a recent review of the ecology of information use by animals with the observation that theoretical work "opens the way to research that may reveal that animals, rather than being capable of using information or not, simply use it when it pays and in ways that are adaptive." In reaching this conclusion, Giraldeau suggests that using information acquired from others is most profitable when individual sampling is costly (Templeton and Giraldeau 1996) or when time available to sample resources personally is short (see also Clark and Mangel 1986; Barta and Szep 1991; Stohr 1998). Hypothetically, under such stressful foraging conditions the ability of individuals to evaluate patch quality for themselves is reduced, and the relative value of vicariously acquired information is enhanced. Evolution should, therefore have favored individuals with sufficient cognitive flexibility to vary their relative dependence on individually and socially acquired information in response to variation in temporal constraints on their opportunities to forage.

Our laboratory has, for many years, used social influences on the foraging behavior of Norway rats *(Rattus norvegicus)* as a model system to explore ways in which socially acquired information biases the food choices of rodents (for reviews see Galef 1976, 1988, 1996). In the course of this work, we have shown that after a recently fed rat (a "demonstrator") interacts with a naive conspecific (an "observer"), the observer increases its relative intake of whatever food its demonstrator ate (Galef and Wigmore 1983; Galef et al. 1984). Such use of public information (Valone 1989) in food selection can be particularly important to rats that have to select a balanced diet in an environment containing both nutrient-deficient and nutritionally adequate, potential foods.

When we allowed rats housed individually to choose for 7 days among four foods, three both palatable and deficient in protein and one both unpalatable and protein-rich, our subjects failed to learn to focus ingestion on the protein-rich food and lost significant amounts of weight (Beck and Galef 1989). On the other hand, rats placed in the same situation with demonstrator rats trained to eat the

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protein-rich food developed a strong preference for it and grew normally (Beck and Galef 1989). Further, the less time that rats had to sample among foods, the less able were they to focus ingestion on the nutritionally adequate food available to them (Galef and Whiskin 1997).

Experiment 1

Here, we determined whether the extent to which naive rats make use of socially acquired information to guide their food selection in an environment containing patches that varied in nutritional value (Beck and Galef 1989; Galef et al. 1991) is influenced by the time they have to sample resources for themselves. We gave naive observer rats the opportunity to sample among four foods for either 2 or 5 h day^{-1}. Three of the foods available to the observers were protein-deficient, and one was protein-rich. Half the observers given access to food for 2 h day^{-1}, and half those given access to food for 5 h day^{-1} could interact with a demonstrator rat that ate only the protein-rich food. If observers make greater use of public information when opportunities for individual resource sampling are relatively short, we would expect an interaction between the duration of sampling opportunities available to observers and the effects of information acquired from demonstrators on observers' intake of protein-rich food.

Methods

Subjects

We used as observers 40 experimentally naive Long-Evans rats obtained from Charles River Canada (St. Constant, Quebec) at 42 days of age. An additional 20 rats that had served as observers in previous experiments served here as demonstrators.

Apparatus

The experiment was conducted in six enclosures each measuring 1 × 1 × 0.3 m. Enclosures were constructed of hardware cloth and angle iron, and each was divided into two compartments of equal size (referred to below as observer's and demonstrator's compartments) by a hardware-cloth partition (1-cm grid) that separated each observer rat from its demonstrator (Fig. 1). Demonstrators' and observers' compartments each contained a harborage site [a wooden nest box (30 × 30 × 15 cm) with a single entrance (5x5 cm)] and a water bottle.

Foods

During the experiment, we presented each observer with four distinctively flavored foods. Three of these foods

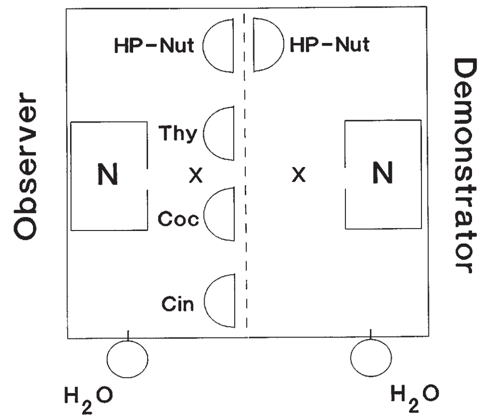

Fig. 1 Overhead schematic of the apparatus used in experiments 1 and 2 (*Nut* nutmeg-flavored diet, *Thy* thyme-flavored diet, *Coc* cocoa-flavored diet, *Cin* cinnamon-flavored diet, *H_2O* water, *N* nest, *X* locations where we placed food bowls during the habituation stage of experiments)

(Diet Cin, Diet Coc and Diet Thy) were relatively poor in protein (4.4% protein by weight); the forth (Diet HP-Nut) was relatively rich in protein (17.7% protein by weight). A diet containing 12% by weight protein is considered adequate for normal growth and development in young rats (Anonymous 1980).

We prepared each of the three protein-poor foods by adding either 1% by weight McCormick's Fancy Ground Cinnamon (Diet Cin), 2% by weight Hershey's Pure Cocoa (Diet Coc), or 1% by weight Club House Ground Thyme (Diet Thy) to a mix containing: (1) 80% by weight protein-free basal mix (Teklad Diets, Madison, Wis., USA, catalogue no. TD 86146; in g kg^{-1}: 808.5 corn starch, 108.1 vegetable oil, 54.1 mineral mix, 7.0 cod-liver oil, and 2.7 vitamin mix), (2) 10% corn starch, (3) 5% granulated sugar, and (4) 5% high-protein casein (Teklad Diets, catalogue no. 160030).

The single protein-rich food (Diet HP-Nut) was prepared by adding 1% Club House Ground Nutmeg to a mix containing: (1) 80% by weight protein-free basal mix and (2) 20% high-protein casein. As we had intended, Diet HP-Nut, lacking palatable sugar, loaded with unpalatable casein (Kon 1931), and flavored with nutmeg, proved the least palatable of the four diets when, in a pilot study, we offered all simultaneously to hungry young rats.

We presented foods to both demonstrators and observers in semi-circular stainless steel food cups (10 cm diameter, 5 cm deep) attached to the hardware cloth partition separating demonstrator's and observer's compartments. Four of these cups were located in the observer's compartment and one in the demonstrator's compartment, and the latter was placed opposite the observer's cup containing Diet HP-Nut (Fig. 1). What cannot be seen in Fig. 1 is that, across observers, we counter-balanced the location of the food cup containing Diet HP-Nut within the array of four food cups presented to them. However, the food cup in the demonstrator's compartment always contained Diet HP-Nut and was always placed opposite the food cup in the observer's compartment that contained Diet HP-Nut.

To prevent spillage, we filled each food cup to less than half its depth. Each food cup still contained more food than a rat would eat in 24 h.

Procedure

We randomly assigned observers to "demonstrator" and "no-demonstrator" groups (n = 20/group), then randomly assigned half of the subjects in each of these two groups to 2-h and 5-h feeding conditions. We then placed individual observers in the observer's compartment of each enclosure (Fig. 1) and a demonstrator in the demonstrator's compartment of those enclosures containing observers assigned to the two demonstrator groups. At the time we first introduced demonstrators and observers into enclosures, no food bowls were present in them.

We then habituated both observers and demonstrators to the experimental situation and to their feeding schedules. For 3 consecutive days, we placed food bowls containing powdered Purina Rodent Laboratory Chow 5001 (Ralston-Purina, Woodstock, Ontario), the food on which both demonstrators and observers had been maintained for the preceding week, in both the demonstrator's and observer's compartments of each enclosure in the positions indicated by Xs in Fig. 1. We left food in enclosures containing observers we had assigned to the 2-h condition for 2 h day^{-1} and in enclosures containing observers assigned to the 5-h condition for 5 h day^{-1}.

Twenty-four hours after we had placed the food bowls containing rat chow in enclosures for the last time, we placed four food cups, each containing a different food, in each observer's compartment and a single food cup containing Diet HP-Nut in each demonstrator's compartment (Fig. 1). At the same time each day for 5 consecutive days, we left the food cups in the cages of both demonstrators and observers assigned to the 2-h condition for 2 h day^{-1} and in the cages of demonstrators and observers assigned to the 5-h condition for 5 h day^{-1}.

The experimenter weighed all food cups at the beginning and end of each feeding period, determined the total amount of Diet HP-Nut each observer ate during the last 5 days of the experiment, and calculated the percentage of each observer's intake on each day that was Diet HP-Nut.

Results and discussion

The main results of experiment 1 are presented in Fig. 2. The figure shows the mean amount of Diet HP-Nut eaten by observers assigned to 2-h and 5-h conditions, as a percentage of the total amount of food they ingested during their 5 days of feeding from the cafeteria of four flavored foods only one of which was protein sufficient. Across the 5 days of the experiment, observers with and without demonstrators ate, respectively, an average (± 1 SEM) of 2.69 ± 0.41 and 1.53 ± 0.37 g of Diet HP-Nut/day.

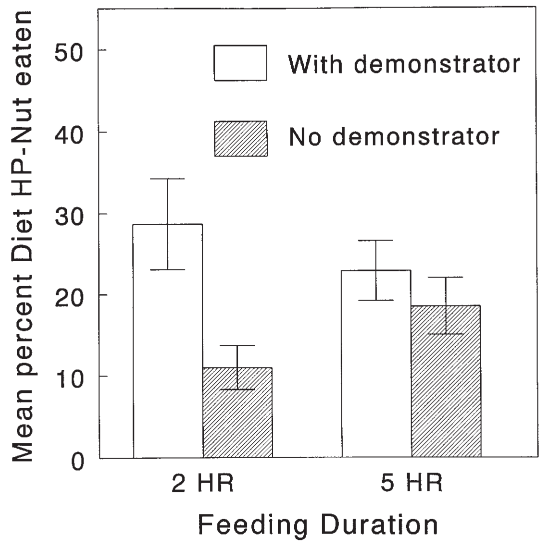

Fig. 2 Mean amount of high-protein, nutmeg-flavored diet (*Diet HP-Nut*) eaten by observers during the 5 days of experiment 1 as a percentage of the total amount of food that observers ingested during those 5 days (*bars* ± 1 SEM)

Results of previous studies of effects of demonstrators on observer food selection in situations similar to the present one led us to expect that observers that had interacted with demonstrators eating Diet HP-Nut would increase their relative intake of Diet HP-Nut (Beck and Galef 1989). Indeed, we found a significant main effect of presence of a demonstrator on the relative amount of Diet HP-Nut observers ate (ANOVA, $F_{1,36}$ = 11.03, P < 0.002). There was, on the other hand, no main effect of the number of hours that food was available to demonstrators and observers on the relative amount of Diet HP-Nut eaten by observers ($F_{1,36}$ = 0.29, P = 0.59). However, as would be predicted on the hypothesis that observers rely more on information acquired from conspecifics when time for resource sampling is relatively short, we did find a significant interaction between the two independent variables presence or absence of a demonstrator and time available for sampling ($F_{1,36}$ = 5.35, P < 0.03). On average, observers with demonstrators and given food for only 2 h day^{-1} ate 3.6 times as much Diet HP-Nut as did observers without demonstrators given equal access to food, whereas observers with demonstrators given access to food for 5 h day^{-1} ate only 1.08 times as much Diet HP-Nut as did observers without demonstrators given equal access to food. As Giraldeau (1997) had predicted, the effect of demonstrators on the food choices of their conspecific observers appeared more pronounced when observers had a relatively short time to sample available resources for themselves.

There is, however, an alternative interpretation of the outcome of experiment 1. In experiment 1, the time that observers had access to food was confounded with: (1) the time that demonstrators had access to food and (2) the time during which observers and demonstrators could interact while demonstrators had access to food. Consequently, differences in the influence of demonstrators on food choices of observers with access to food for 2 or 5 h day^{-1} may not have been due to differences in the use that observers made of information provided by their demonstrators. Rather, the different effect of demonstrators on observers assigned to 2-h and 5-h conditions may have been a result of differences in: (1) information provided to observers by demonstrators fed for different amounts of time, or (2) the time observers in the two conditions had to extract information from feeding demonstrators. We undertook experiment 2 to investigate both these possibilities.

Experiment 2

In experiment 2 we compared the effectiveness of demonstrators fed for either 2 or 5 h day^{-1} in altering the food choices of observers allowed to sample for 2 h day^{-1}. We chose to examine effects of demonstrator schedules of feeding on the diet choices of observers fed for 2 h day^{-1} rather than on the food choices of observers sampling for 5 h day^{-1}, because in experiment 1 only the former observers provided evidence of an effect of public information on their food choices.

Methods

Subjects

We used as observers 30 experimentally naive, 42-day-old rats obtained from Charles River, Canada, and as demonstrators, 20 rats, now 48–56 days old, that had served as observers in experiment 1.

Procedure

We used the same apparatus and foods in experiment 2 as in experiment 1, and the procedure of the two experiments was similar, though in experiment 2 all observers had access to food for only 2 h day^{-1}. As in experiment 1, observers assigned to the 2-h condition shared their enclosures with demonstrators that had access to food for 2 h day^{-1} and observers assigned to the no-demonstrator condition had no demonstrators in their enclosures (again replicating one of the conditions in experiment 1). Observers assigned to the 5-h condition had access to food for only 2 h day^{-1} but shared their enclosures with demonstrators that had access to food for 5 h day^{-1}. We introduced food into the compartments of demonstrators paired with observers assigned to both 2- and 5-h conditions each day at the same time that we introduced food into their respective observers' compartments.

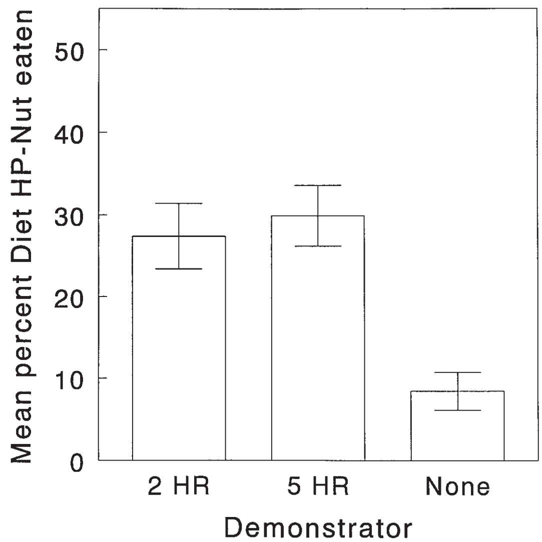

Fig. 3 Mean amount of high-protein, nutmeg-flavored diet (Diet HP-Nut) eaten by observers during the 5 days of experiment 2 as a percentage of the total amount of food that observers ingested during those 5 days (*bars* ± 1 SEM)

Results and discussion

The main results of experiment 2 are presented in Fig. 3. The figure shows the amount of Diet HP-Nut (the relatively unpalatable, high-protein food eaten by demonstrators) ingested by observers as a percentage of the total amount of food the observers ingested during their 5 days of feeding from a cafeteria of four distinctively flavored diets.

Statistical analysis revealed a significant effect of condition on percentage of Diet HP-Nut eaten by observers ($F_{2,27} = 11.75$, $P < 0.0001$. Post hoc tests showed that observers assigned to 2-h and 5-h conditions did not differ from one another in the percentage of Diet HP-Nut that they ate during the last 5 days of the experiment (Tukey's multiple pair-wise comparisons, both $P > 0.05$). However, both observers assigned to the 2-h and to the 5-h condition differed significantly from observers assigned to the no-demonstrator condition in relative amount of Diet HP-Nut eaten (both $P < 0.002$). Observers assigned to 2-h, 5-h and no-demonstrator conditions ate respectively an average (± 1 SEM) of 1.73 ± 0.36, 2.69 ± 0.44, and .93 ± 0.26 g of Diet HP-Nut day^{-1}.

The results of experiment 2 strongly suggest that neither differences in the time demonstrators had access to food nor differences in the time that observers had access to feeding demonstrators was responsible for the interaction between feeding time and effects of demonstrators on observers intake of Diet HP-Nut in experiment 1. To the contrary, the greater influence of public information on the food choices of observers in experiment 1 seems to have reflected differences in time that observers had available for resource sampling.

General discussion

Templeton and Giraldeau (1995, 1996) have shown previously that increased ease of acquiring public information and increased difficulty of individual sampling increase the likelihood that starlings *(Sturnus vulgaris)* will use public information in deciding when to depart a feeding patch. Giraldeau (1997) and Clark and Mangel (1986) have suggested, that as the time available to individuals to forage decreases, they should increase their use of public information in decision making. The results of the present experiments confirm this prediction. They, therefore, suggest that animals might be best viewed not as either able to acquire and use public information or not, but as modifying their dependence on public information in response to environmental conditions (Giraldeau 1997). On this view, a range of ecological variables that theory suggests affect the relative value of socially and individually acquired information to foragers [e.g., environmental stability (Boyd and Richerson 1988), distribution and permanence of food sources (Ward and Zahavi 1973)] should regulate attention paid to public information when foraging.

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