

## Social Influences on the Selection of a Protein-Sufficient Diet by Norway Rats (*Rattus norvegicus*)

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Investigated effects of interactions between naive and knowledgeable rats (*Rattus norvegicus*) on selection of a nutritionally adequate diet by the naive. We found that during a 7-day test, isolated rats choosing among 4 foods, 3 of which were protein-deficient and 1 of which was protein-rich, failed to learn to prefer the protein-rich diet and lost weight. Conversely, those rats that interacted with conspecifics trained to eat the protein-rich diet developed a strong preference for that diet and thrived. The authors also found that Ss were more strongly influenced in their diet selection by the flavor of the foods eaten by conspecifics than by the locations where conspecifics fed. The results suggest that social influence may be important in development of adaptive patterns of diet choice by rats (or other dietary generalists) that need to find nutritionally adequate diets in demanding environments.

Students of dietary self-selection have described two complementary processes that may lead animals foraging in the world outside the laboratory to select nutritionally adequate foods from among the myriad potentially ingestible, beneficial, toxic, and useless substances found in natural habitat. First, animals have the ability to detect the presence of some nutrients in complex foods and can use tastes associated with those nutrients to select valuable foods to eat (Richter, 1943; Rozin, 1976). Second, animals can associate the post-ingestional consequences of a food with its taste and can, therefore, learn to select foods that provide valuable nutrients (Booth, 1985; Harris, Clay, Hargreaves, & Ward, 1933; Rozin, 1976). In the literature, these two abilities—the ability to detect directly some nutrients in foods and the ability to learn about the nutritional value of foods from the consequences of their ingestion—have been treated as sufficient to explain the development of adaptive patterns of food choice by generalists in natural environments (Rozin, 1976).

One can, however, imagine circumstances in which neither direct detection of the taste of nutrients in foods, individual learning about the consequences of eating various foods, nor both processes considered together would be adequate to explain the selection of a nutritionally adequate diet by animals. Dietary generalists such as rats can detect directly the

sensory qualities correlated with only a handful of nutrients (e.g., sugars, salts, fat, and water) from among dozens of substances required for growth, self-maintenance, and reproduction. The ability of rats to learn about the nutritional value of ingested substances is also limited and need not result in adaptive food choices (see Westoby, 1974, for review). As the number of potential foods available for an animal to sample and the time to onset of the rewarding consequences of eating a nutritionally valuable food increase (Harriman, 1955; Harris et al., 1933; Rozin, 1969), and as the relative palatability of a food containing a necessary nutrient decreases (Kon, 1931; Scott & Quint, 1946; see Epstein, 1967, for review), the ability of an animal to acquire a preference for a nutritionally valuable food rapidly declines. Thus, although in benign environments the sensory-affective systems (Young, 1959) and learning abilities of individuals often prove adequate to the task of diet selection, in more challenging situations (where an animal may find many useless, potential foods to sample, where some needed nutrients are available only in unpalatable foods, and where foods have long-delayed, post-ingestional consequences), the probability that an isolated individual will find an adequate diet before exhausting its internal reserves can be quite low.

Many vertebrate generalists live throughout their lives as members of social groups. All mammals and most birds spend their first weeks or months of life in intimate association with a parent or parents who, by virtue of their very reproductive success, demonstrate the nutritional adequacy of the foods they have been eating. A naive juvenile, maturing in a demanding environment and unable to learn to identify an adequate diet by itself, may prosper simply by allowing its sampling of foods to be guided by the food choices of either its parents or other adults that it observes feeding. Socially acquired information concerning the foods others eat (Galef, 1986, in press) may provide a complement or supplement to individual learning that facilitates identification of valuable foods.

This series of experiments was undertaken to examine the possibility that naive, juvenile rats living in circumstances in which they were unable to select a nutritionally adequate diet

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for themselves could learn to choose a nutritionally adequate diet if allowed to interact with adult conspecifics that were doing so.

Experiment 1

Free-living, adult omnivores may be challenged occasionally by a failure of one or another of the foods on which they have come to depend. To survive, every juvenile must develop de novo a nutritionally adequate diet composed of solid foods. Because in natural circumstances it is juvenile animals that must most frequently solve the problem of diet selection, the study of how generalists develop nutritionally adequate diets ought to focus on the young (Galef & Beck, in press).

In this experiment we determined whether both weanling and adolescent rats, either in isolation or in a social context, could develop a preference for a single, protein-rich diet when it was presented together with a number of more palatable, protein-poor diets. We anticipated that in the test situation we used, isolated animals would have difficulty identifying the nutritionally adequate diet. Rats cannot directly detect the presence of protein in food, so detection of the nutritionally adequate food on the basis of its sensory qualities was not possible in our experimental situation. Furthermore, to make individual learning about the consequences of eating the protein-rich diet difficult, we both provided several alternative foods for our subjects to choose among (Harris et al., 1933; Rozin, 1969) and placed the needed protein in the least palatable of these foods (Kon, 1931; Scott & Quint, 1946).

Method

Subjects

Thirteen weanling (70 to 90 g) and 26 adolescent (150 to 175 g), male, Long-Evans rats (*Rattus norvegicus*) served as subjects in this experiment. All were born and reared in the McMaster University vivarium and all were descended from breeding stock acquired from Charles River Canada (St. Constant, Quebec). An additional 47 (175 to 200 g) male rats from the McMaster University colony served as demonstrators.

Diets

During the experiment each subject was presented with four diets. Three of these diets were both relatively palatable and relatively poor in protein (4.4% protein by weight); one was both relatively unpalatable and relatively rich in protein (17.5% protein by weight). (A 12%-protein diet is considered adequate for young rats; *Guide to the Care and Use*, 1980). Each of the three protein-poor diets was composed of 80% by weight protein-free, basal mix (Teklad Diets, Madison, Wisconsin, Catalogue No. TD 86146; in g/kg, 808.5 g corn starch, 108.1 g vegetable oil, 7.0 g 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, Catalogue No. 160030). The three, different, protein-poor diets were flavored with, respectively, 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).

The single protein-rich diet was composed of 80%-by-weight protein-free, basal mix and of 20% high-protein casein. One-percent-by-weight Club House ground nutmeg was added to the high-protein diet (Diet HP-Nut) to give it a distinctive flavor and smell. Diet HP-Nut, lacking any palatable sugar, loaded with unpalatable casein (Kon, 1931), and flavored with nutmeg (which previous experiments have suggested was the least preferred of the four flavors we used), proved, as we had intended, to be the least preferred of the four diets when all were offered to hungry young rats in a 2-hr simultaneous choice.

Apparatus

The feeding behavior of subjects and demonstrators was observed in 1 m wide x 0.3 m high x 1 m deep cages that were constructed of angle iron and hardware cloth, floored with galvanized sheet metal, and carpeted to a depth of 2 to 3 cm with woodchip bedding. Each cage (see left panel of Figure 1) contained a single 30 x 30 cm, wooden, nest box with two 5 x 5 cm entrances and a watering station. The diets were presented in round, 10-cm diameter, Pyrex bowls placed in the positions indicated in Figure 1a.

Procedure

The experiment was performed in three stages:

*Demonstrator training.* Demonstrators were housed individually and trained with a taste-aversion conditioning procedure, to avoid

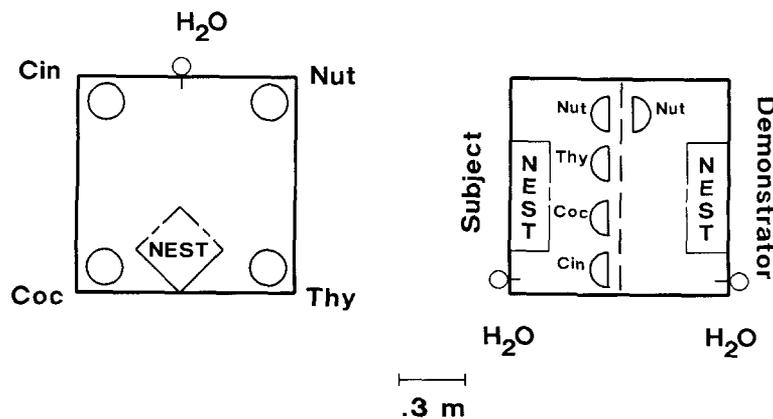


Figure 1. Overhead schematic of apparatuses used in Experiment 1 (left) and Experiments 2 and 3 (right).

eating each of the three, protein-poor diets (Diets Cin, Coc, and Thy). Each demonstrator was first food-deprived for 12 hr and was then given access for 2 hr to a weighed food bowl containing Diet Cin. Following the 2-hr period of access to Diet Cin, each demonstrator was injected intraperitoneally with 10-g/kg, 2% LiCl solution. The demonstrators were next given 34 hr to recover from the effects of toxicosis while maintained ad lib on powdered Purina Laboratory Rodent Chow. After recovery from toxicosis, each demonstrator was trained first to avoid Diet Coc, then to avoid Diet Thy by the same procedure that had been used to condition an aversion to Diet Cin. One hour after pairing of LiCl with Diet Thy, each demonstrator was given ad lib access to high-protein, nutmeg-flavored diet (Diet HP-Nut) for 24 hr.

Given the rationale for the present study, it would have been best to train demonstrators to eat Diet HP-Nut by allowing them to learn that each available alternative diet was inadequate and that eating any one exclusively or all three in combination caused illness. Unfortunately, the older demonstrators became, the more likely they were to attack subjects placed in their cages. If we had not used artificial training techniques to speed the demonstrators' learning of aversions to Diets Coc, Cin, and Thy, they would have become too old during training to allow subjects to be placed safely with them. However, even using the less-than-ideal methods that practical considerations required, we were able to examine the effect that a demonstrator's eating nutritious Diet HP-Nut had on the acquisition of a preference for that diet by naive subjects.

**Habituation.** Subjects within each age-weight class were randomly assigned to groups and, depending on the group to which a given subject was assigned, placed either alone or with demonstrators in an apparatus. Subjects assigned to the Weanling-No Demonstrator Group ( $n = 7$ ) and to the Adolescent-No Demonstrator Group ( $n = 11$ ) were each placed alone in an apparatus. Subjects assigned to the Weanling-Three Demonstrator Group ( $n = 6$ ), Adolescent-One Demonstrator Group ( $n = 8$ ), and Adolescent-Three Demonstrator Group ( $n = 7$ ) were each placed in an apparatus with either one or three demonstrators, as appropriate.

A bowl containing powdered Purina Laboratory Rodent Chow (Diet P) was placed in the middle of each apparatus, and all subjects and demonstrators were left undisturbed for 24 hr. This 24-hr period of habituation of subjects and demonstrators, both to one another and to the apparatus, had been found in earlier studies to reduce variance in the amount eaten by subjects during the test phase of the experiment described in the next section.

**Testing.** Immediately after habituation, the bowl containing Diet P was removed from each apparatus and four, 10-cm diameter, round, Pyrex food bowls containing, respectively, Diets Cin, Coc, Thy, and HP-Nut were placed in the corners of the apparatus in the locations indicated in the left panel of Figure 1. For the next week the subjects and demonstrators were left undisturbed, except for daily weighing of subjects and refilling of foodbowls.

### Data Analysis

To determine the efficiency of subjects' diet selections in this experiment, we examined the cumulative change in body weight of subjects as a percentage of their respective body weights at the start of the test phase of the experiment. To make these percentage scores suitable for parametric statistical analyses, they were arcsine transformed.

### Results and Discussion

The main results of Experiment 1 are presented in Figure 2, which shows the mean cumulative percent changes in body

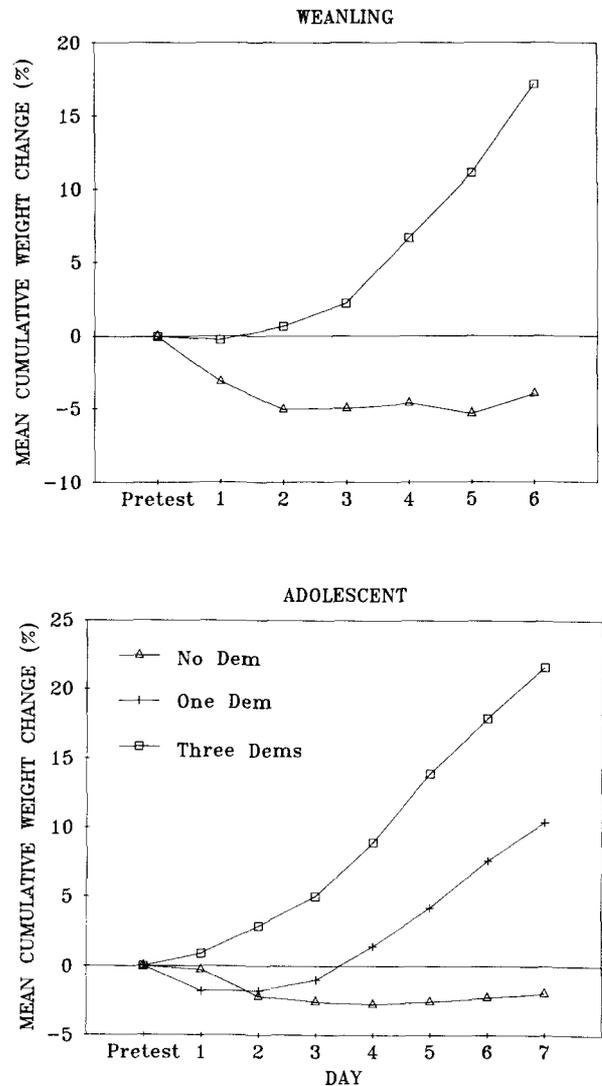


Figure 2. Mean cumulative percentage weight change of weanling (top) and adolescent (bottom) subjects during the test phase of Experiment 1. (Dem = demonstrator).

weight of, respectively, weanling and adolescent subjects that were caged either alone or with trained demonstrators during the test phase of the experiment. As can be seen in the upper panel of Figure 2, weanling subjects with three demonstrators gained a significantly greater percentage of their starting weight during the experiment than did weanling subjects feeding in isolation, Student's  $t(11) = 3.20, p < .004$ .

Similarly, as can be seen in the lower panel of Figure 2, adolescent subjects also benefited appreciably from the presence in their respective enclosures of demonstrators trained to eat the nutritionally adequate Diet HP-Nut. During the 7 days of the experiment, those adolescents interacting with demonstrators gained a significantly greater percentage of their starting body weight than did those adolescents choosing among foods in isolation,  $F(2, 23) = 19.74, p < .001$ .

Post hoc analyses of the weight gains of adolescent subjects revealed (a) that adolescent subjects sharing their enclosure with a single demonstrator gained a significantly greater percentage of body weight than did isolated, adolescent subjects (Tukey's test,  $q = 12.4$ ,  $p < .01$ ) and (b) that adolescent subjects interacting with three demonstrators gained a significantly greater percentage of body weight than did adolescent subjects interacting with but a single demonstrator (Tukey's test,  $q = 11.2$ ,  $p < .05$ ).

The results of Experiment 1 thus demonstrated that both weanling and adolescent rats that lived in an environment where they failed to select a nutritionally adequate diet for themselves chose an adequate diet if they had the opportunity to interact with conspecifics eating that diet. The results of Experiment 1 also revealed certain problems that both guided and restricted the design of later experiments. First, those weanling rats tested in isolation did so poorly in the diet-selection task that many became seriously debilitated during the 6 days of testing. For ethical reasons, it was decided not to continue to use weanlings in this series of studies.

Second, although the data of Experiment 1 provided evidence consistent with the view that interaction with knowledgeable conspecifics facilitated selection of adequate diets by naive, young rats, that evidence was indirect. In three of the five groups, demonstrators and subjects were eating from the same food bowls, making it impossible to determine the actual pattern of diet selection exhibited by subjects. Perhaps subjects with and without demonstrators ate similar proportions of Diets HP-Nut, Thy, Coc, and Cin. The presence of a demonstrator or demonstrators may have either increased the amount of all four diets eaten by subjects or reduced subjects' energy expenditures for thermoregulation, thus enhancing their weight gain by means other than directing feeding to the protein-rich Diet HP-Nut.

## Experiment 2

In this experiment the procedures used in Experiment 1 were modified to permit the food intake of adolescent subjects to be measured directly.

### Method

#### Subjects

Twelve, experimentally naive, male rats, weighing 150 to 175 g at the beginning of the experiment, served as subjects. An additional 18, 175- to 200-g, male rats served as demonstrators.

#### Apparatus

Experiment 2 was conducted in  $1 \times 1 \times .3$ -m cages, each divided in half by a screen (1-cm grid) that separated each subject from its respective demonstrator (see Figure 1, right panel). Each of the two compartments in each cage (referred to herein as, respectively, the subject's and demonstrator's compartments) contained both a watering station and a  $30 \times 15 \times 15$ -cm wooden nest box with a single  $5 \times 5$  cm entrance.

### Procedure

Experiment 2 was conducted in two stages:

**Habituation.** Subjects were randomly assigned to No Demonstrator ( $n = 6$ ) and Three Demonstrator ( $n = 6$ ) Groups, and each subject was placed alone in the subject's compartment of an apparatus. The demonstrator's compartment of each apparatus that contained a subject assigned to the No Demonstrator Group was left empty, whereas three demonstrators were placed in the demonstrator's compartment of each apparatus containing a subject assigned to the Three Demonstrator Group.

After the subjects and demonstrators were appropriately distributed, all were given ad lib access for 24 hr to a bowl containing Diet P placed in the middle of their respective compartments. The subjects and demonstrators were then left undisturbed for 24 hr to become habituated to the experimental situation.

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

### Results and Discussion

The main results of Experiment 2 are presented in Figure 3, which shows the mean amounts of Diet HP-Nut eaten by subjects in Three Demonstrator and No Demonstrator Groups as a percentage of the total amount that subjects ate daily during testing.

Analyses of food choices of subjects revealed that subjects in the Three Demonstrator Group ate both more Diet HP-

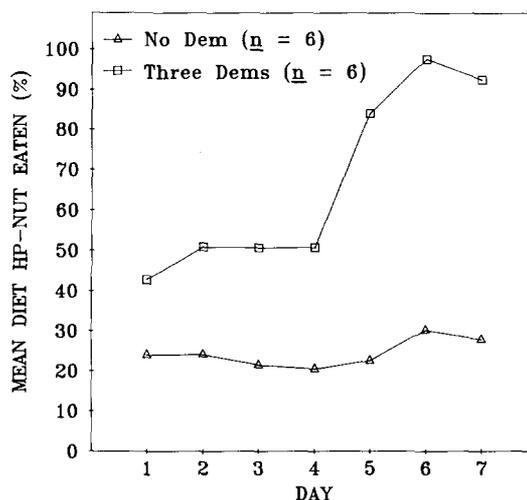


Figure 3. Mean amount of high-protein, nutmeg-flavored diet (Diet HP-Nut) ingested as a percentage of total amount eaten daily by isolated subjects (No Dem) and subjects choosing diets in the presence of demonstrators (Three Dems) during testing in Experiment 2.

## Method

Nut, Student's  $t(10) = 2.44, p = .04$ , and a greater percentage of Diet HP–Nut, Student  $t(10) = 3.26, p < .01$ , throughout the 7 days of testing than did subjects in the No Demonstrator Group. As one might expect, the correlation between the total amounts of Diet HP–Nut eaten by individual subjects during the 7 days of the experiment and their total percentage of weight gain during the same period was significantly positive (Pearson's  $r = .87, p < .001$ ).

The data clearly indicate that the presence of demonstrators eating Diet HP–Nut significantly increased the intake of that diet by subjects and this increased intake of Diet HP–Nut was highly correlated with increased gains in body weight.

### Experiment 3

Taken together, the results of Experiments 1 and 2 show that the success of naive rats in selecting an adequate diet can be influenced by interaction with conspecifics eating that nutritionally adequate diet. However, the results of these experiments provided no information as to how social influence was exerted on subjects by their demonstrators.

Previous studies of social influences on diet choice by rats have shown (a) that both adult and juvenile rats prefer diets that they have smelled on other rats (Galef, Kennett, & Wigmore, 1984; Galef & Stein, 1985; Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984) and (b) that juvenile rats, but not adult rats, prefer to eat in locations where other rats are feeding (Galef, 1977b; Galef & Clark, 1971). Thus, both local enhancement effects (Thorpe, 1963) and the influence of olfactory cues on food preference (see Galef, 1986, for review) might have been responsible for the observed effects of demonstrators on diet selections by subjects in Experiments 1 and 2. Experiment 3 was undertaken to determine whether (a) the smell of Diet HP–Nut on a demonstrator, (b) the physical presence of a demonstrator in the vicinity of a food bowl containing Diet HP–Nut, or (c) both of these would influence the diet choices of naive, adolescent subjects.

### Subjects

Eighteen, experimentally naive, male, 150- to 175-g, Long-Evans rats served as subjects and an additional 18 of their conspecifics, 175 to 200 g in weight, served as demonstrators.

### Apparatus

The present experiment was conducted in the apparatus illustrated in the right panel of Figure 1 and described in the *Apparatus* section of Experiment 2.

### Procedure

The procedure of this experiment was identical to that of Experiment 2, except in (a) the number of demonstrators with which each subject interacted, (b) the foods fed to demonstrators, and (c) the locations where demonstrators were fed. In this experiment each subject was placed across a screen partition from a single demonstrator. After habituation each subject was assigned to one of three groups.

The subjects assigned to the Same Food–Same Place Group ( $n = 6$ ) each shared an apparatus with a demonstrator that had access to a single food cup containing Diet HP–Nut. Each demonstrator's food cup containing Diet HP–Nut was placed directly across the screen partition from each subject's food cup containing Diet HP–Nut (see Figure 4, Panel A). Thus, subjects assigned to the Same Food–Same Place Group were treated identically to subjects assigned to the Three Demonstrator Group of Experiment 2, except that each subject in the Same Food–Same Place Group of this experiment interacted through the screen partition with a single demonstrator rather than with three demonstrators.

Each subject assigned to the Same Food–Different Place Group ( $n = 6$ ) interacted with a demonstrator eating Diet HP–Nut from a food cup located directly across the screen partition from each subject's food cup containing Diet Cin (see Figure 4, Panel B). As the name of the Same Food–Different Place Group implies, the subjects in this group were exposed to demonstrators eating the high-protein, nutmeg-flavored diet in a location distant from the location where each subject's own bowl of high-protein, nutmeg-flavored diet was placed.

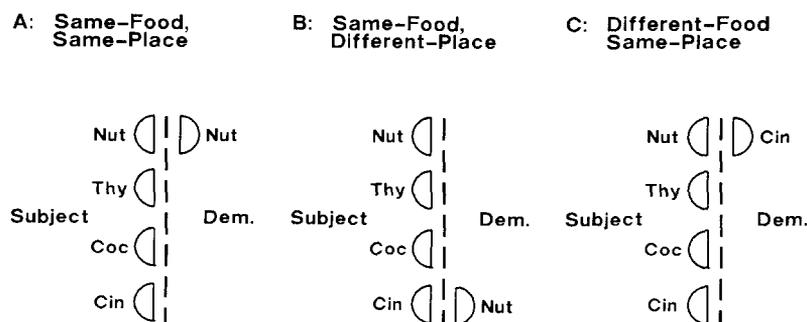


Figure 4. Overhead schematic of the positions of food cups presented to subjects and demonstrators in the Same Food–Same Place (Panel A), Same Food–Different Place (Panel B), Different Food–Same Place (Panel C) Groups in Experiment 3. (Nut = nutmeg-flavored diet; Cin = cinnamon-flavored diet; Thy = thyme-flavored diet; Coc = cocoa-flavored diet; and Dem. = demonstrator).

Last, those subjects assigned to the Different Food-Same Place Group ( $n = 6$ ) each shared an apparatus with a demonstrator eating Diet Cin directly across the screen partition from the subject's food cup containing Diet HP-Nut (see Figure 4c).

For the week of the experiment, the subjects and demonstrators were left undisturbed except for daily weighing of food cups and subjects.

### Results

The main results of Experiment 3 are presented in Figure 5, which shows, respectively, the mean amount of Diet HP-Nut eaten by subjects in each of the three groups as a percentage of the total amount eaten daily by subjects during

testing (Figure 5, top panel) and the mean percent cumulative weight change exhibited by subjects in each of the three groups (Figure 5, bottom panel).

Because there was extreme heterogeneity of variance across groups in the amount of Diet HP-Nut that they ate ( $F_{\max} = 20.3$ ), statistical analyses of diet intake were carried out on log-transformed data. We found a significant effect of treatment on the total amount of Diet HP-Nut eaten by subjects during the 7 days of the test phase of the experiment,  $F(2, 15) = 5.61, p < .025$ . Furthermore, protected  $t$  tests (Wike, 1985) revealed that subjects in the Different Food-Same Place Group ate significantly less Diet HP-Nut during the 7 days of the experiment than did subjects in the Same Food-Same Place Groups (least significant difference [LSD] = .42,  $p < .01$ ) and that subjects in the Same Food-Same Place Group did not differ from subjects in the Same Food-Different Place Group in the percentage of Diet HP-Nut that they ate.

As would be expected, given the observed, positive correlation between the amount of Diet HP-Nut eaten by subjects and their percentage weight gain in the test situation (Pearson's  $r = .750, p < .001$ ), there was also a significant effect of treatment on the percentage weight gain shown by subjects assigned to the three groups,  $F(2, 15) = 3.85, p < .05$ . Protected  $t$  tests revealed that subjects in the Different Food-Same Place Group ate significantly less Diet HP-Nut than did subjects in each of the other two groups (LSD = .67, both  $ps < .01$ ).

Subjects in the Different Food-Same Place Group were exposed to a demonstrator eating Diet Cin in the vicinity of each subject's food cup containing Diet HP-Nut. If the food eaten by demonstrators influenced diet selection by subjects, then one would expect subjects in the Different Food-Same Place Group (i.e., subjects whose demonstrators were eating Diet Cin), to eat a greater percentage of Diet Cin than subjects in either of the other two groups, whose demonstrators were eating Diet HP-Nut.

As can be seen in Figure 6, which shows the mean amount of Diet Cin, as a percentage of the total amount of low-protein diets (Diets Cin, Coc, and Thy) eaten by subjects in each of the three groups during the 7 days of testing, there was a significant effect of treatment on intake of Diet Cin,  $F(2, 15) = 5.51, p < .025$ . Protected  $t$  tests revealed that subjects in the Different Food-Same Place Group ate significantly more Diet Cin than did subjects in either the Same Food-Same Place or Same Food-Different Place Groups (LSD = 29.3, both  $ps < .01$ ).

### Discussion

All results of Experiment 3 consistent with the hypothesis that the food choices of adolescent subjects were more strongly influenced by the foods that other rats were eating than by the locations where those rats were feeding. These findings ought not, of course, be used to infer that the location where adult rats eat cannot be an important influence on the feeding behavior of young rats. As mentioned in the introduction to this experiment, in other situations, particularly those where

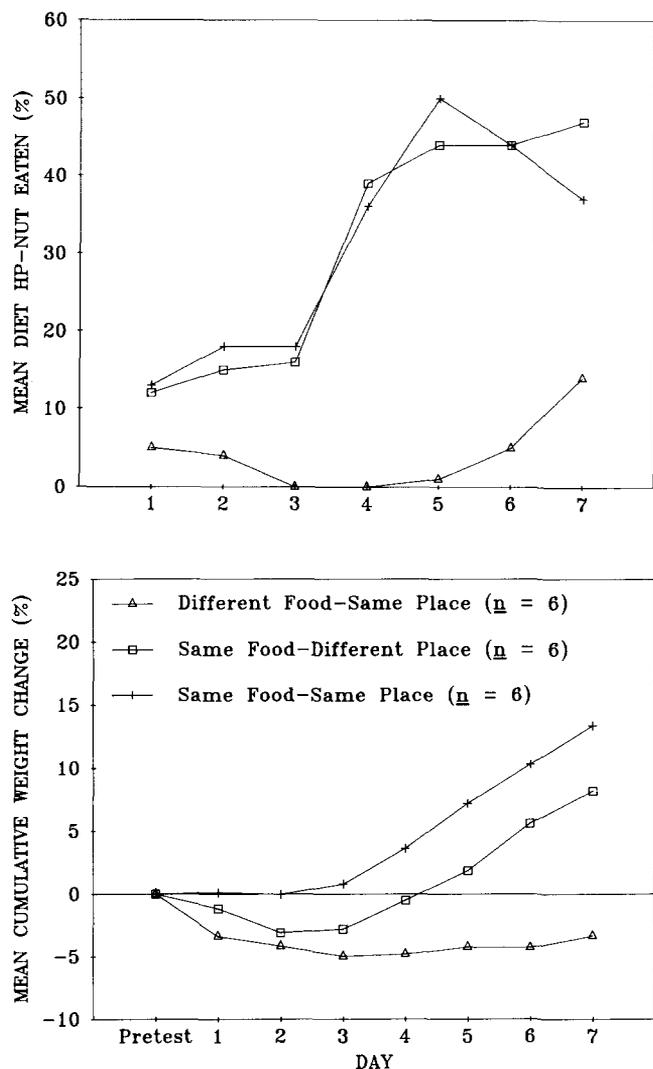


Figure 5. Mean amount of high-protein, nutmeg-flavored diet (Diet HP-Nut) ingested as a percentage of total amount eaten daily by subjects during testing (top) and mean cumulative percentage weight change of subjects (bottom) in the three groups of Experiment 3.

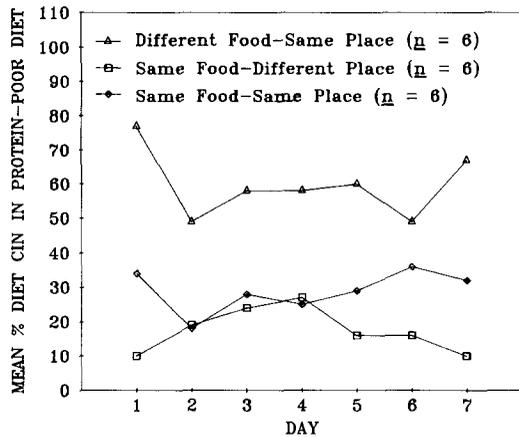


Figure 6. Mean amount of cinnamon-flavored diet (Diet Cin) ingested as a percentage of total amount of protein-poor, cinnamon-, cocoa-, and thyme-flavored diets eaten daily by subjects in the three groups of Experiment 3 during testing.

the same food is available at several locations, the feeding site selection of young rats is profoundly influenced by where adult or juvenile conspecifics are feeding (Galef, 1977a; Galef & Clark, 1971; Strupp & Levitsky, 1984).

### General Discussion

In the attempt to explain how generalist feeders, living in the world outside the laboratory, come to select nutritionally adequate diets, attention has focused on the specific hungers, learned aversions, and learned appetites exhibited by individual animals. Little attention has been paid to the fact that during at least the early part of their lives, many generalists live as members of social groups and that naive, group-living animals can exploit more informed others as sources of information about what foods to eat and what foods to avoid eating.

A series of articles from our laboratory have demonstrated profound effects of social interaction on the foraging patterns and diet choices of rats (reviewed in Galef, 1977a, 1986, in press). The results of the present series of experiments extend these earlier findings by showing that in environments where individual rats were unable to learn to select a nutritionally adequate diet from among an array of alternatives, social interaction of naive rats with successful conspecifics could facilitate the acquisition of adaptive diet choices by the naive. Our data suggest that socially acquired information can enable young rats to survive, even to thrive, in environments where many would succumb if they had to depend on their individual abilities to select nutritionally adequate diets.

When a new area is colonized by members of a generalist species, most immigrants may fail to find foods that meet their dietary needs. Many may die. However, those individuals that, for whatever reason, find an adequate diet in circumstances where others fail can serve as models both for less successful contemporaries and for members of future generations. Presence of successful models could make benign

otherwise undesirable habitat (Galef & Beck, in press). The ability of rats and, presumably, of other vertebrate generalists to be guided in their choice of foods by the food choices of conspecifics ought not to be ignored in future discussions of the development of adaptive patterns of diet choice by free-living animals.

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