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Use of social information by sodium- and protein-deficient rats: test of a prediction (Boyd & Richerson 1988)

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Boyd & Richerson (1988 Social Learning: Psychological and Biological Perspectives, pp. 29–48) predicted from formal models of the evolution of social learning that an animal should rely more heavily on socially acquired information when seeking a nutrient that it has difficulty learning to select for itself than when seeking a nutrient it can readily identify. We compared the extent to which Norway rats, Rattus norvegicus, seeking either sodium (which they can easily identify) or protein (which they cannot identify), relied on information acquired from recently fed conspecific demonstrators when selecting a food. Consistent with Boyd & Richerson's prediction, when choosing between two unfamiliar, distinctively flavoured foods rich in both protein and sodium, protein-deprived rats showed significantly greater social influence on their food choices than did sodium-deprived rats.

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On the final page of an overview of formal models predicting circumstances under which natural selection should favour reliance on social learning at the expense of individual learning, Boyd & Richerson (1988, page 44) proposed that, ... for a particular species, there will be some aspects of diet about which it will be difficult for individuals to learn what is best, but there will be other aspects about which it will be easy for individuals to learn. The models predict that the former will be acquired disproportionately by social learning and the latter disproportionately by individual learning. As far as we know, there has been no empirical test of this prediction despite the availability of an appropriate model system in Norway rats, R. norvegicus.

Norway rats are dietary generalists that, like other mammals examined to date, find it easy to detect some nutrients in potential foods, but difficult to detect others (Galef 1989, 1991; Rozin & Schulkin 1990). For example, sodium-deficient rats show enhanced ingestion of sodium salts the very first time that they are rendered sodium deficient (Epstein & Stellar 1955) and show a preference for a sodium-rich food within seconds of first exposure to it (Wolf 1969). Conversely, protein-deficient rats offered

Correspondence: B. G. Galef, Jr, Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, Ontario, Canada, L8S 4K1 (email: galef@mcmaster.ca). a choice between a protein-rich and protein-deficient diet, have considerable difficulty learning to prefer the foods that contain protein, although over time, they show an increase in the amount of protein-rich diet that they consume. The time that it takes protein-deficient rats to learn to focus ingestion on a food rich in protein depends on a number of variables including the number of foods available, their relative palatabilities and the latency with which ingestion of a protein-rich food alleviates symptoms of deficiency (for reviews, see Epstein 1967; Lat 1967; Galef 1991). However, learning to focus ingestion on a protein-deficient diet invariably takes longer than learning to focus attention on a sodium-deficient diet.

The prediction from the formal models that Boyd & Richerson (1988) review is clear. Food choices of protein-deprived rats should be more strongly affected by socially acquired information than food choices of sodium-deprived rats.

To compare reliance on socially acquired information of sodium- and protein-deprived rats, we used an experimental paradigm (Galef 2002) that has been used in our laboratory for more than 20 years (for reviews, see Galef 2003, 2005). In brief, after a naïve rat (an observer) interacts with a conspecific (a demonstrator) that has recently eaten a distinctively flavoured food, the observer shows a significant enhancement of its preference for the food that its

demonstrator ate (Galef & Wigmore 1983). For example, after interacting with a demonstrator rat fed cinnamon-flavoured food, an observer rat offered a choice between cinnamon- and cocoa-flavoured food will eat significantly more cinnamon-flavoured food than an observer rat offered the same choice after interacting with a demonstrator rat fed cocoa-flavoured food (Galef & Wigmore 1983). In the experiment reported here, we compared the susceptibility of protein- and sodium-deprived rats to such social influence on their food choices.

An important potential confound when comparing the magnitude of social influences on food choice in animals deprived of, and therefore seeking, different nutrients lies in potential differences in the degree of discomfort of subjects in different deprivation states. For example, it is possible that, in the present experiment, sodium-deprived rats felt less ill than protein-deprived rats. If so, any observed difference in the susceptibility of sodium- and protein-deprived animals to social influences on their food choices might not be the result of differences in the difficulty they would have in learning individually about sodium and protein, but to differences in the susceptibility to social influence of animals experiencing different levels of dissatisfaction with their current state (Schlag 1998; Laland 2004). To control, at least in part, for this possibility, we compared the susceptibility to social influence on food choice of subjects experiencing both high and low levels of protein deprivation with subjects experiencing a mild state of sodium deprivation.

METHODS

Subjects

Thirty-six 8- to 9-week-old Long—Evans female rats acquired from Charles River Canada (St Constant, Quebec, Canada) served as observers. They weighed between 206.9 and 261.2 g (mean \pm SE = 227 \pm 4.9 g) at the time that they were tested for susceptibility to social influence on their food choices. An additional 36 rats, aged 10–11 weeks, that had served as observers in previous experiments, served as demonstrators in the present experiment.

Apparatus

Throughout the experiment, we housed both demonstrators and observers individually in stainless steel, wiremesh hanging cages, measuring $20 \times 20 \times 34$ cm. We presented food to all subjects in semicircular, stainless steel food cups (10 cm diameter and 5 cm deep). To prevent spillage, we filled food cups to only half their depth.

Procedure

Deprivation of protein

To induce protein deficiency, we fed observers, for 1 week, Teklad Basal Mix for Adjusted Protein (TD 86146, Teklad Mills, Madison, WI, U.S.A.) to which we had added either 4% by weight High Protein Casein (CA 160030) to

make 4% protein diet or 8% by weight High Protein Casein to make 8% protein-deficient diet (The Canadian Council on Animal Care recommends a minimum of 12% protein for maintaining protein in adult rats).

Deprivation of sodium

To induce a mild sodium deficiency, we fed observers Teklad sodium-deficient diet (TD 90228: sodium-deficient diet) for 1 week while giving them demineralized water to drink

Diets used during social induction and testing

We prepared diets for use during testing for social influence on food choice by mixing either 1 g of powdered cinnamon (McCormick Canada, London, Ontario: cinnamon-flavoured diet) or 2 g of Hershey's Cocoa (Hershey's Canada Inc., Mississauga, Ontario, Canada: cocoa-flavoured diet) with sufficient powdered Teklad Rodent Diet (W) 8640 (diet 8640) to bring the mixture to 100 g. Diet 8640 is a commercial laboratory rodent chow that contains both sufficient protein (22.6%) and sufficient sodium (0.40%) to support normal growth, development and reproduction in rats.

Experimental procedures

To begin, we weighed each observer, then randomly assigned 12 observers to each of three conditions: low-protein diet, high-protein diet and sodium-deprived. For 7 consecutive days, we provided sodium-deficient diet and distilled water to subjects assigned to the sodium-deprived condition and tap water and either 4% protein diet or 8% protein diet to subjects assigned, respectively, to severe and mild protein-deprivation conditions. At the end of the 7 days of deprivation, we reweighed each observer and determined its weight gain or loss during the preceding week.

Social learning

Seventy-two hours before the end of the 7-day period of maintenance of observers on their deficient diets, we placed the 36 demonstrators on a 23-h/day schedule of food deprivation, feeding them diet 8640 for 1 h/day for 2 consecutive days. After a third 23-h period of deprivation, we fed 18 demonstrators weighed samples of cinnamon-flavoured diet and 18 demonstrator weighed samples of cocoa-flavoured diet for 1 h. Immediately after this 1-h feeding period, we placed a demonstrator in each observer's cage, assigning demonstrators to observers so that half of the observers in each of the three conditions received a demonstrator fed cinnamon-flavoured diet and the rest received a demonstrator fed cocoa-flavoured diet. We then left demonstrators and observers undisturbed to interact for 30 min.

Testing observers

At the end of the 30-min period of interaction between demonstrators and observers, we removed the demonstrator from each observer's cage and, for 23 h, offered each observer two weighed food cups, one containing cinnamon-flavoured diet and the other cocoa-flavoured diet. We reweighed the cups and calculated the percentage of each observer's total intake that was of the diet that its demonstrator had eaten (i.e. for observers that interacted with demonstrators fed cinnamon-flavoured diet, grams of cinnamon-flavoured diet eaten/total amount eaten \times 100, and for observers that interacted with demonstrators fed cocoa-flavoured diet, grams of cocoa-flavoured diet eaten/total amount eaten \times 100), 4 and 23 h after we introduced food cups containing each diet into observers' cages.

Statistical Tests

Because of significant heterogeneity of variance in the data describing the percentage that observers ate of their respective demonstrators' diets (Bartlett's statistic corrected = 8.36, P < 0.02), we used nonparametric statistics for analysing those data.

Ethical Note

The McMaster University Animal Research Ethics Board approved the procedures used in this experiment on 23 August 2004 by AUP Number 04-06-28.

RESULTS

Effects of Deprivation

During the 7-day period of deficiency induction, observers assigned to the mild protein-deprivation condition lost $5.6 \pm 1.9\%$ (mean \pm SEM) of their initial body weights, whereas those assigned to the severe protein-deprivation condition lost $9.9 \pm 1.5\%$ of their initial body weights, and subjects assigned to the sodium-deprivation condition lost $7.0 \pm 1.0\%$ of their initial body weights. During the same 7-day period, a group of 12 female rats of the same age and weight as subjects in the experiment maintained on ad libitum diet 8640 and tap water gained $16.3 \pm 1.5\%$ of their initial body weights. Thus, although all animals assigned to experimental conditions lost weight relative to control animals fed the nutritionally balanced diet 8640 ($F_{44} = 8.71, P < 0.001$; Bonferroni multiple comparisons tests, all t values > 2.49, all P values < 0.05), subjects assigned to the three deficient groups lost equivalent amounts of weight (one-way ANOVA: $F_{33} = 2.10$, P = 0.14) with protein-deprived subjects losing both slightly less weight (mild protein-deprivation condition) and slightly more weight (severe protein-deprivation condition) than subjects assigned to the sodium-deprivation condition.

Ingestion by Demonstrators

All demonstrators ate more than 5 g of cinnamon- or cocoa-flavoured diets during the 1-h feeding period that immediately preceded their interaction with observers.

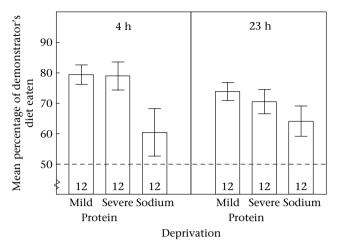


Figure 1. Mean \pm SE percentage demonstrators' diets eaten by protein-deficient and sodium-deficient observers during 4 h (left panel) and 23 h (right panel) of testing.

Results of Testing

At the end of 4 h of testing, the amount of demonstrator's diet consumed by rats in the protein-deprivation conditions was approximately 20 percentage points higher than that consumed by rats in the sodium-deprivation condition (Kruskal–Wallis one-way ANOVA: $H_2 = 6.50$, P < 0.04; Fig. 1). In contrast, at the end of 23 h of testing, the percentage of demonstrator's diet eaten no longer differed between the sodium-deprived and two protein-deprived groups ($H_2 = 2.47$, P = 0.29; Fig. 1).

Seventeen of the 24 observers assigned to protein-deprivation conditions (i.e. those subjects expected to require some time to learn whether a diet contained a nutrient that they needed) ingested a smaller percentage of their demonstrator's diet during the entire 23-h of testing than during the first 4 h of testing (Wilcoxon matched-pairs signed-ranks test: T = 77, P < 0.05). Apparently, as protein-deprived observers learnt that the two diets available to them had similar postingestive effects, and consequently, that the information that they had received from their demonstrators was irrelevant (Galef & Whiskin 1998, 2001) they gradually abandoned reliance on the information they had extracted from their respective demonstrators.

DISCUSSION

The finding that observers assigned to the sodium-deprivation condition (that faced a relatively easy aspect of diet about which to learn individually) showed significantly less social influence on their food choices during the first 4 h of testing than observers assigned to the two protein-deprivation conditions (that faced a relatively difficult aspect of diet about which to learn individually) is entirely consistent with Boyd & Richerson's (1988) prediction as to the relative influence of socially acquired information on food choices of animals seeking nutrients that they

find relatively easy or relatively difficult to identify independently.

The need for empirical examination of predictions from formal theory as to the conditions that determine the relative influence of socially acquired information on decision making in animals is widely recognized (e.g. Laland 2004; Galef 2006). The present experiment is but one of a number of experiments either completed (e.g. Galef & Whiskin 2006; for review, see Galef 2006) or currently underway in our laboratory designed to explore the applicability of predictions of factors (see Laland 2004 for review) that formal models predict should affect the magnitude of the influence of socially acquired information on the behaviour of Norway rats deciding which of two foods to ingest. The results of such studies indicate that the way forward will be both long and hard. With respect to the present experiment, discovery of a single circumstance in which the difficulty that members of a single species have in learning individually to select appropriate foods predicts the extent to which they rely on socially acquired information in diet selection is but a first step in assessing the generality of the rule of thumb that Boyd & Richerson (1988) deduced from first principles.

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