

# Protein Deficiency Magnifies Social Influence on the Food Choices of Norway Rats (*Rattus norvegicus*)

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The food choices of protein-deprived juvenile rats were more profoundly affected by interaction with conspecifics than were the food choices of protein-replete juvenile rats. When choosing among four different-flavored, protein-deficient diets, protein-deprived rats ate significantly more of the diet eaten by a conspecific demonstrator than did protein-replete rats. These data suggest that the food choices of the relatively less successful members of a population are most affected by social interaction. Consequently, the mean effect of social interaction on diet selection in a population of Norway rats is likely to be positive.

Results of studies in several laboratories indicate that naive "observer" rats will exhibit enhanced preference for a food after interaction with a conspecific "demonstrator" that has eaten that food. When offered a choice between two foods (diets A and B), those observer rats that interact with demonstrators previously fed diet A show a greater preference for diet A than do those observer rats that interact with demonstrators previously fed diet B (Galef, Kennett, & Wigmore, 1984; Galef & Wigmore, 1983; Grover et al., 1988; Heyes & Durlach, 1990; Posadas-Andrews & Roper, 1983).

Such social influences on food choice can play an important role in the survival of rats faced with the need to select a nutritionally adequate diet from a cafeteria of potential foods. For example, Beck and Galef (1989) allowed young rats to choose among four distinctively flavored foods. Three of these foods were both protein deficient and relatively palatable and one was both protein rich and relatively unpalatable. The experimental situation had been designed to make it difficult for individual rats to learn to select the protein-rich food (Galef & Beck, 1990; Westoby, 1974), and as expected, only 2 of 24 young rats tested in isolation developed a preference for the protein-rich food during a 1-week test period. In contrast, 25 of 27 subjects that shared their enclosures with demonstrator rats that had been trained to eat the relatively unpalatable, protein-rich food developed a preference for the protein-rich food during the week-long test. Subjects interacting with trained demonstrators thrived, whereas subjects choosing among foods in isolation lost weight and became sickly. Beck and Galef (1989) interpreted these results as suggesting that, in natural environments, where individual trial-and-error learning is unlikely to lead omnivores to self-select an adequate diet from among potential foods, social

learning could markedly increase the probability of survival (Galef, in press; Galef & Beck, 1990).

There is a possible difficulty with the hypothesis that social interaction facilitates selection of nutritionally adequate diets by rats living in challenging habitat. Imagine two rats ( $\alpha$  and  $\beta$ ). Rat  $\alpha$  is a healthy individual that has been eating protein-rich food A; rat  $\beta$  has been eking out a marginal existence, subsisting on protein-poor food B, and is malnourished. As a consequence of interaction between rats  $\alpha$  and  $\beta$ , both rat  $\beta$ 's probability of eating nutritious food A and rat  $\alpha$ 's probability of eating deficient food B should increase. It appears, at least superficially, that social influence does as much harm to rat  $\alpha$  as it does good for rat  $\beta$ .

The problem posed by social induction of preferences for inferior foods is probably small because the long-term cost to healthy rat  $\alpha$  of being socially induced to eat an inadequate food that it could then learn to avoid would be relatively minor. Alternatively, the long-term benefit to sickly rat  $\beta$  of being socially induced to sample a nutritious food that it could then learn to eat would be relatively large. Still one feels some unease at proposing a diet-selection mechanism that, of itself, has equal potential for good and ill.

If it were the case that healthy rats influenced conspecifics to eat the foods that they were eating, whereas sickly rats influenced conspecifics to avoid the foods that they were eating, then there would be no problem. However, evidence from several studies suggests that healthy and sickly demonstrators are equally effective in enhancing their observers' preferences for foods (Galef, McQuoid, & Whiskin, 1990; Galef, Wigmore, & Kennett, 1983; Grover et al., 1988).

The probability of socially acquired information interfering with, rather than enhancing, adaptive food choices by rats could also be reduced if the magnitude of social influence on diet selection varied as a function of the internal states of rats. For example, if those rats that were doing well at selecting foods (i.e., that were well nourished) were relatively resistant to social influence on their food choices, whereas those rats that were malnourished and ill were relatively susceptible to social influence, then the immediate benefits of social influence would tend to be greater than the immediate costs.

Determining whether deficient rats are more susceptible than replete rats to social influences on their food choices is

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not so straightforward a matter as it might appear at first glance. In particular, one cannot simply pair naive-deficient and naive-replete rats with demonstrators trained to select a nutritionally adequate food from among an array of foods and then see whether deficient subjects eat more nutritionally adequate food than do replete subjects.

First, and perhaps trivially, unless each subject is physically separated from its respective demonstrator, there is no way to determine how much of each food was eaten by subjects and how much was eaten by their demonstrators. Second, and less trivially, deficient subjects might experience greater reinforcement than replete subjects from eating nutritionally adequate food. Consequently, deficient subjects might learn to eat nutritionally adequate food more rapidly than replete subjects (Gibson & Booth, 1986), even if deficient subjects were no more susceptible than replete subjects to social influences on their food selection. Third, it is always possible that deprivation might cause changes in flavor preferences that only accidentally resulted in increased preference for the nutritionally adequate food (Richter, 1942–1943). Consequently, our experiment was designed to ensure that: (a) demonstrators and the subjects with which demonstrators were paired fed from separate feeding sites, (b) each of the foods among which replete and deficient subjects chose were equally ineffective in alleviating the deficiency state that had been induced in deprived subjects, and (c) there were no significant changes in the food preferences of subjects as a function of their respective deprivation states. Condition a was met by physically separating demonstrators from observers; condition b was met by providing subjects with only deficient diets to choose among, so that they could not learn from post-ingestional consequences which diet to eat; and condition c was controlled by examining the food choices of replete and deficient subjects in the absence of social influence.

## Method

### Subjects

Thirty-two male Long-Evans rats, weighing 150 to 175 g at the start of the experiment, served as subjects. All were born and reared in the vivarium of the McMaster University Psychology Department to breeding stock acquired from Charles River Canada (St. Constant, Quebec). Sixteen additional male rats weighing 175 to 200 g from the same source served as demonstrators. Both subjects and demonstrators had been maintained since weaning (at 21 days of age) in sibling groups of 4 on ad lib Purina Rodent Laboratory Chow #5001 and water in a temperature- and humidity-controlled colony room on a 12:12-hr light/dark cycle. At the beginning of the experiment, the 32 subjects were assigned randomly to deprivation and control conditions.

### Diets

**Deprivation and habituation.** During both the 7-day deprivation period and 1-day habituation period (described in *Procedure*), subjects in both deprivation and control conditions were maintained on diets composed of protein-free basal mix (Teklad Diets, Madison, Wisconsin, catalog number TD 89044; in g/kg, 808.5 g sucrose, 108.2 g coconut oil, 27.0 g cod liver oil, 54.0 g mineral mix, 2.3 g vitamin

mix) and high-protein casein (Teklad Diets, catalog number 160030). Subjects in two deprivation conditions ( $n = 8$  per condition) were fed a diet containing 6% by weight casein (5.3% by weight protein), whereas subjects in two control conditions ( $n = 8$  per condition) were fed a diet containing 20% by weight casein (17.5% by weight protein). A 12% by weight protein diet is considered adequate for young rats (*Guide to the Care and Use of Experimental Animals*, 1980).

**Testing.** During the 1-week period of testing (described in *Procedure*), each subject was offered an ad lib choice among four distinctively flavored, protein-poor foods. Each of these four protein-poor foods was composed of 80% by weight protein-free, basal mix (Teklad Diets, Madison, Wisconsin, catalog number TD 86146; in g/kg, 808.5 g corn starch, 108.1 g vegetable oil, 7.0 cod liver oil, 54.1 g mineral mix, and 2.7 g vitamin mix), 10% corn starch, 5% granulated sugar, and 5% high-protein casein (Teklad Diets, catalog No. 160030). The four different, protein-poor foods were flavored with, respectively, 1% by weight McCormick's fancy ground cinnamon (Diet Cin), 2% by weight Hershey's pure cocoa (Diet Coc), 1% by weight Club House ground thyme (Diet Thy), or 1% by weight Club House ground nutmeg (Diet Nut). Previous experiments have shown that Diet Nut was the least preferred of the four foods used (Beck & Galef, 1989).

### Apparatus

The experiment was conducted in cages ( $1 \times 1 \times .3$  m), each divided in half by a screen (1-cm grid) that separated each subject from its respective demonstrator (see Figure 1). Each of the two compartments in each cage (referred to later as, respectively, subjects' and demonstrators' compartments) contained both a wooden nest box ( $30 \times 15 \times 15$  cm) with a single entrance ( $5 \times 5$  cm) and a water bottle.

### Procedure

The experiment was conducted in three stages: deprivation, habituation, and testing.

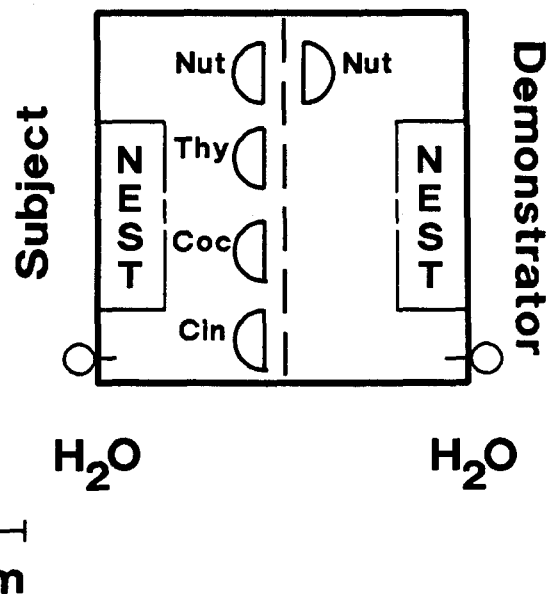


Figure 1. Overhead schematic of apparatus used to measure susceptibility to social influence on diet choice. (Nut = nutmeg; Thy = thyme; Coc = cocoa; Cin = cinnamon; H<sub>2</sub>O = water.)

**Deprivation.** Subjects were assigned randomly to deprivation ( $n = 16$ ) and control ( $n = 16$ ) conditions and placed in groups of 4 in shoebox cages ( $38 \times 30 \times 15$  cm) where, for 7 consecutive days, each group had ad lib access to Teklad Diet 89044 mixed with either 6% casein by weight (deprivation condition) or 20% casein by weight (control condition).

**Habituation.** At the end of the 7-day deprivation period, each of 8 deprived and 8 control subjects (those subjects assigned to demonstrator/deprivation and demonstrator/control groups) were placed in the subject's compartment of an apparatus with a demonstrator in the demonstrator's compartment. The remaining 8 deprived and 8 control subjects (those subjects assigned to no demonstrator/deprivation and no demonstrator/control groups) were each placed in the subject's compartment of an apparatus with no demonstrator in the demonstrator's compartment. A bowl containing whichever diet a subject had eaten during the deprivation stage of the procedure was then placed in the center of each subject's compartment and a bowl containing Teklad Diet 89044 with 20% casein was placed in each demonstrator's compartment. Subjects and demonstrators were then left undisturbed for 24 hr. This 24-hr period of habituation of subjects to the experimental situation had been found in an earlier study (Beck & Galef, 1989) to reduce variance in the amount eaten by subjects during the testing phase of the experiment.

**Testing.** At the end of the 24-hr habituation period, the food bowls were removed from demonstrators' and subjects' compartment, and each subject was presented with four 10-cm diameter semicircular food cups, each containing a different-flavored, protein-deficient diet. The four food cups were attached, in the positions indicated in Figure 1, to the screen partition separating each subject's compartment from its demonstrator's compartment. As also indicated in Figure 1, a food cup containing Diet Nut was placed in each demonstrator's compartment directly across the screen partition from each subject's food cup containing Diet Nut. For the following week, subjects and demonstrators were left undisturbed except for daily weighing of all food cups.

**Data Analysis**

Data were discarded from subjects ( $n = 8$ ) spilling food on more than 1 day of Testing, leaving 6 subjects in each of the four groups (demonstrator/deprivation, demonstrator/control, no demonstrator/deprivation, and no demonstrator/control).

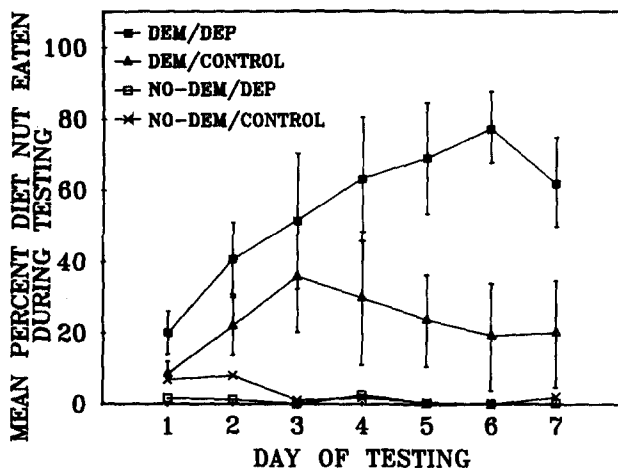


Figure 2. Mean percent Diet Nut eaten by subjects on each day of testing. (Flags =  $\pm 1$  SEM; DEM = demonstrator; DEP = deprivation.)

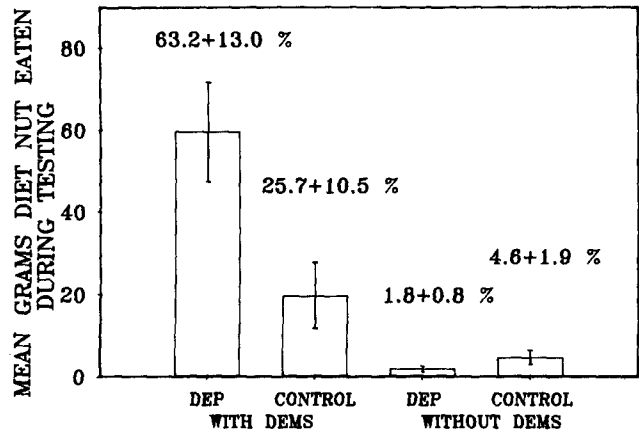


Figure 3. Mean total amount (g) of Diet Nut eaten across all 7 days of testing by subjects in each of the four groups. (Numbers above histograms indicate the mean percent Diet Nut eaten across all 7 days of testing by subjects in each of the four groups. Flags =  $\pm 1$  SEM; DEP = deprivation; DEMS = demonstrators.)

Because percentage scores are not normally distributed, all percentage scores were arcsine transformed before they were used in parametric statistical tests.

**Results**

The main results of Experiment 1 are presented in Figure 2, which shows, for each day of testing, the mean amount of Diet Nut eaten by the 6 subjects in each group, as a percentage of the total amount of food that each subject ate on that day. As one would expect from the results of previous studies (Beck & Galef, 1989), during the 7 days of the experiment, subjects in groups with demonstrators ate a significantly greater percentage of Diet Nut than did subjects in groups without demonstrators, repeated measures analysis of variance (ANOVA),  $F(1, 5) = 21.82, p < .006$ . More important for the hypothesis under investigation, there was a significant interaction between deprivation state and presence of a demonstrator on the percentage of Diet Nut subjects ate during testing, repeated measures ANOVA,  $F(1, 5) = 8.50, p < .034$ . As can also be seen in Figure 2, subjects in the demonstrator/deprivation group ate a larger percentage of Diet Nut than did subjects in the demonstrator/control group, repeated measures ANOVA,  $F(1, 5) = 6.64, p < .049$ .

The amount of target food (Diet Nut) eaten by subjects during the week-long test period was as important an index of subjects' diet choice as was the percentage of target food that subjects ate. As can be seen in Figure 3, which shows the amount of Diet Nut eaten by subjects during the 7-day test: (a) subjects with demonstrators ate more Diet Nut than did subjects without demonstrators,  $F(1, 1) = 23.82, p < .0002$ , (b) the amounts of Diet Nut eaten by deprived and control subjects without demonstrators did not differ using Student's  $t$  test,  $t(1) = 2.43, p = ns$ , and (c) there was a significant interaction between deprivation state and presence of a demonstrator in determining the amount of Diet Nut eaten,  $F(1, 1) = 8.47, p < .009$ . These data indicate that protein deprivation

vation both increased the effects of social interaction on food choice and failed to increase preference for the flavor of Diet Nut.

While taking measurements of subjects' daily diet choices, it became apparent that there were systematic differences in the diet sampling patterns of protein-deprived and protein-replete subjects without demonstrators: Subjects in the no demonstrator/deprivation group tended to concentrate their intake on a single diet during each day of testing, changing their preferred diet from one day to the next; subjects in the no demonstrator/control group spread their intake more evenly across the four diets on each day of testing. Rozin (1969) described similar differences in the diet sampling patterns of thiamine-deficient and replete rats choosing among four different foods for 8 hr/day.

To compare systematically the diet-sampling patterns exhibited by protein-deficient and control subjects, we calculated the percentage of each subject's total intake that it took from the food which it ate most of on each day of testing, a measure we refer to here as a subject's percent modal diet intake. The upper panel of Figure 4 shows, for each day of testing, the mean percent modal diet intake of protein-deprived and control subjects without demonstrators. As is evident from inspection of the upper panel of Figure 4, protein-deficient subjects without demonstrators concentrated their daily intake on a single diet to a greater extent

than did control subjects without demonstrators, repeated measures ANOVA,  $F(1, 5) = 25.27, p < .001$ .

It is possible that a constant level of socially induced bias acting on the different underlying patterns of diet sampling exhibited by protein-deficient and control subjects produced the difference in amount of Diet Nut eaten by subjects in demonstrator/deprivation and demonstrator/control groups described in Figures 2 and 3. However, reference to the lower panel of Figure 4, which shows the mean percent modal diet intake during testing of subjects in demonstrator/deprivation and demonstrator/control groups reveals no significant difference in the diet sampling patterns of subjects in those two groups during testing, repeated measures ANOVA,  $F(1, 5) = 1.43, p = .29$ . It is, therefore, difficult to see how differences in the diet sampling patterns of protein-deprived and control subjects could account for the observed differences in Diet Nut intake exhibited by subjects in demonstrator/deprivation and demonstrator/control groups.

It is perhaps also worth mentioning that we have performed the experiment reported here twice. The first experiment we ran differed from the present one only in the diets fed to subjects during the deprivation and habituation stages of the experiment (Beck, 1990). In the first experiment, as in the present one, during testing: (a) deprived subjects without demonstrators ate no more Diet Nut than did replete subjects without demonstrators, (b) protein-deprived subjects with demonstrators ate significantly more Diet Nut than did replete subjects with demonstrators, and (c) the percent modal diet intake of protein-deprived subjects without demonstrators was significantly higher than the percent modal diet intake of control subjects without demonstrators.

There was also one important difference between the outcome of the present experiment and that of our first experiment. In the first experiment, intake of Diet Nut by protein-deprived subjects with demonstrators was significantly greater than that of control subjects with demonstrators on each of Days 3 to 7 of testing, but not across all 7 days of testing. Furthermore, the interaction between presence of a demonstrator and deprivation condition was significant on each of Days 5 to 7 of testing but not across all 7 days of testing. We have not investigated the cause of this difference in the time course of the effects of protein deprivation on social influence. However, it is possible that the variability reflected differences between repetitions in the degree of protein deprivation of subjects in protein-deprived groups at the beginning of the testing phase.

## Discussion

The tendency of rats to be influenced in their patterns of food choice by the food choices of others would permit those rats making inferior food choices to deflect the adaptive patterns of food choice of their more successful fellows. Workers both in our laboratory and elsewhere had expected that successful rats might protect themselves against such malevolent influence by preferring foods eaten by healthy demonstrators and ignoring or avoiding foods eaten by ill demonstrators. However, the results of several experiments suggest that rats do not use such a strategy (Galef et al., 1990; Galef et al., 1983; Grover et al., 1988).

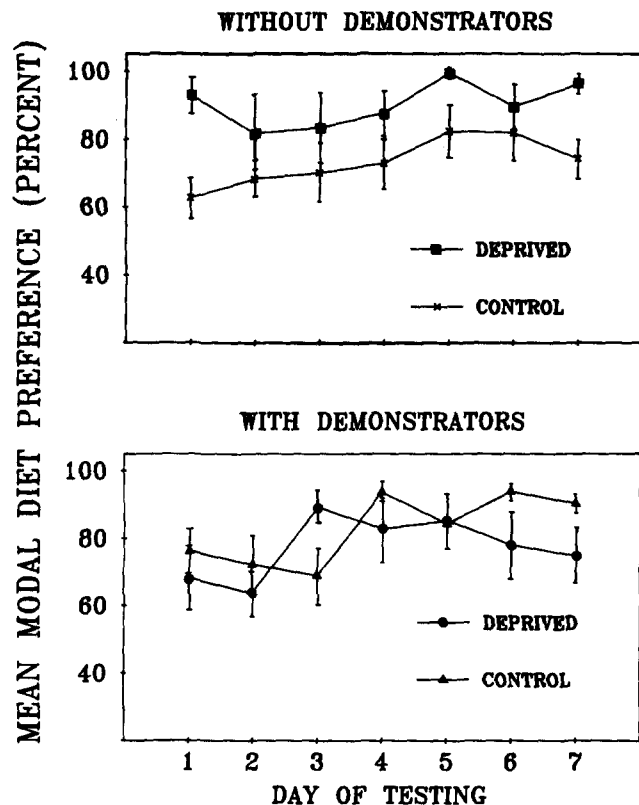


Figure 4. Mean modal diet preference of subjects without demonstrators (upper panel) and with demonstrators (lower panel) on each day of testing (Flags =  $\pm 1 SE_M$ ).

How then can social influence on dietary preference be adaptive if rats are affected equally by conspecifics of high and low fitness? The results reported here suggest that although the state of health of a demonstrator is not a determinant of the effectiveness of that demonstrator in modifying the food choices of its observers, the state of health of observers does effect the extent to which they exhibit socially induced modifications of their food choices. Protein-deficient rats exhibit greater effects of social influence on their food selection than do protein-replete rats. Consequently, individuals of presumably low fitness will be more profoundly influenced in their food selections by interaction with their fellows than will individuals of presumably high fitness. Therefore, social influences on food choice will, on average, increase fitness.

Some years ago, Deutsch (1962, p. 273) suggested that a useful distinction can be made between "the conditions which determine the ability to imitate and those which determine the desire to imitate." In the present case, a parallel distinction might be made between those conditions affecting the ability to extract social information about food choice and those conditions influencing the motivation to acquire and to use such information. It does not seem reasonable to suggest that the ability of rats to determine what foods conspecifics have been eating would increase with protein deficiency. Rather it seems probable that the motivation to acquire or to use information about the foods that others are eating would increase in protein-deficient rats. Deprived rats might interact with demonstrators more frequently than might replete rats, thus acquiring more information from demonstrators than replete rats; alternatively, the behavior of deprived rats might be more profoundly affected than that of replete rats by whatever information they did acquire from demonstrators. In either case, the present results indicate that the internal state associated with protein deficiency increases the magnitude of social influences on the feeding behavior of Norway rats.

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