

**The role of social information in the development  
of  
preferences for nutritious foods by Long-Evans rats.**

**By**

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**Socially acquired preferences for nutritious foods by rats.**

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**TITLE: The role of social information in the development of preferences for nutritious foods  
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## **Abstract**

It has long been assumed that animals select nutritionally adequate diets via innate and learned preferences for nutritious foods. However, animals typically fail to select a nutritionally adequate diet when a) more than two or three alternative diets are available, b) a needed nutrient is available only in a relatively unpalatable food, and c) recovery from nutrient deficiency is delayed. Because these three conditions are likely to occur in natural settings, the inability of animals to select adequate diets under such conditions suggests that our current understanding of diet selection in nature is in need of revision.

The present research indicated that failures on the part of animals to select adequate diets have been due to the artificial testing conditions used in previous diet-selection experiments. Animals in previous experiments were tested in isolation, and have therefore been denied a source of dietary information available to their wild counterparts: the diet selection behaviour of others. In the present research, rats rapidly developed preferences for a protein-rich food under the three conditions listed above when they were exposed to others feeding upon the protein-rich diet. Present data indicated that rats adopted the preferences of others by matching what other rats ate, rather than matching where others ate.

The responses of rats to the feeding behaviour of others seem well-matched to the goal of obtaining reliable and accurate dietary information from others. For example, rats were more likely to match a diet preference if several others are displaying the same diet preference rather than if just one other exhibited that preference. Such a behaviour might serve to prevent rats from adopting an idiosyncratic, maladaptive preferences; it seems

unlikely that several rats would display the same idiosyncratic maladaptive preference.

Rats were also more likely to match the diet choices of large rats than small rats. Because large rats in the wild are more likely to have acquired beneficial diet preferences than those of small rats, the tendency to preferentially match the diet choice of large rats would result in superior diet choices.

The degree to which rats match the diet choices of others while nutrient deprived and nutrient replete also suggests an adaptive interpretation. Nutrient-deprived rats matched the diet choices of others to a greater extent than did rats that were either recovering from nutrient-deprivation or completely recovered from nutrient-deprivation. The mechanism underlying the enhanced tendency of nutrient-deprived rats to match the diet choices of others did not appear to be an enhanced susceptibility to social influence. Rather, nutrient deprivation rendered rats more likely to restrict their diet choice to a single food. Thus, when nutrient-deprived rats were exposed to a demonstrator, they showed a greater tendency than non-deprived rats to restrict their feeding to the demonstrator's diet.

Taken together, the results obtained in the present research indicated that social cues are a vital source of dietary information. In order to obtain a complete understanding of how rats, and, undoubtedly, other animals as well, select diets in natural settings, it is necessary to obtain a clearer understanding of the role of social influences in diet selection.

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## Chapter I

### Introduction

The question of how wild animals find nutritious food in natural environments that contain myriad nutrient-poor and toxic foods has been addressed by psychologists since the early part of this century. The modern consensus is that animals have two complementary mechanisms that allow them to find nutritious foods: a set of innate preferences for gustatory qualities that are correlated with the presence of nutrients in foods (Richter, 1943; Rozin, 1976) and a capacity to learn to prefer nutritious foods (Harris, Hargreaves and Ward, 1933; Rozin, 1976).

At birth, rats, humans, and members of other omnivorous species tend to prefer foods that are sweet, slightly salty, or greasy to those lacking these qualities. To the extent that sweet, salt, and greasy sensations are correlated with the presence of, respectively, sugars, salt, and fats, the taste of a food can bias animals to eat nutritious foods. However, because the correlation between the flavor of food and its nutrient composition is not perfect, animals cannot rely upon their innate preferences to select an adequate diet. Relative palatability may bias feeding toward foods that are likely to be nutritious, but palatability is not a reliable guide to nutritional content.

Omnivores must learn to prefer those foods that contain proteins or amino acids (e.g. Booth and Simson, 1971; Simson and Booth, 1974; Baker, Booth, Duggan, and Gibson, 1987), vitamins (e.g. Rozin, 1965; Garcia, Ervin, Yorke, and Koelling, 1967),

minerals other than sodium (e.g. Scott, Verney, and Morrissey, 1950; Rodgers, 1967; Chesters and Quarterman, 1970), and starch (e.g. Booth, 1972; Booth, Lovett, and McSherry, 1972) by associating the physiological consequences of ingesting each nutrient with the taste of the food containing it. Because most preferences for nutritious foods must be learned, differential success in learning to prefer nutritious foods accounts for a sizeable portion of the variance in success of animals searching for nutritious food. Because of the relationship between successful learning and successful diet selection, the learning mechanism responsible for the formation of taste-consequence associations has apparently been shaped by natural selection so as to increase the likelihood that adaptive, rather than maladaptive, associations develop.

Three properties of learning, involved in diet selection, differ in such marked ways from other forms of associative learning that the three properties have been interpreted as specific adaptations for forming taste-consequence associations: (a) Asymptotic learning often occurs in a single trial (Garcia, McGowan, and Green, 1972); (b) gustatory stimuli are more likely to become associated with the consequences of ingestion than are stimuli in other modalities (Garcia and Koelling, 1966), and, finally, (c) associations between flavors and consequences are formed even if there is a delay of as much as 12 hr between ingestion and the onset of internal consequences of ingestion (Revusky, 1968; Smith and Roll, 1967).

While these three characteristics of learning processes involved in diet selection increase the likelihood that adaptive associations will develop, they do not guarantee this outcome. Westoby (1974) described three features of a diet-selection situation that interfere with the formation of adaptive associations between the taste of a food and its internal consequences. Adaptive diet preferences will not be formed if: (a) the physiological consequences of nutrient ingestion occur after the 12 hr "association window" has closed,

(b) the animal is not in a deficient state when it eats the nutritious food, and (c) the relative unpalatability of a nutritious food prevents the animal from eating enough of the food to detect the positive consequences contingent upon its ingestion.

Westoby's list of conditions that interfere with the formation of adaptive diet preferences is not, however, exhaustive. In addition, an adaptive preference for a nutritious food would fail to develop if: (d) two foods were eaten in rapid succession and the beneficial consequences of ingestion became associated with the wrong food (Rozin, 1969), or (e) the large number of nutrient-poor foods in an environment prevents an animal from adequately sampling a nutrient-rich food (Harris, Clay, Hargreaves and Ward, 1933).

The above list of five conditions under which animals fail to develop adaptive food preferences may be understood by viewing the process by which adaptive associations are formed as composed of three distinct stages. In order for an animal to form an adaptive food preference, the animal must first sample a nutritious food; it must then detect the positive consequences of ingesting the nutritious food, and finally, it must attribute those positive consequences to the nutritious food. To simplify this discussion, I will refer to these three stages of adaptive preference formation as sampling, detection, and attribution. Animals fail to develop adaptive preferences under the five conditions (a-e) listed above because each condition prevents animals from successfully passing through one or more of the three stages of adaptive preference formation. Condition (e) interferes with sampling, conditions (a),(b), and (c) interfere with detection of nutrients, and conditions (a) and (d) interfere with correct attribution.

Animals exhibit a variety of behaviours which increase the likelihood that they will successfully pass through the three stages of diet selection. First, nutrient-deficient animals develop aversions to the foods they are eating; they thus increase the likelihood that they will sample novel foods which might contain the missing nutrient (Rozin, 1967; Simson

and Booth, 1974). Second, deficient animals tend to eat only one food in any single feeding bout, and sometimes eat only one food for an entire day (Rozin, 1969). Such a feeding pattern would ensure that an animal ate enough of a nutrient-rich food to detect its positive effects, and that an animal would attribute these positive effects to the correct diet. Third, as mentioned above, animals form associations between tastes and internal consequences of ingestion that occur up to 12 hours later (Garcia, McGowan, and Green, 1970). Because the physiological effects of many nutrients can be delayed, a 12-hr association window makes it possible for even the delayed positive effects of a food to be attributed to that food. Finally, animals are more likely to associate positive consequences of ingestion to a novel diet than to a known diet (Revusky and Bedarf, 1967; Shettleworth, 1972). By attributing recovery to a novel food, rather than to a known food, animals further increase the likelihood that they will correctly attribute positive consequences of ingestion to the correct food because the foods a deficient animal has subsisted on cannot contain a missing nutrient. Therefore, a deficient animal that only attributes recovery to novel foods that it has eaten is more likely to make a correct attribution.

Given the diversity of mechanisms that increase the probability that adaptive food preferences will develop, one might presume that animals rarely fail to select an adequate diet. Yet there have been many reports, especially in the early diet-selection literature, of animals failing to develop adaptive food preferences when made to choose among two or more foods.

Several aspects of the nutrient environment affect success in such a cafeteria-feeding task. The palatability of diets is apparently an important factor; animals often fail to make adaptive choices in a selection task when needed nutrients are present only in a relatively unpalatable food (Kon, 1931; Scott and Quint, 1946). For example, Kon (1931) found that rats showed great variance in their preference for casein. Rats that ate 2g of

casein in a single meal subsequently came to prefer the casein and gained weight, whereas those that did not eat 2g of casein failed to develop a preference for it and eventually died of protein deficiency. In this instance, the low relative palatability of casein reduced intake of a nutrient source, thereby interfering with nutrient detection.

Another parameter affecting success on selection tasks is the number of alternative diets. For example, Harris et al. (1933) found that the likelihood that a rat would develop a preference for a thiamine-rich food declined as the number of alternative diets increased. Indeed, in the Harris et al. (1933) study, no rat came to prefer the thiamine-rich food when five thiamine-poor alternatives were available. Unfortunately, it is not clear which stage of the nutrient recognition process is affected by increasing the number of alternatives. This manipulation could simply reduce the likelihood that a rat would sample the nutrient-rich food. Alternatively, a greater number of selections could cause animals to eat less of any one diet, reducing the likelihood that they would eat enough thiamine-rich diet to detect a change in internal state. Finally, the greater number of diets could increase the likelihood of attribution errors.

A review of Harris et al.'s (1933) data from individual rats given either six or eight alternatives seems to indicate that different rats failed for different reasons. One unsuccessful rat did not sample the thiamine-rich diet during the week of testing. Other unsuccessful rats ate small quantities of the thiamine-rich diet on several different days of testing. These rats could either have failed to detect the consequences of the nutrient, or attributed them to the incorrect diet. Without knowing how much nutrient a deficient animal must eat to detect its effects, it is not possible to discriminate between these explanations.

Failures to find nutritious food can also occur when a needed nutrient produces slow recovery from deficiency (Young and Wittenborn, 1940; Harriman, 1955). Such

failures must, to a great extent, be due to attribution errors. In humans, the first physiological signs of recovery from vitamin A or vitamin D deficiency occur ten days after vitamin therapy is begun (Park, 1939). If a second unfamiliar food, deficient in vitamins A or D, is eaten in the ten day period before recovery begins, then a maladaptive association is likely to be formed.

If diet selection failures occurred under conditions that could never occur in the world outside the laboratory, then they could simply be viewed as laboratory phenomena of little relevance to the study of adaptive diet-selection behaviour. Yet the laboratory conditions under which animals often fail to find adequate nutrients closely match conditions one would expect to find in natural settings. The natural environment of omnivores often contains a multitude of potential foods varying in palatability and nutrient composition, the very conditions under which laboratory animals typically fail to select nutritionally adequate diets. It is, therefore, quite surprising that wild animals manage to survive and reproduce, given the poor diet-selection abilities expressed by animals in the laboratory under conditions simulating those found in nature.

The discrepancy between the conditions required by laboratory animals to select adequate diets, and the conditions present in nature is puzzling. If the diet-selection abilities of laboratory animals are representative of those of wild animals, then why have animals not evolved mechanisms to find nutrients under conditions present in their natural environments? On the other hand, if the diet-selection abilities of laboratory animals are not representative of those of wild animals, and wild animals are capable of finding adequate nutrients under conditions in which laboratory animals fail, then what limits the diet-selection ability of laboratory animals? The discrepancy also raises questions about the manner in which diet-selection behaviour has been investigated. Because the conditions under which animals fail to select adequate diets have been recognized for at least 30 years,

one would assume that the failure of laboratory animals to find adequate nutrients under simulated natural conditions would be considered a major theoretical problem. Yet the discrepancy between the diet-selection capacity of laboratory animals, and the diet-selection capacity required in the natural environment, is not even addressed by modern investigators. An explanation for this absence of interest can be found in the history of diet-selection research.

### A history of diet-selection research

Psychologists first became interested in the ability of animals to find nutritious food following Evvard's (1915) report in a journal of nutrition that pigs showed a natural ability to select adequate diets.

"When the appetite is given full control of what shall be eaten it is surprising to note how well the pigs naturally select the specific feeds which swine herdsman have long since approved as of the best, and what is equally surprising the pigs show marked avoidance of those feeds usually considered as ill-adapted to swine." (Evvard, 1915, p. 375)

Evvard's finding was made at a time in which it was generally believed that animal's possess fixed behavioural traits that can only be slightly modified by experience. This misconception can be found in the writings of many of the prominent psychologists of the day.

"If the thousand babies born this week in New York city were given equal opportunities they would still differ in much the same way and to much the same extent as they will in fact differ." (Thorndike, 1913, p. 127)

"... the structure which must later develop into the anatomical mechanism of instinct is already present in the fertilized egg of the given species." (Watson, 1914, p. 152)

The misconception that behaviour is controlled by fixed instincts was already a part of the diet-selection literature when Evvard made his discovery. For example, Turro (1910) (cited in Mursell, 1925) suggested that specific hungers for protein, carbohydrates, and fats arise from a 'tropic center' located somewhere in the basal ganglia. Carlson (1912) was also of the opinion that hunger is an inherited trait. However, as the following quotation shows, Carlson believed that the instinctive desire for food may be modified by experience.

"Must we not look for the primary basis of appetite in a desire for food as the expression of an inherited mechanism, primarily independent of, but subsequently modified by, the individual experience? In other words, have we not in appetite for food conditions as primitive and essentially fixed by inheritance as in the case of the sexual desires or 'instincts'?" (Carlson, 1912, p. 186)

As one might expect, Evvard's finding was interpreted as a demonstration that animals have an innate ability to select nutritionally adequate diets (e.g. Osborne and Mendel, 1918; Mitchell and Mendel, 1921). Thus, when Osborne and Mendel (1918) repeated Evvard's basic experiment using rats under more controlled conditions, they assumed that diet-selection behaviour is governed by instinct. This assumption, coupled with the truism that animals must make adequate diet choices in order to survive and reproduce, led them to the following conclusion.

"The success with which animals living in their natural environment nourish themselves must depend upon the exercise of choices in which instinct and appetite play a significant part. ... the biological evidence of the survival and well-being of innumerable species testifies to the success of their instinctive dietary habits." (Osborne and Mendel, 1918, p. 19)

Osborne and Mendel's assumption that it is logically necessary that animals have an innate ability to make adaptive diet choices apparently led them to a biased interpretation of their own experimental results. Their experimental procedure was to compare the weight gain of two groups of rats matched for both sex and weight. Rats in the experimental condition were given a choice between a complete diet and one low either in protein or in specific amino acids. Rats in the control group were fed only the complete diet. In their discussion, Osborn and Mendel summed up their results in the following manner.

"Although in these few experiments the growth was not the maximum that might have been expected, nevertheless nine out of ten rats soon ate such proportions of the two foods offered in each case as to enable them to grow at a nearly normal rate." (Osborne and Mendel, 1918, p. 27)

If one looks closely at Osborne and Mendel's original data, a different conclusion emerges. In nine of the ten matched pairs, animals given a choice of diets gained less weight than their control group partners (Sign test,  $x=1$ ,  $p = .011$ ). After being given the diet choice for twenty days, experimental subjects weighed 38 percent less than control subjects, and still weighed 23 percent less after 40 days of testing. Also, the experimental animals displayed great variance in their preference for the two diets. This high variance resulted in large differences in weight gain; while one experimental subject gained more weight than any control subject during the first 20 days of testing, two other experimental subjects barely maintained their initial body weight during the same period. If rats in the experimental group had an "innate" propensity to find nutrients, neither their poor general performance nor their highly variable success would be expected.

In Osborne and Mendel's discussion, results which contradicted their presupposition that rats have an innate ability to select adequate diets were not mentioned. Instead, Osborne and Mendel concluded that the outcome supported the conclusion that

animals have an innate ability to make beneficial diet choices. Apparently, Osborne and Mendel's logical argument that animals must have the ability to find nutrients in order to survive made them less critical of their own results than they might otherwise have been.

The period following Osborne and Mendel's experiment was characterized by a heated conflict over whether or not animals have an innate ability to select adequate diets. The conflict was fueled by the fact that similar procedures yielded radically different results. For example, Beadles, Braman, and Mitchell (1930) gave rats a selection task very similar to the one used by Osborne and Mendel (1918), a choice between a low protein diet, deficient in cystine and a complete diet. In contrast to the results reported by Osborne and Mendel (1918), Beadles, Braman, and Mitchell (1930) found no evidence that rats could distinguish between the two diets. Similarly, Pearl and Fairchild (1921) found that free-feeding hens ate less protein and fat, yet did not differ in egg production or apparent health from birds grown on commercial feed. Yet when Tomhave and Mumford (1931) attempted to replicate Pearl and Fairchild's experiment, their hens lost weight, and exhibited cannibalism, slow moulting, and low egg production.

An illuminating example of a pair of experiments that yielded contradictory results is provided by Kon (1931) and Richter, Holt, and Barelare (1938). Both Kon and Richter et al. tested the ability of rats to compose adequate diets from isolated nutrients. Kon found rats to be extremely poor at this task; Richter et al. found rats to be extremely proficient. The discrepancy in results has been attributed to the different methods used by Kon (1931) and by Richter et al. (1938) to choose the nutrient sources offered in the selection task (Epstein, 1961). Kon simply obtained his nutrients from commercial sources. Richter et al. used a rather more elaborate method to choose the diets they presented to their subjects.

Richter et al. performed a pilot experiment in which they determined the survival time of rats allowed to eat only one of several different sources of a nutrient. For example,

to pick a source of fat Richter et al. restricted rats to a diet of one of the following: olive oil, lard, cod liver oil, wheat germ oil, perilla oil, or peanut oil. Because rats lived longest on olive oil, this was the source of fat later used in the diet-selection test. Richter et al.'s rationale for choosing nutrient sources in this way was that it was "better than making a priori selections on the basis of our theoretical knowledge of the nutritional value of the foodstuffs" (Richter et al., 1938, p. 736). Evidently Richter et al. feared that animals might not select adaptively simply because an adequate diet could not be composed from arbitrarily-chosen nutrient sources. This is a peculiar fear given that Richter et al. had only to feed control animals a diet made up of the nutrient components to determine if animals could compose a nutritionally adequate diet from those components. Osborne and Mendel (1918) and Kon (1931) had used such a control group in their earlier experiments.

Epstein (1961) proposed that the selection criterion used by Richter et al. (1938) selected for diet components that were actually sources of several nutrients rather than just one. He argued that the survival time of animals restricted to a single food would have been longest for those foods containing several different nutrients. The foods Richter et al. offered their subjects would, therefore, have predisposed subjects towards finding adequate nutrients. If an animal failed to detect a nutrient in the nutrient's nominal source, it could still obtain the nutrient from other available foods. For example, if an animal failed to obtain its protein from the nominal protein source, casein, it could readily acquire sufficient protein from the nominal vitamin B source, yeast. The disparity between the outcomes obtained by Kon (1931) and those obtained by Richter et al. (1938) can, therefore, be attributed to differences between the nutrient environments used in their respective experiments. While Kon composed his nutrient environment from nutrient sources selected arbitrarily, Richter et al. unintentionally chose nutrient sources that predisposed animals towards finding adequate nutrients.

The theory of diet selection proposed by Richter in Richter et al. (1938) to explain the success of animals selecting among isolated nutrients was an extension of Osborne and Mendel's (1918) theory. While Osborne and Mendel suggested that instinctive dietary habits allow animals to make adaptive diet choices, Richter went on to propose that these habits took the form of innate preferences for the tastes of nutrients.

"The results showed that the rat has a special appetite not only for salt and sugar, but also for protein, carbohydrate, sodium, calcium, phosphorus, potassium, and the vitamins." (Richter, et al., 1938, p. 744)

Richter's willingness to accept this elaborate explanation of his results apparently arose from the juxtaposition of two logical arguments. The first argument, which originated in Osborne and Mendel's (1918) paper, was that it is logically necessary for animals to have the ability to select adequate diets.

"The survival of animals and humans in the wild state in which the diet had to be selected from a great variety of beneficial, useless, and even harmful substances is proof of this ability." (Richter et al., 1938, p. 734)

The second argument was founded on the assumption that animals cannot form associations between events occurring far apart in time, an ability animals require if they are to associate the gustatory qualities of a food with its internal consequences. Richter reasoned that animals must therefore be able to identify nutrients by their tastes, or not at all.

"There are those who believe that all self-selection choices are based on experience, or a trial and error process ... But certainly this does not apply to normal animals in which the effects of eating any substance, except possibly a strong poison, do not appear usually for many hours or even days." (Richter et al., 1938, p. 742)

Thus, Richter had "proven" that it was logically necessary both that animals have an innate ability to make adaptive food choices, and that the sole mechanism underlying this ability is innate preferences for nutrients.

Richter's "proof" placed him into an awkward position in relation to the diet-selection literature, since it made failures to select an adequate diet logically impossible. The many experiments (e.g. McCandlish, 1923; Nevens, 1927; Beadles, Braman, and Mitchell, 1930; Kon, 1931; Tomhave and Mumford, 1931; Harris, Clay, Hargreaves, and Ward, 1933; Wilder, 1937) that had shown animals to be incapable of selecting adequate diets posed a definite problem.

Richter's solution was simply to discount those results that did not conform to the outcome made necessary by his logical proof. In his review of the diet-selection literature, Richter cited nine experiments which reported successful diet-selection, yet only one in which animals failed to self-select adequate nutrients (Richter et al. 1938). The failure he mentioned occurred in Kon's (1931) study, about which he wrote that rats given a choice of diet components "did not thrive as well as when these substances were offered in a composite mixture." (Richter et al. 1938, p. 735). This is putting it rather mildly. One-half of the rats given Kon's diet-selection problem died of malnutrition. Those that survived weighed 40 percent less than controls after 69 days of testing (Kon, 1931).

In addition to showing bias in the papers he cited, Richter also showed a tendency to misrepresent the views of the authors of the papers he did cite. To give his theory historical roots, Richter quoted a single sentence from Mursell (1925) which, when taken out of context, suggested that Mursell accepted Richter's concept of innate preferences for nutrients. In an attempt to explain why different societies typically consume the same proportions of nutrients, Mursell wrote,

"Probably the best hypothesis covering these facts is that of certain positive chemotropisms which operate to set up cravings for specific substances." (Mursell, 1925, p. 321)

However, the context in which this sentence was written makes it clear that Mursell was not suggesting that humans have infallible innate cravings for specific nutrients, but rather that we have much more general biases towards nutrients. Indeed, later in the same paper he explicitly stated that diet selections are not made on the basis of innate preferences for the taste of nutrients.

"Any attempt to explain the food preferences of humanity on the basis of inherently pleasant or unpleasant tastes and odors is doomed to break down hopelessly, and in fact it is far truer that we like what we eat than that we eat what we like. It is notorious that uneducated taste is the most misleading of guides, and easily permits us to starve in the midst of plenty, or to eat noxious and poisonous substances. So the whole problem of nutritional education turns on training the individual to enjoy the right things, a matter of no small difficulty in a civilization like our own, where a bewildering dietary profusion of the most unequal values is provided for almost every one." (Mursell, 1925, p. 326)

Richter showed a similar bias in reporting Dove's (1935) conclusions.

"Recently Dove (1935) also reported that chickens were able to make advantageous selections from a variety of natural foods. According to him, this ability varied from animal to animal and was dependent on genetic factors." Richter et al. (1938, p. 735)

This gives the impression that Dove believed that diet selections are based completely upon genetic predispositions. In fact, Dove believed that genes were responsible for only a portion of the variance in diet selection, and suggested that environmental factors, notably those of the social environment, were equally important.

"... the final form and function of the organism is dependent not alone upon hereditary and environmental (nutritional) factors and their interactions, but also upon those social factors expressed as the interaction between individuals." (Dove, 1935, p. 529)

Richter's studies and writings, and the biased views they contained, had a profound influence on the growing field of diet-selection research. Indeed, it is difficult to find a demonstration of successful diet selection published after 1938 in which one of Richter's studies is not cited. However, it was not Richter's general theory of diet selection that had the greatest long-term impact. Rather, Richter's great influence came from his demonstrations of successful diet selection and his arguments as to why animals must be able to select adequate diets.

Richter's theory, that all diet selections are made via innate preferences for nutrients, derived most of its power from the supposition that the potential alternative mechanism of diet selection, trial-and-error learning, was not possible due to the length of the delay between ingestion and the physiological consequences of ingestion. This argument so convinced contemporary scientists that clear demonstrations of a learned component to successful diet selection (Harris, et al., 1933; Scott and Verney, 1947; Tribe and Gordon, 1953) were either ignored or treated as special cases. It was not until Garcia and Koelling (1966) demonstrated that internal stimuli are much more likely to become associated with gustatory stimuli than are external stimuli, that research on the learned component of diet preferences began in earnest.

Three pieces of evidence have been used to prove that some diet preferences are acquired rather than inborn: (a) Animals deficient in a nutrient do not show an immediate preference for a diet containing the nutrient, but come to prefer it some time after ingestion. This form of evidence has been used to demonstrate that learning is important in the development of preferences for foods containing thiamine (Rozin, Wells, and Mayer, 1964), protein (Simson and Booth, 1974; Peragoy, Zimmerman, and Strobel, 1972), zinc (Chesters and Quarterman, 1970) and calcium (Hughes and Wood-Gush, 1971). (b) Even after an animal has recovered from deficiency, it continues to prefer a diet it ate while

recovering from deficiency. Rozin (1965) used this type of evidence to argue that preference for thiamine-rich diets is learned. (c) After an animal develops a preference for a flavored, nutrient-rich diet, it will continue to prefer ingesta with that flavor even when the nutrient is removed. This form of evidence was used to demonstrate learned preferences for foods containing the B vitamins (Harris, et al., 1933; Scott and Verney, 1949; Tribe and Gordon, 1955), and protein (Booth and Simson, 1971).

General acceptance of a learned component of diet selection was accompanied by a shift in the meaning of the term "ability", as it was used in the diet-selection literature. In Richter's theory of diet selection, the ability to select nutritious food was considered to be an innate trait. If the nutrient environment allowed it, an animal with such an innate ability to make adaptive diet selections would infallibly select an adequate diet. Thus, any failure in diet selection was taken as evidence that animals do not have the ability to choose nutritious food.

After the learning theory displaced Richter's theory as the generally accepted theory of diet selection, it was no longer deemed necessary for animals to always succeed on diet-selection tasks in order for them to possess the ability to select adequate diets. Because trial-and-error learning does not inevitably result in adaptive behaviour, the learning theory of diet selection does not imply that animals will unfailingly solve diet-selection problems. Thus, after the general acceptance of the learned component of diet selection, isolated failures to find adequate nutrients were not taken as evidence against the presence in animals of an ability to select nutritious food. Rather, such failures were considered to be manifestations of the inherent fallibility of the learning mechanism. For this reason, the discovery of the learned component of diet selection was a primary factor in resolution of the conflict over whether or not animals have the ability to select adequate diets.

Examples of successful diet selection were considered to be expressions of the ability possessed by animals to choose nutritious food; diet-selection failures were not accepted as evidence against this ability. This tendency to differentially weight examples of successful diet selection and unsuccessful diet selection was made explicit in a review article by Overmann (1976).

"Animals do exhibit the ability to select and regulate their ingestion of nutrients. This ability has been demonstrated in a number of species, under a variety of conditions, and with a host of different nutrient sources. Although this diversity of methods, animals, and foodstuffs adds substantial evidence to the validity of dietary self-selection abilities, it has also contributed to an apparent lack of reliability. Comparisons between studies are difficult and contradictory findings are common. As Rozin (1968) has pointed out, however, positive demonstrations of selection or regulation must be considered more convincing than negative findings of lack of selection or regulation."  
(Overmann, 1976, p. 228)

General acceptance of the importance of learning in diet selection made a further contribution to resolution of the question of whether animals have the ability to select adequate diets. After the importance of the learned component of diet selection was generally acknowledged, the focus of research shifted away from investigations of the success of animals in various diet-selection tasks, toward the investigation of the learning mechanisms that enable animals to be successful in diet-selection tasks. This shift in focus promoted resolution of the conflict over whether animals possess an ability to select adequate diets in two ways. Most obviously, the shift in focus caused researchers to devote their energies to investigating the characteristics of the learning mechanisms of diet selection, and therefore to neglect the question of how successful animals actually are at selecting adequate diets. More importantly, the shift in focus led to a plethora of studies of the learning mechanisms involved in diet selection. In contrast to earlier studies, the intent of these later studies was not to determine whether animals would learn to prefer foods under a variety of conditions. Rather, the intent of these studies was to determine whether

animals had any capacity whatsoever to learn to prefer diets containing nutrients, and to discover the properties of the processes involved in such learning. The conditions used in these experimental investigations of the learning mechanisms were, therefore, selected to maximize the probability that learning would occur.

In most studies that explored the learning mechanisms underlying diet selection, nutrient-deficient animals were presented with the choice of only two foods: a nutrient-deficient food and a nutrient-rich food (e.g. Tribe and Gordon, 1953; Rozin, 1965; Rozin, Wells, and Mayer, 1964; Garcia, Ervin, Yorke and Koelling, 1967). Prior to testing, animals were often made highly deficient in a single nutrient (e.g. Scott and Verney, 1947; Garcia, et al., 1967; Rodgers and Rozin, 1966; Rodgers, 1967). Also, most studies of learning mechanisms investigated the ability of animals to learn to prefer foods containing the fast-acting B vitamins (see Rozin, 1967 for a review).

Virtually all investigations into the mechanisms involved in the development of learned preferences for nutritious foods showed animals to be capable of developing preferences for nutrient-rich foods under these conditions. Thus, the diet-selection literature became filled with demonstrations of successful diet selection, effectively overshadowing earlier demonstrations of diet-selection failures. The disparity between the number of reports of successful and unsuccessful diet selection made it appear that animals fail to select nutritious foods only under special conditions, when in fact it is successful diet selection which occurs only under special conditions.

By the end of the 1960s there was a general consensus among psychologists that the behavioural repertoire expressed by laboratory animals is sufficient to allow them to compose an adequate diet in a natural environment. This belief is supported by three pieces of evidence: (a) The vast majority of diet-selection studies have found animals to be capable of choosing nutritious food. (b) It is logically necessary that laboratory animals possess

the ability to select adequate diets, since their wild ancestors were able to survive in their natural environment (Osborne and Mendel, 1918; Richter et al., 1938; Lat, 1967). (c) It is generally believed that animals have only two means by which they can find nutritious foods: either they innately prefer the taste of a needed nutrient, or they develop learned preferences for those foods which produce positive physiological effects due to their nutrient content. Thus, the capacity to choose nutritious foods provided by these two mechanisms must be sufficient to allow animals to find adequate nutrients.

Each of these three pieces of evidence in favor of the thesis that animals behave in such a way as to enable them to select adequate diets is suspect. The fact that there have been a plethora of studies showing that laboratory animals are capable of selecting adequate diets demonstrates only that the laboratory conditions used in these studies were conducive to successful diet selection. The conditions used in these studies were poorly representative of those likely to be encountered in nature. As discussed previously, laboratory animals typically fail to find adequate nutrients when a selection task is used which simulates natural conditions. Indeed, if wild animals could only find nutritious food under the unnaturally benign environmental conditions in which laboratory animals can find nutritious food, there would be few wild animals left alive.

The second and third pieces of evidence used to support the view that the diet-selection behaviour of laboratory animals would allow them to select adequate diets in a natural environment are logical arguments based upon an unverified assumption. Both pieces of evidence assume that wild animals have only two sources of dietary information available to them: innate and learned preferences for the taste of nutritious foods. If wild animals have a third source of dietary information available to them which has not been made available to laboratory animals, then the argument that laboratory animals must be able to select adequate diets because wild animals are able to do so, and the argument that

the innate and learned preferences expressed by laboratory animals must be sufficient to allow animals to select adequate diets in a natural setting, are both rendered invalid.

In fact, there is already a great deal of evidence in the diet-selection literature that animals utilize a third source of dietary information in addition to innate and learned preferences. As early as 1935 Dove provided anecdotal evidence that animals acquire dietary information not only from the taste of food and the internal consequences of ingesting food, but from social interactions as well.

"Observations by the writer on the feeding habits of the young of horses, cattle, swine, goats, rabbits, chicks and other domesticated animals indicate that the young learn very early to follow and imitate the mother in the time of feeding and in the foods consumed." (Dove, 1935, p. 528)

More recently, Weiskrantz and Cowey (1963) found that rhesus monkeys would consume only small quantities of novel foods unless they witnessed another monkey ingesting them. Similarly, Turner (1964) discovered that sparrows would avoid novel foods unless exposed to a conspecific feeding upon them. Rats have also been found to be affected by the feeding behaviour of conspecifics. They will preferentially eat at feeding sites where others are eating (Galef and Clark, 1971), and where others have left residual scent cues (Galef and Heiber, 1976; Galef and Beck, 1985). Furthermore, rats prefer novel foods they have previously smelled on the breath of a conspecific (Galef and Wigmore, 1983; see Galef, 1986 and Galef, 1989 for a review of this literature).

The advantages of using the social environment as a source of dietary information seem clear. By using social information a wild animal could avoid the costly process of individually sampling novel foods of unknown nutritional value. The fact that an animal is alive attests to the adequacy of its diet selections throughout its lifetime. A wild animal

could obtain accurate dietary information at a low cost to itself simply by matching the diet choices of another animal.

Laboratory findings of social influences on diet selection strongly suggest that wild animals can use their social environment as a source of dietary information. If laboratory animals have indeed been deprived of this source of dietary information available to wild animals, then the failure of laboratory animals to find adequate nutrients under conditions likely to prevail in the wild is explicable. Only when laboratory animals are supplied with all the sources of dietary information available to wild animals would one predict that laboratory animals should be as capable as wild animals of finding adequate nutrients. The possibility that wild animals use their social environment as a source of dietary information also implies that our current understanding of the ways in which wild animals select adequate diets, based as it is upon the study of isolated laboratory animals, may be distorted and in need of substantial revision. The present research was undertaken to determine how important the social environment is for successful diet selection in nutrient environments that simulate some essential aspects of natural nutrient environments.

## **Chapter II: The effect of presence of demonstrators on ability to select a protein-rich diet.**

The purpose of the present series of experiments was to determine whether a rat made to choose among several diets of varying protein content benefited from the presence of others making adaptive diet selections.

### **EXPERIMENT 1**

Experiment 1 was performed to determine whether juvenile rats are more likely to develop a preference for a protein-rich diet when in the presence of older rats displaying a preference for this diet. The nutrient environment used was one in which isolated animals often find it difficult to find adequate nutrients: there were several alternative diets available (Harris, Clay, Hargreaves, and Ward, 1933; Rozin, 1969), and the protein source was a relatively unpalatable diet (Kon, 1931; Scott, 1946).

#### **Method**

##### *Subjects*

Thirteen, juvenile, male, Long-Evans, experimentally-naive rats from the McMaster colony, weighing 70-90 g, descendants of breeding stock acquired from Charles River, Canada (St. Constant, Quebec) served as subjects. An additional 18 male Long-Evans rats, weighing 175-200 g, served as demonstrators.

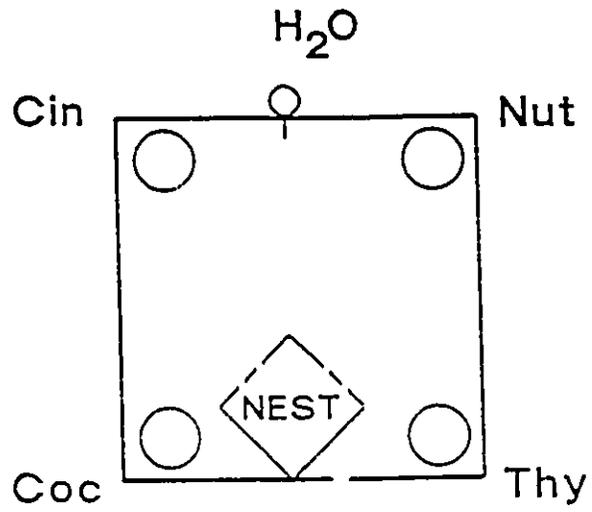
### *Test Diets*

Rats chose among three relatively-palatable, protein-poor diets (4.4% protein) and one relatively-unpalatable protein-rich diet (17.5% protein). The protein-poor diets were composed of 80% by weight basal mix (Teklad Diets, Madison, WI; catalogue # TD 86146; in g/kg, 808.5 g corn starch, 108.1g vegetable oil, 7.0g Cod liver oil, 54.1g Mineral mix, 2.7g vitamin mix), 10% corn starch, 5% granulated sugar, and 5% casein (Teklad Diets, catalogue # 160030). The three protein-poor diets were each given a specific flavor by adding either 1% McCormick's fancy ground cinnamon, 2% Hershey's cocoa, or 1% Club House ground thyme to them. The sole protein-rich diet was composed of 80% basal mix and 20% casein and was flavored with 1% Club House ground nutmeg. For ease of writing, the protein-poor diets will be referred to as Diets Cin, Coc, Thy (abbreviations of their flavorings), and the protein-rich diet as Diet HP-Nut (abbreviation of high-protein nutmeg diet).

### *Apparatus*

The present experiment was conducted in 1x1x0.3-m cages constructed of angle iron and hardware cloth and floored with galvanized sheet metal covered to a depth of 2-3 cm with wood-chip bedding. Each cage contained a single 30x30-cm, wooden nest box with two 5x5-cm entrances, and a watering station (see Fig. 1). All diets were presented in circular, 10-cm-diam., Pyrex food bowls.

**Fig. 1. Schematic diagram of the apparatus used in Experiments 1, 2, and 7. The diet labels refer only to the flavorings used in the diets. The nutrient compositions of diets used in each experiment are described in the text.**



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### *Procedure*

The experiment was performed in three steps.

**Step 1. *Demonstrator training.*** Each demonstrator was housed individually and trained to avoid the three protein-poor diets (Diets Cin, Coc, and Thy) by conditioned taste-aversion training. Each demonstrator was first food-deprived overnight for 12 hr, then given access to a weighed food bowl containing Diet Cin for 2 hr. After it was ascertained that a given demonstrator had eaten Diet Cin, the demonstrator was immediately injected interperitoneally with 1% of its body weight of a 2% wt/vol LiCl solution. Each demonstrator was then given ad lib access to powdered Purina Laboratory Rodent Chow (Diet P) for 34 hr. Aversion training was repeated using Diet Coc and Diet Thy. Following aversion training to Diet Thy, each demonstrator was given ad lib access to Diet HP-Nut for 58 hr.

**Step 2. *Habituation.*** Subjects were randomly assigned to either an Experimental Group ( $n=6$ ) or a Control Group ( $n=7$ ) and were placed individually in testing enclosures. Three demonstrators were then placed into the testing enclosure of each subject in the Experimental group. For the next 24 hr, all rats were given ad lib access to water and a bowl that contained Diet P placed in the center of the testing enclosure. This 24-hr period of habituation of subjects and demonstrators, both to one another and to the apparatus, had been found in pilot studies to markedly reduce variance in the amount eaten by subjects during Step 3 described below.

**Step 3. *Testing.*** Following habituation, the bowl that contained Diet P was removed from each testing enclosure and replaced with bowls that contained the four test diets, one test diet in each corner, as illustrated in Figure 1. For the next 6 days, subjects and demonstrators were left undisturbed except for a daily weighing of food bowls and subjects.

## Results

The presence of demonstrators trained to feed exclusively upon the protein-rich diet had a profound effect upon the amount that juvenile subjects grew during the 7 days of testing. As shown in Fig. 2, subjects in the Experimental group gained a significantly greater percentage of their initial body weight during testing than did isolated subjects (Student t-test,  $t(11)=3.20$ ,  $p=.0042$ , one-tailed). While only 29 percent of the isolated juveniles gained weight during the six days of testing, 83 percent of juveniles tested in the presence of demonstrators did so.

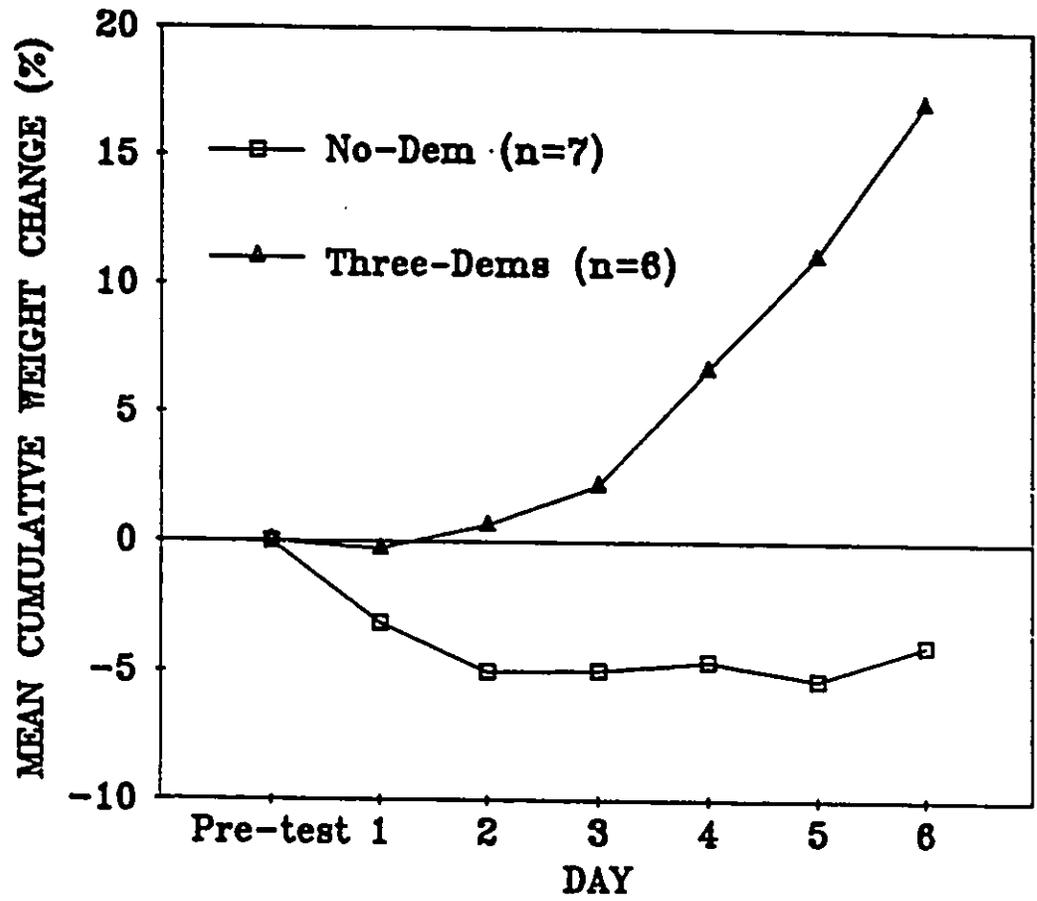
## Discussion

Assuming that the substantial weight gain displayed by weanling rats exposed to demonstrators was due to their preference for the protein-rich diet, the present results suggest that social influences can play an important role in the diet selections of young rats. This finding is not surprising given the advantage that a weanling could derive from using social information to solve diet-selection problems. By utilizing social information, weanlings can learn about the nutrient environment without engaging in the slow, and therefore costly, enterprise of sampling foods of unknown nutritional value. In addition, the accuracy of dietary information a weanling can derive from social sources is almost certainly greater than information it can obtain from its own foraging experience. The simple fact that an animal is alive attests to its ability to find adequate nutrients. Thus, if there is a certain risk, no matter how small, that a weanling will develop maladaptive diet preferences, it could avoid that risk by adopting the preferences of an older conspecific.

The more difficult the diet-selection task is, the greater the benefit of adopting a solution discovered by an older conspecific.

Unfortunately, the testing procedure used in the present experiment did not allow the actual diet choices of subjects exposed to demonstrators to be monitored. Without such measures the possibility remains that the observed difference in weight gain between the experimental and control groups was merely a consequence of a difference in their total dietary intake. This explanation of the substantial weight gains made by animals exposed to demonstrators is examined in Experiment 3 of this thesis.

**Fig. 2. Mean cumulative percent weight change of juvenile subjects choosing diets either in isolation, or in the presence of three demonstrators trained to eat a protein-rich diet (Diet HP-Nut).**



## EXPERIMENT 2

The main purpose of Experiment 2 was to determine whether the diet choices of adolescent rats, like those of weanling rats, are susceptible to social influences. If adolescent rats are not responsive to social influence, then their lack of responsiveness would suggest that the role of social influences is limited to establishing an initial diet for weanlings and juveniles.

Experiment 2 also examined the effect of using several, rather than a single demonstrator, on the diet choices of juvenile rats.

### Method

#### *Subjects and Test Diets*

Twenty-six, adolescent, male, Long-Evans, experimentally-naive rats, weighing 150-175 g, descendants of breeding stock acquired from Charles River, Canada (St. Constant, Quebec) served as subjects. An additional 29 rats, weighing 175-200 g served as demonstrators. The four test diets described in Method of Experiment 1 were used.

#### *Apparatus*

The test enclosure described in Method of Experiment 1 was used (see Fig. 1). All diets were presented in circular, 10-cm-diam., Pyrex food bowls.

#### *Procedure*

The procedure used in the present experiment was the same as that used in Experiment 1, except for two minor changes. Three conditions were used in the present

experiment rather than two: isolated animals ( $n=11$ ), animals that selected diets in the presence of a single demonstrator ( $n=8$ ), and animals that selected in the presence of three demonstrators ( $n=7$ ). In addition, the testing period was lengthened to one week.

## Results and Discussion

The main results of Experiment 2 are presented in Fig. 3, which shows the cumulative percentage weight gain of subjects in the three groups. An ANOVA conducted on cumulative percent weight gain data indicated that adolescent rats benefited as much from the presence of others displaying adaptive diet preferences as did weanling rats ( $F(2,23)=19.74$ ,  $p=.00005$ ). Post-hoc analysis revealed that subjects exposed to a single demonstrator gained a significantly higher percentage of their initial body weight than did isolated animals (Newman-Keuls post-hoc analysis,  $W_r=12.38$ ,  $p<.01$ ) and that subjects with three demonstrators gained a greater percentage of their initial weight than either subjects exposed to just one demonstrator (Newman-Keuls post-hoc analysis,  $W_r=11.16$ ,  $p<.05$ ), or isolated subjects (Newman-Keuls post-hoc analysis,  $W_r=23.54$ ,  $p<.01$ ). While only 27 percent of isolated subjects gained weight during the week of testing, 87 percent of the subjects with one demonstrator gained weight, and 100 percent of those with three demonstrators gained weight. No isolated subject gained as much weight as any subject with three demonstrators.

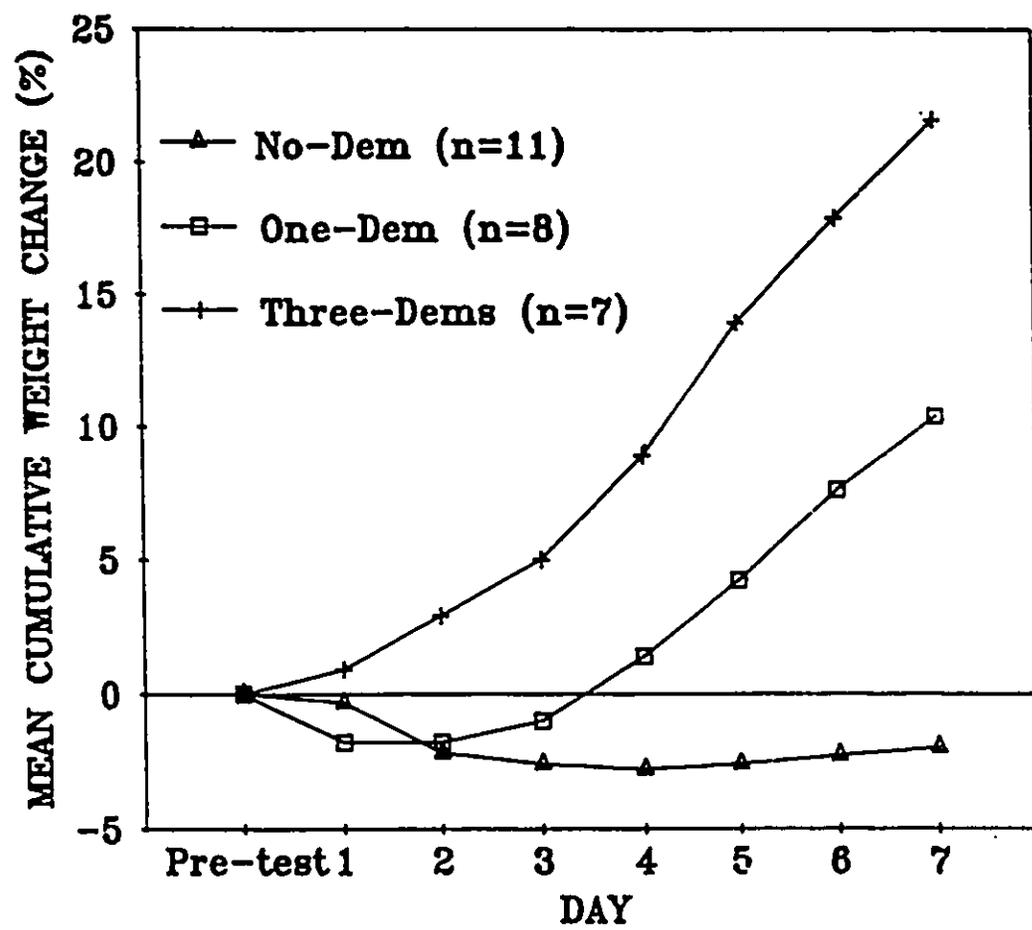
Unfortunately, because subjects in the two experimental groups were tested in the presence of demonstrators, it was not possible to directly measure diet choice behaviour. Without such measures one cannot rule out the possibility that observed differences in weight gain were due to differences in total intake. Experiment 3 examines this possibility.

Assuming that the differences in weight gain were indeed due to differences in diet selection behaviour, the results of the present experiment suggest that the role of social factors in diet selection extends beyond the weaning period. One can point to two major advantages that a rat would gain from remaining sensitive to social influences after weaning. First, many nutrient deficiencies would develop after weaning. For example, the internal reserves of vitamin B in the weanling rat allow it to grow normally for 10 days when fed a diet completely lacking the vitamin (Rozin, 1967). A diet containing small yet insufficient quantities of vitamin B might allow a rat to reach adolescence or even young adulthood before the effects of deficiency appeared. The present results suggest that an animal which failed to acquire information about a nutrient source as a weanling, and that subsequently became nutrient deficient as a juvenile, could still access social information in order to correct its deficiency. Second, it is possible that the source of a needed nutrient being exploited by a rat might disappear from the environment, perhaps due to seasonal fluctuation. A juvenile rat that could not use social information to find a new source of this nutrient would be at a severe disadvantage.

Another aspect of the present results that deserves discussion is the fact that rats housed with three demonstrators gained a significantly greater percentage of their initial weight than animals with a single demonstrator. A likely explanation for this outcome is that the critical social interactions that allow diet information to be transferred occur earlier in the testing phase if several demonstrators are present rather than if only one demonstrator is present. It is not impossible that such a graded response to social influence has adaptive consequences. One might speculate that a rat that was more likely to adopt a diet preference when several rats displayed the preference would have an advantage over a rat that did not match its response to the number of animals displaying the preference. If several rats prefer the same diet, then the diet may be more likely to contain a needed nutrient than if a

single rat prefers it. While a single rat may express an idiosyncratic preference for a nutrient-poor diet, it is less likely that several rats would express the same idiosyncratic preference.

**Fig. 3. Mean cumulative percent weight change of adult subjects choosing diets in isolation, in the presence of a single demonstrator trained to eat a protein-rich diet (Diet HP-Nut), or in the presence of three trained demonstrators.**



### EXPERIMENT 3

The results of Experiments 1 and 2 showed that naive animals presented with a diet-selection task gained substantially more weight when tested with a knowledgeable conspecific than when tested alone. However, because subjects and demonstrators were housed together in Experiments 1 and 2, it was not possible to monitor the actual diet choices of subjects. In the present experiment an apparatus was used which separated subjects from their demonstrators, thereby allowing diet selections to be monitored directly.

#### Method

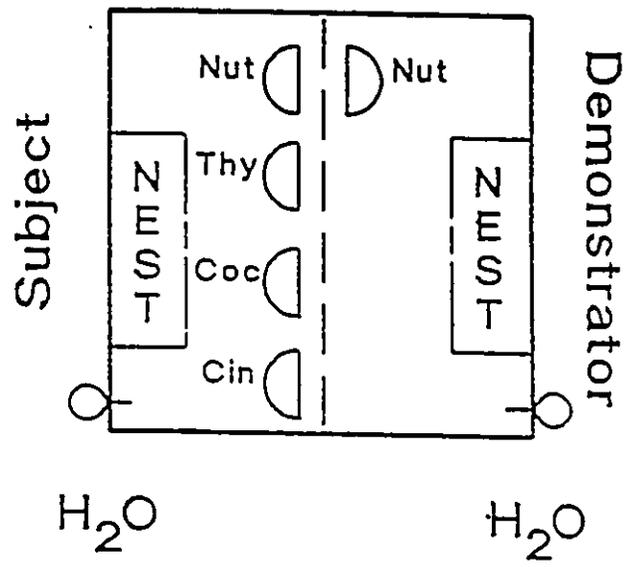
##### *Subjects and Test diets*

Twelve experimentally naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 18 rats, weighing 175-200 g served as demonstrators. The four test diets described in Method of Experiment 1 were used.

##### *Apparatus*

The present experiment was conducted in the same 1x1x.3-m cages used in Experiments 1 and 2, except that the cages were divided in half by a hardware-cloth barrier (grid size 1x1 cm) that separated subjects from their respective demonstrators. Each side of the divided enclosure contained a single 30x15-cm, wooden nest-box with one 5x5-cm entrance, and a watering station (See Fig. 4).

**Fig. 4. Schematic diagram of the apparatus used in Experiments 3,8,9,10,11,12, and 13. The diet labels refer only to the flavorings used in the diets. The nutrient compositions of diets used in each experiment are described in the text.**



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### *Procedure*

The experiment was conducted in two steps.

**Step 1. *Habituation.*** Subjects were randomly assigned to Experimental ( $n=6$ ) and Control Groups ( $n=6$ ) and individually placed in the subject compartments of the divided enclosures (See Fig. 4). Three demonstrators were then placed in the demonstrator compartment of the cage of each Experimental subject. The demonstrator compartments of the cages of subjects in the Control Group were left empty. Subjects and demonstrators were then given ad lib access to powdered Purina Laboratory Rodent Chow (Diet P) for 24 hr.

**Step 2. *Testing.*** Following habituation, bowls containing Diet P were removed from the testing enclosures and each subject was given four metal, semi-circular, 10-cm-diam. food bowls, each containing a different test diet. These food cups were attached to the dividing screen and contained the test diets in the order Diet Cin, Coc, Thy, and HP-Nut from the front of the cage to the back (See Fig. 4). Demonstrators were each given a single food bowl containing Diet HP-Nut. This bowl was attached to the dividing screen immediately opposite each subject's bowl containing Diet HP-Nut (see Fig. 4). For the next week, subjects and demonstrators were left undisturbed except for a daily weighing of food bowls and subjects.

## Results and Discussion

Subjects were influenced by the feeding behaviour of their respective demonstrators even under the conditions of the present experiment, in which direct physical contact between subject and demonstrator was prevented. An analysis of diet choices showed that the higher growth rate of subjects with demonstrators, relative to isolated subjects, was due to their significantly greater preference for the protein-rich Diet HP-Nut (see Fig. 5). As Fig. 5 shows, subjects with demonstrators ate a significantly greater proportion of the protein-rich diet during testing (Student  $t$ -test,  $t(10)=-2.52$ ,  $p=.015$ , one-tailed)\*. Indeed, by the end of the testing period, Diet HP-Nut made up 92.5 percent of the food intake of subjects with demonstrators, but only 27.8 percent of the intake of subjects without demonstrators. While only one of the six isolated subjects ate more than 90 percent of its total intake from the Diet HP-Nut bowl on one of the testing days, all six subjects with demonstrators did so.

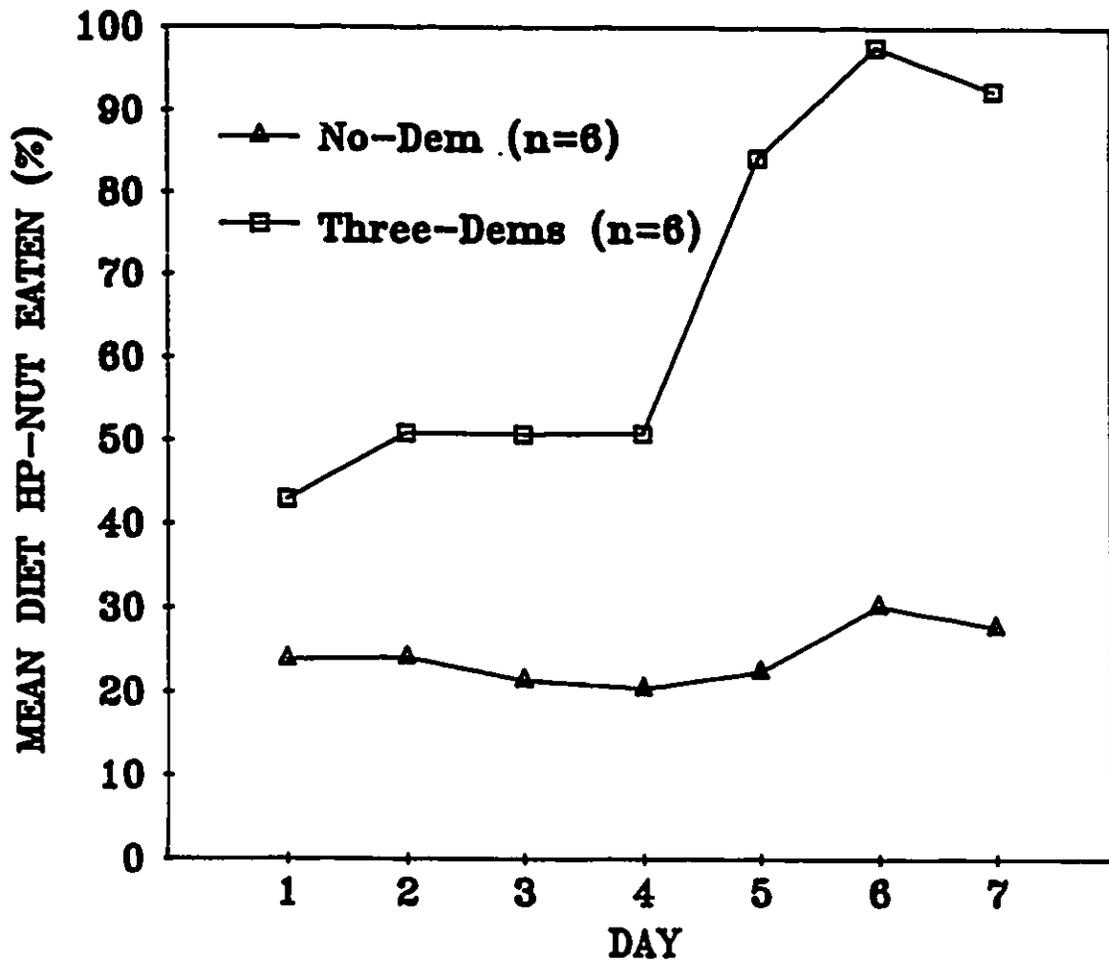
As can be seen in Fig. 6, subjects exposed to demonstrators gained a greater percent of their initial body weight than did subjects that selected diets in isolation. However, this difference did not reach significance using a Student  $t$ -test (Student  $t$ -test,  $t(10)=1.42$ ,  $p=.09$ , one-tailed). It is likely that the lack of significance is a Type II error, both because two repetitions of the basic procedure used in Experiment 3 (Experiments 6 and 8) did yield significant differences in weight gain, and because non-parametric statistical analysis of the present data indicated there was a significant difference between the weight gain of isolated subjects and subjects exposed to a demonstrator (Mann-Whitney  $U$  test,  $U=7$ ,  $p=.0465$ , one-tailed).

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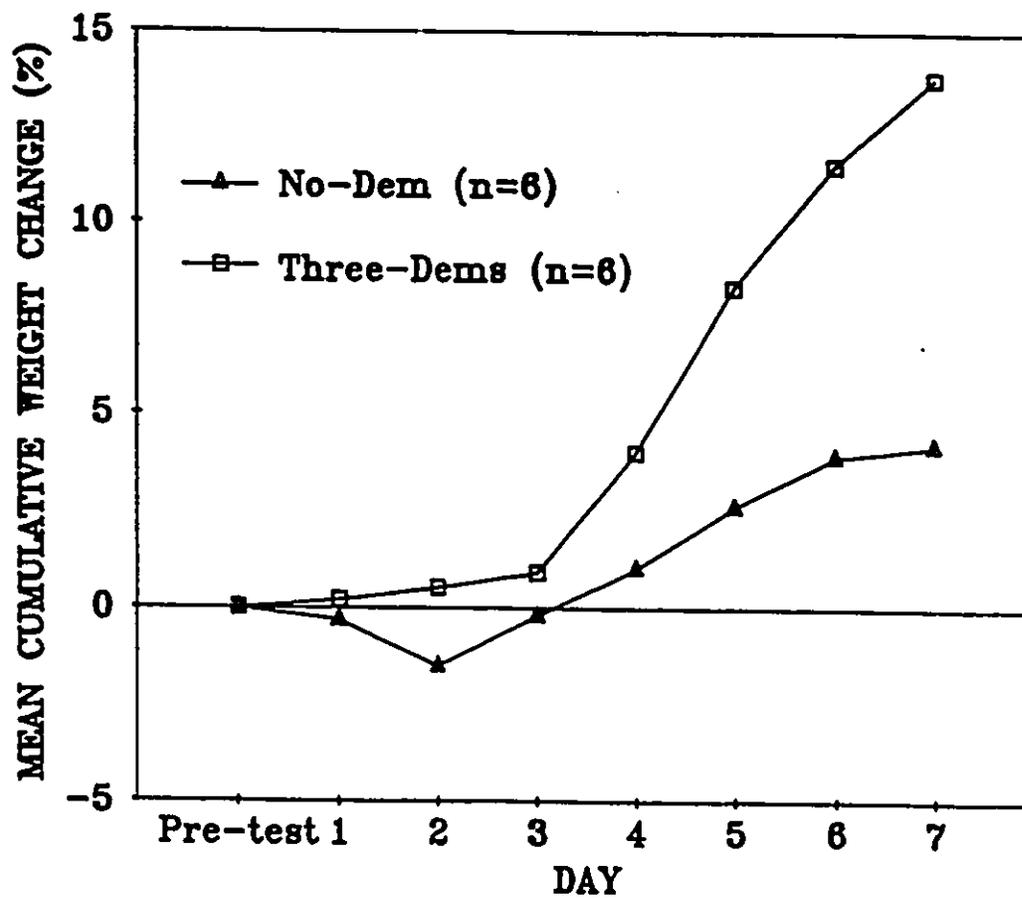
\* Throughout this paper percentage scores of diet preference were transformed using an Arcsin transform prior to statistical analysis:  $Y'=\text{Arcsin}(\text{Sqrt}(Y))$ .

Because subjects were separated from their demonstrators in the present experiment, it was possible to determine the strength of the relationship between intake of protein-rich diet by subjects and their weight gain. Percent intake of Diet HP-Nut by animals in both groups during the week of testing was significantly correlated with total weight change during testing (Pearson  $r=+.844$ , Student  $t$ -test,  $t(10)=4.98$ ,  $p<.0005$ , one-tailed). The positive correlation indicates that the amount of weight gained was indeed related to the proportion of protein-rich diet ingested.

**Fig. 5. Mean amount of Diet HP-Nut ingested, as a percentage of total intake, by isolated subjects and by subjects choosing diets in the presence of three demonstrators eating Diet HP-Nut in the demonstrator compartment of the divided enclosure.**



**Fig. 6. Mean cumulative percent weight change of subjects choosing diets either in isolation, or in the presence of three demonstrators eating a protein-rich diet (Diet HP-Nut) in the demonstrator compartment of the divided enclosure.**



**Chapter III: The relative control of where and what a demonstrator ate over subject diet choice.**

Taken together, the results of the series of experiments presented in Chapter II strongly suggest that the success of naive rats in a diet-selection task was enhanced by the presence of others making adaptive diet selections. Subjects that were tested in the presence of demonstrators that had been trained to prefer the protein-rich diet ate a significantly higher proportion of this diet during the 7 day testing period (Experiment 3), and gained a significantly greater percentage of their initial body weight (Experiments 1 and 2), than subjects tested in isolation.

However, the results obtained in these experiments do not reveal what form this social influence took. Other studies have shown that the diet choice of rats is affected by both the type of food eaten by others (Galef, Kennet, and Wigmore, 1984; Galef and Wigmore, 1983; Galef and Stein, 1985), and by where others are feeding (Thorpe, 1963; Galef, 1977; Galef and Clark, 1971). The purpose of the present series of experiments was to determine the extent to which rats in the present paradigm responded to these two types of social information. By discovering the mechanism by which rats match the diet choices of others when selecting nutritious foods, it should be possible to develop a more accurate picture of how social information is used by wild rats to make beneficial diet choices. For example, if rats are only able to use social information to orient towards a food site and cannot gain information about the type of food to eat from others, then rats

would be forced to individually sample the diets at the location at which a demonstrator fed in order to obtain precise dietary information. If, however, rats obtain information about the actual foods being eaten by others, then they could forego this potentially costly individual sampling.

## EXPERIMENT 4

In the present experiment, I examined whether the presence of a demonstrator which had recently fed upon a protein-rich diet was in itself sufficient to cause subjects to choose a diet adequate in protein.

### Method

#### *Subjects and Test diets*

Sixteen experimentally-naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 16 rats, weighing 175-200 g, served as demonstrators. The four test diets described in Method of Experiment 1 were used in the present experiment.

#### *Apparatus*

The present experiment was conducted in the divided enclosure described in Method of Experiment 3 (see Fig. 4).

#### *Procedure*

The experiment was conducted in two steps.

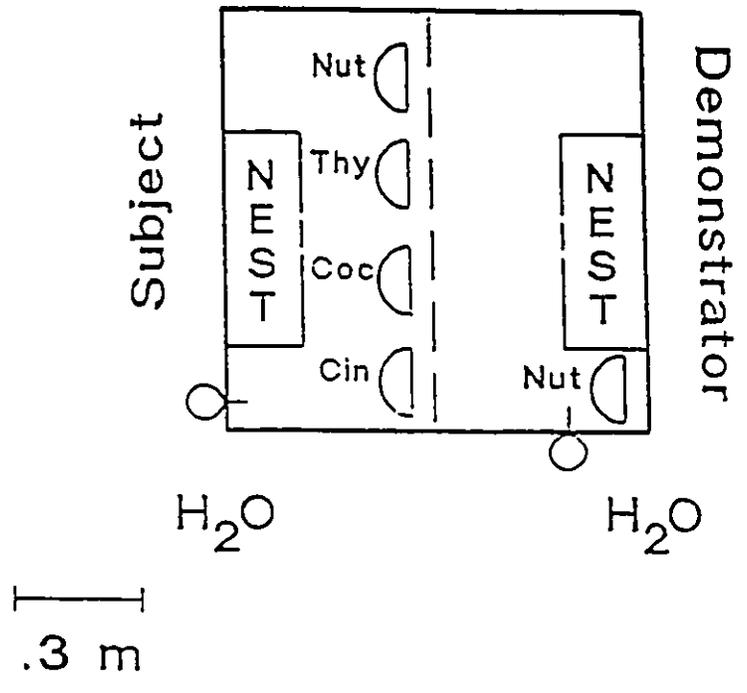
**Step 1. *Habituation.*** Subjects were randomly assigned to Same-Food ( $n=8$ ) and Different-Food ( $n=8$ ) conditions and individually placed in the subject compartments of the divided enclosures. A single demonstrator was placed in each of the adjacent demonstrator compartments. Subjects and demonstrators were then given ad lib access to powdered Purina Laboratory Rodent Chow (Diet P) for 24 hr.

**Step 2. Testing.** Following habituation, bowls containing Diet P were removed from the testing chambers and each subject was given four metal, semi-circular, 10-cm-diam., food bowls each containing a different test diet. These food bowls were attached to the dividing screen and contained the test diets in the order Diet Cin, Coc, Thy, and HP-Nut from the front of the cage to the back. Demonstrators caged adjacent to subjects in the Same-Food Group were each given a single food bowl containing Diet HP-Nut. This bowl was placed in the corner of the demonstrator compartment furthest from the subject's food bowl containing Diet HP-Nut (see Fig. 7). Demonstrators of subjects in the Different-Food group were fed Diet P from a bowl placed in the same distant corner of their compartment in which Demonstrators assigned to Same-Food Group subjects fed. For the next week subjects were left undisturbed except for daily weighing of food bowls and subjects.

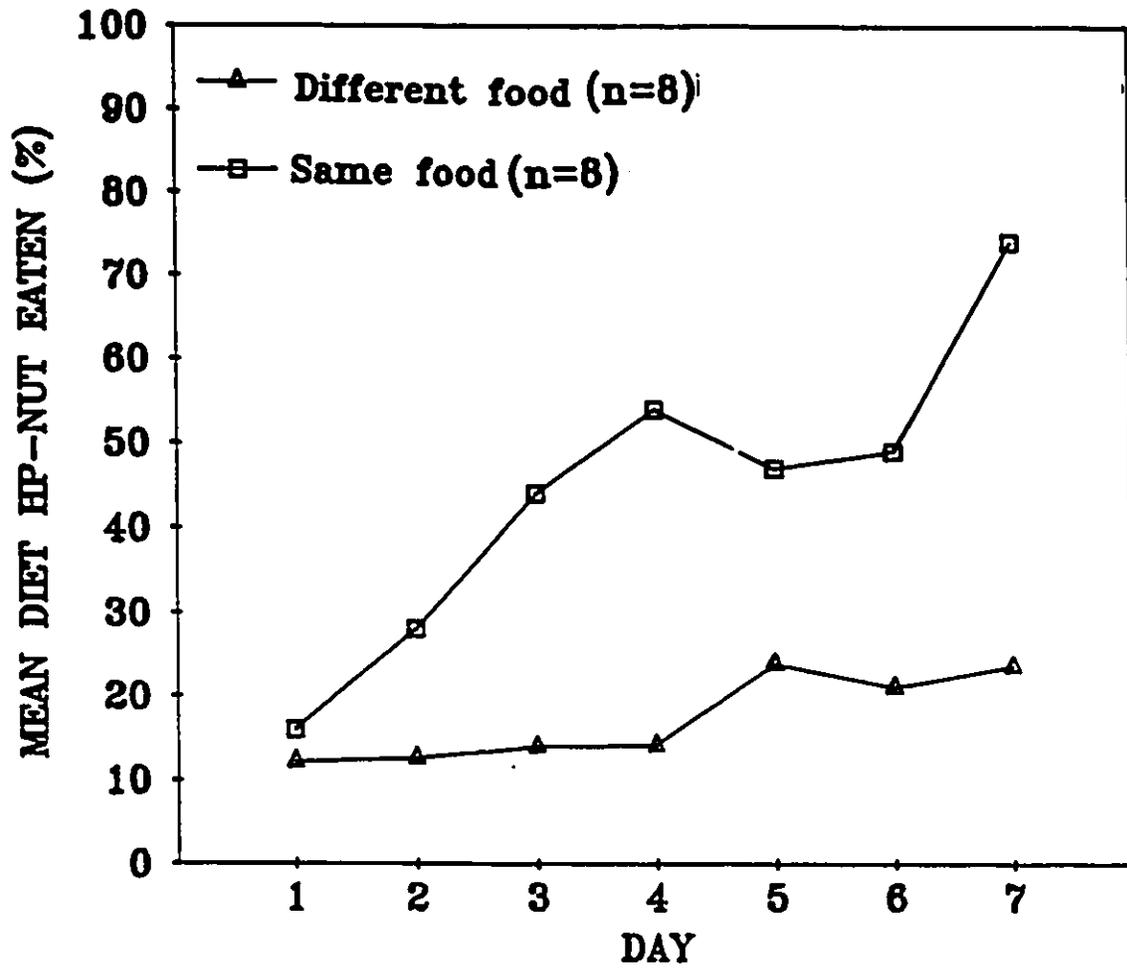
## Results and Discussion

The results of the present experiment indicate that the a subject did not have to be in the presence of a demonstrator while the demonstrator fed in order to show a tendency to match the demonstrator's diet choice. As suggested by an examination of Fig. 8, and as confirmed by statistical test, subjects in the Same-Food group ate a greater proportion of Diet HP-Nut than did subjects in the Different-Food group over the week of testing (Student t-test,  $t(14)=1.98$ ,  $p=.033$ , one-tailed). Also, subjects in the Same-Food group gained a significantly greater percent of their initial weight during testing than did subjects in the Different-Food group (Student t-test,  $t(14)=2.21$ ,  $p=.021$ , one-tailed; see Fig. 9).

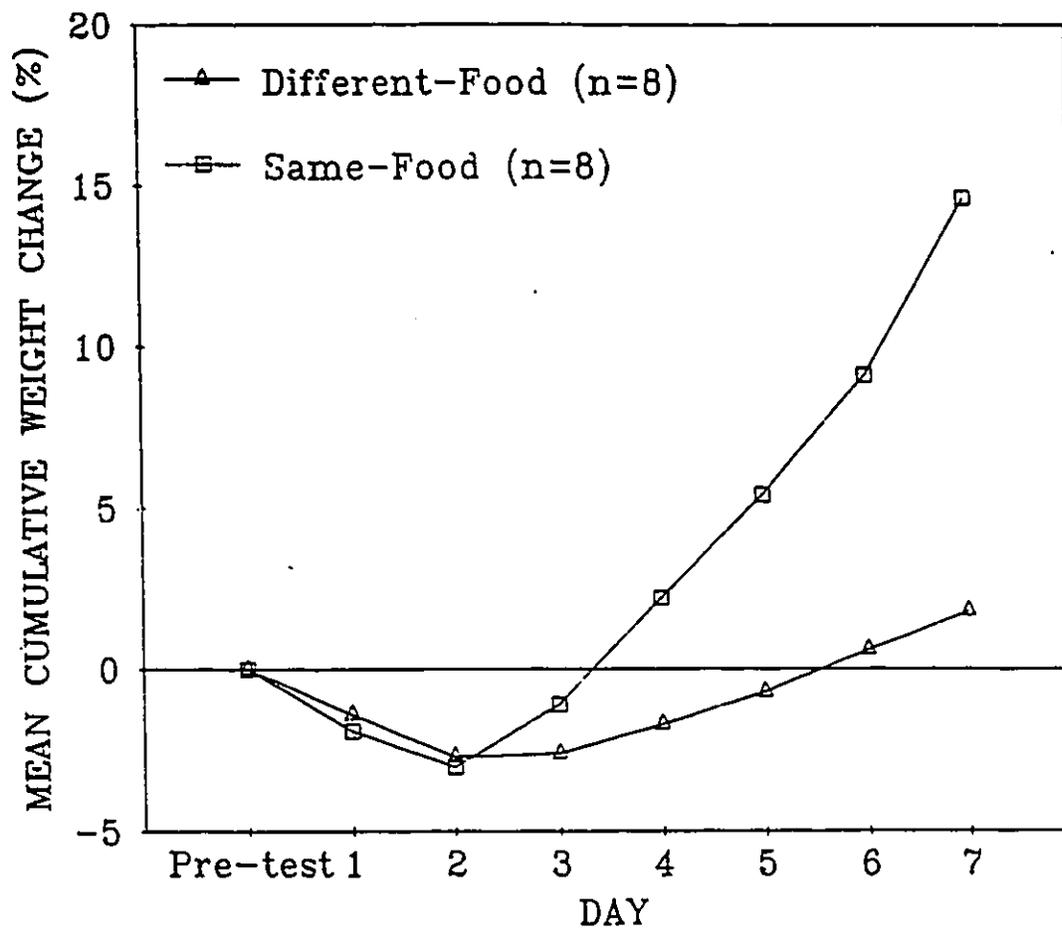
Fig. 7. Schematic diagram of the apparatus used in Experiments 4 and 5.



**Fig. 8. Mean amount of Diet HP-Nut ingested, as a percentage of total intake, by subjects in the Same-Food and Different-Food conditions.**



**Fig. 9. Mean cumulative percent weight change of subjects in the Same-Food and Different-Food conditions.**



The present results agree with Galef and Wigmore's (1983) finding that rats were biased by the diet choice of others even when separated from them by a wire mesh screen. Galef and Wigmore (1983) showed that rendering rats anosmic by treating them with Zinc Sulphate eliminated their tendency to match the diet choice of their respective demonstrators, suggesting that rats were influenced in their diet selection by scent cues that remained on the breath of demonstrators after they fed. Galef and Wigmore (1983) suggested that rats could use their ability to detect olfactory cues on the breath of others to exploit foods that are intermittently available in the environment. A colony of rats, they argued, could serve as an "information-center", providing rats with access to information collected by numerous rats foraging individually.

The present results suggest that olfactory cues might also be used by rats to find needed nutrients that are present in relatively unpalatable foods when several more palatable alternative diets are available.

## EXPERIMENT 5

While Experiment 4 showed that subjects do not have to be in the presence of a demonstrator while it feeds in order to be influenced by the demonstrator's diet choice, it did not exclude the possibility that the location at which a demonstrator fed might also influence subject diet selection. The present experiment directly tested this possibility.

### *Subjects and Test diets*

Thirteen experimentally-naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 13 rats, weighing 175-200 g, served as

demonstrators. The four test diets described in Method of Experiment 1 were used in the present experiment.

### *Apparatus*

The present experiment was conducted in the divided enclosure described in Method of Experiment 3 (see Fig. 4).

### *Procedure*

The experiment was conducted in two steps.

Step 1. Habituation. The habituation procedure described in Method of Experiment 4 was used in the present experiment.

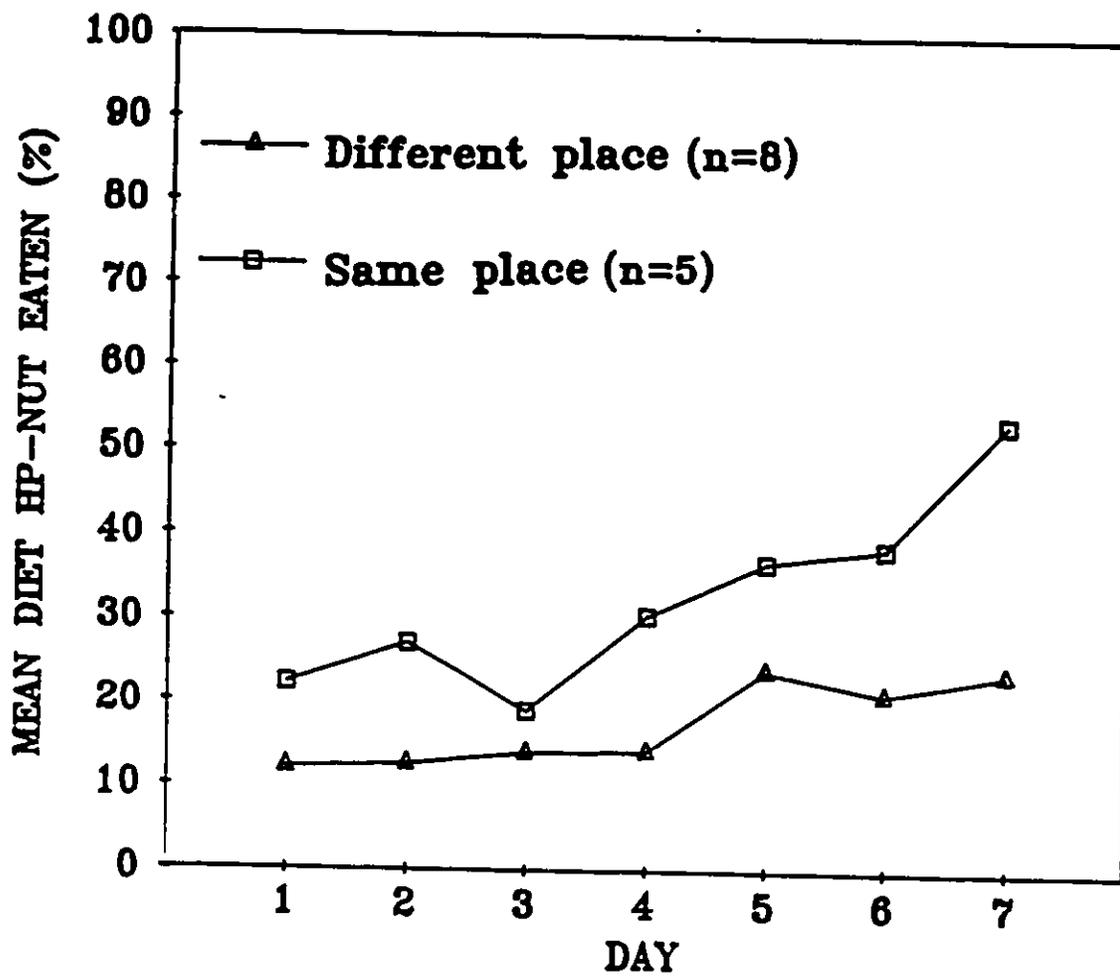
Step 2. Testing. Following habituation, all bowls containing powdered Purina Laboratory Rodent Chow (Diet P) were removed from the testing chambers and each subject was given four metal, semi-circular, 10-cm-diam. food bowls, each containing a different test diet. These food cups were attached to the dividing screen and contained the test diets in the order Diet Cin, Coc, Thy, and HP-Nut from the front of the cage to the back. Demonstrators assigned to the Same-Place group ( $n=5$ ) were each given a single food bowl containing Diet P. This bowl was attached to the dividing screen immediately opposite the bowl in each subject's compartment that contained Diet HP-Nut (see Fig. 4). Demonstrators in the Different-Place group ( $n=8$ ) were also fed Diet P, but from a bowl placed in the corner of the demonstrator compartment furthest from the bowl in each subject's compartment that contained Diet HP-Nut (See Fig. 7). For the next week, subjects and demonstrators were left undisturbed except for a daily weighing of both food bowls and rats.

## Results and Discussion

The presence of a demonstrator at a feeding site did not have a significant effect upon the diet choices of subjects. As shown in Fig. 10, subjects in the Same-Place group ate a slightly higher percentage of Diet HP-Nut during testing than subjects in the Different-Place group. However, the difference in the percentage of Diet HP-Nut eaten between the two groups was not statistically significant (Student t-test,  $t(11)=1.03$ ,  $p=.17$ , one-tailed). Indeed, the two groups did not significantly differ in proportion of Diet HP-Nut intake on any testing day (see Table 1 for significance levels). Weight gain data also suggests that subjects in the Same-Place group were slightly better at finding an adequate diet than subjects in the Different-Place group (see Fig. 11). Yet as with Diet HP-Nut intake, the two groups did not differ significantly in their weight gain (Student t-test,  $t(11)=.988$ ,  $p=.18$ , one-tailed).

The present results do not conform to those of Galef and Clark (1971) in which it was found that the presence of a rat at a feeding site affected diet choice. If the disparity of results was not simply due to a Type II error in the present experiment, then the disparity of results could be due to either of two major procedural differences between the present study and that of Galef and Clark (1971): (a) Subjects in the present study were given a choice of four diets rather than just two. (b) The wire mesh screen that separated subjects and demonstrators in the present experiment might have reduced the influence that the presence of a demonstrator at a feeding site has upon diet selection.

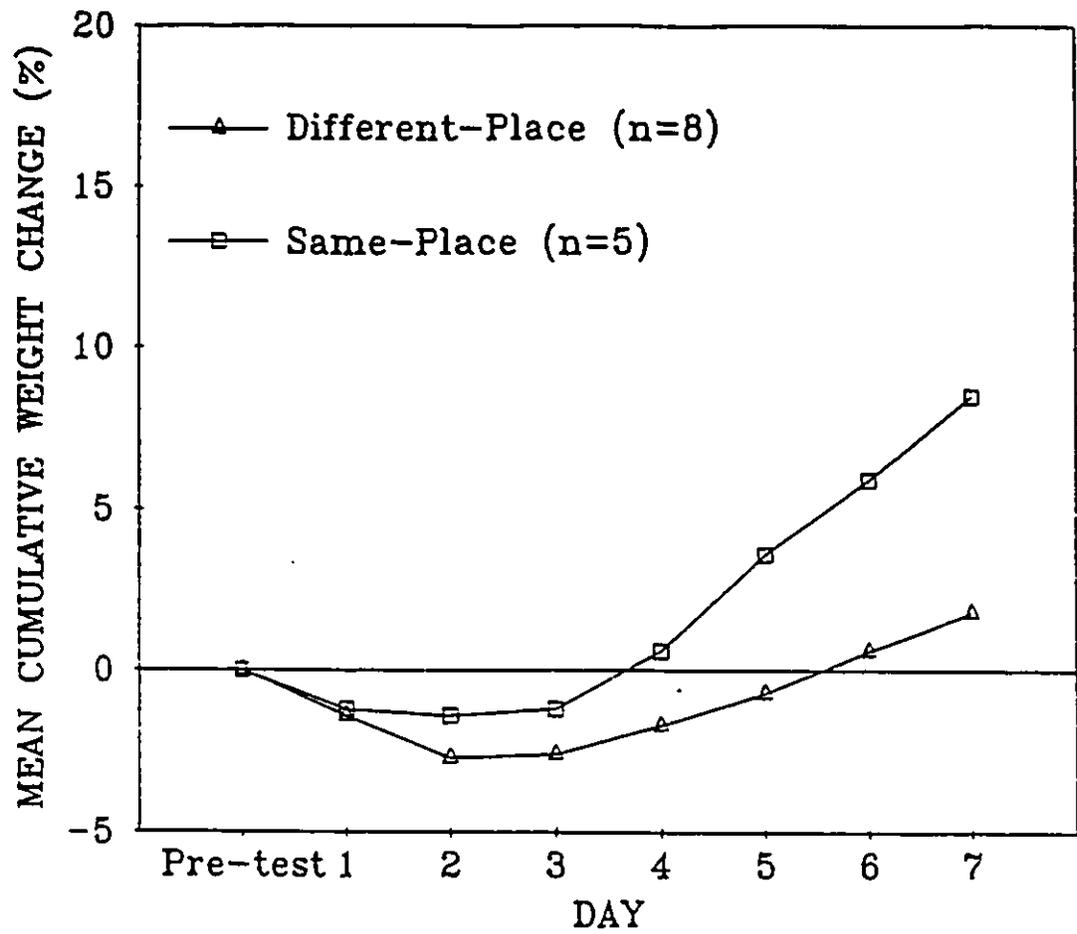
**Fig. 10. Mean amount of Diet HP-Nut ingested, as a percentage of total intake, by subjects in the Same-Place and Different-Place conditions.**



**Table 1. Results of Student t-tests comparing the amount of Diet HP-Nut eaten, as a percentage of total intake, by subjects in the Same-Place and Different-Place conditions.**

|               | Day  |      |     |      |     |     |      |
|---------------|------|------|-----|------|-----|-----|------|
|               | 1    | 2    | 3   | 4    | 5   | 6   | 7    |
| t(11)         | 1.01 | 1.27 | .22 | 1.21 | .89 | .96 | 1.42 |
| p(one-tailed) | .18  | .11  | .40 | .13  | .20 | .18 | .09  |

**Fig. 11. Mean cumulative percent weight change of subjects in the Same-Place and Different-Place conditions.**



## EXPERIMENT 6

Taken together, the results of Experiments 4 and 5 were consistent with the view that the diet selections of subjects were more influenced by what a demonstrator fed upon than by where a demonstrator fed. The present experiment directly tested this possibility.

### Method

#### *Subjects and Test diets*

Eighteen rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 18 rats, weighing 175-200 g served as demonstrators. The four test diets described in Method of Experiment 1 were used in the present experiment.

#### *Apparatus*

The present experiment was a conducted in the divided enclosure described in Method of Experiment 3.

#### *Procedure*

The experiment was conducted in two steps.

Step 1. *Habituation*. The habituation procedure described in Method of Experiment 4 was used in the present experiment.

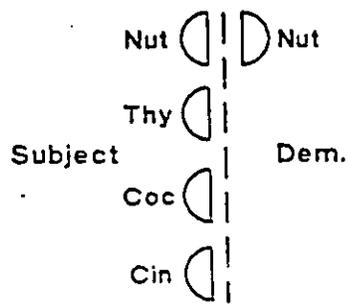
Step 2. *Testing*. Following habituation, bowls containing powdered Purina Laboratory Rodent Chow (Diet P) were removed and each subject was given four metal, semi-circular, 10-cm-diam. food bowls each containing a different test diet. These food

cups were attached to the dividing screen and contained the test diets in the order Diet Cin, Coc, Thy, and HP-Nut from the front of the cage to the back.

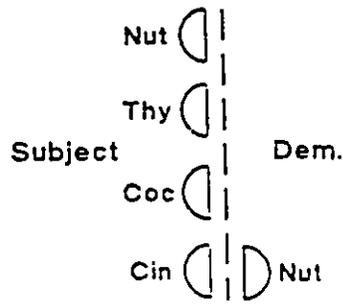
Both the locations at which demonstrators were fed, and the diet that they were fed varied among three groups ( $n=6$ /group). Demonstrators assigned to subjects in the Same-Food/Same-Place condition were fed from a bowl containing Diet HP-Nut placed directly opposite the location at which subjects were presented with Diet HP-Nut (see Fig. 12a). Demonstrators assigned to subjects in the Same-Food/Different-Place condition were fed Diet HP-Nut directly opposite where subjects were presented with a bowl containing Diet Cin (see Fig. 12b). Demonstrators assigned to subjects in the Different-Food/Same-Place condition were fed Diet Cin directly opposite where their subjects were presented with Diet HP-Nut (see Fig. 12c). For the next week subjects were left undisturbed except for a daily weighing of food bowls and rats.

**Fig. 12 a,b,c. The arrangement of diets used in the Same-Food/Same-Place, Same-Food/Different-Place, and Different-Food/Same-Place conditions.**

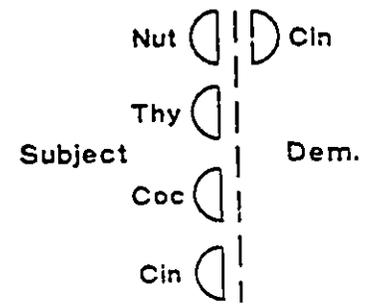
**A: Same-Food  
Same-Place**



**B: Same-Food  
Different-Place**



**C: Different-Food  
Same-Place**

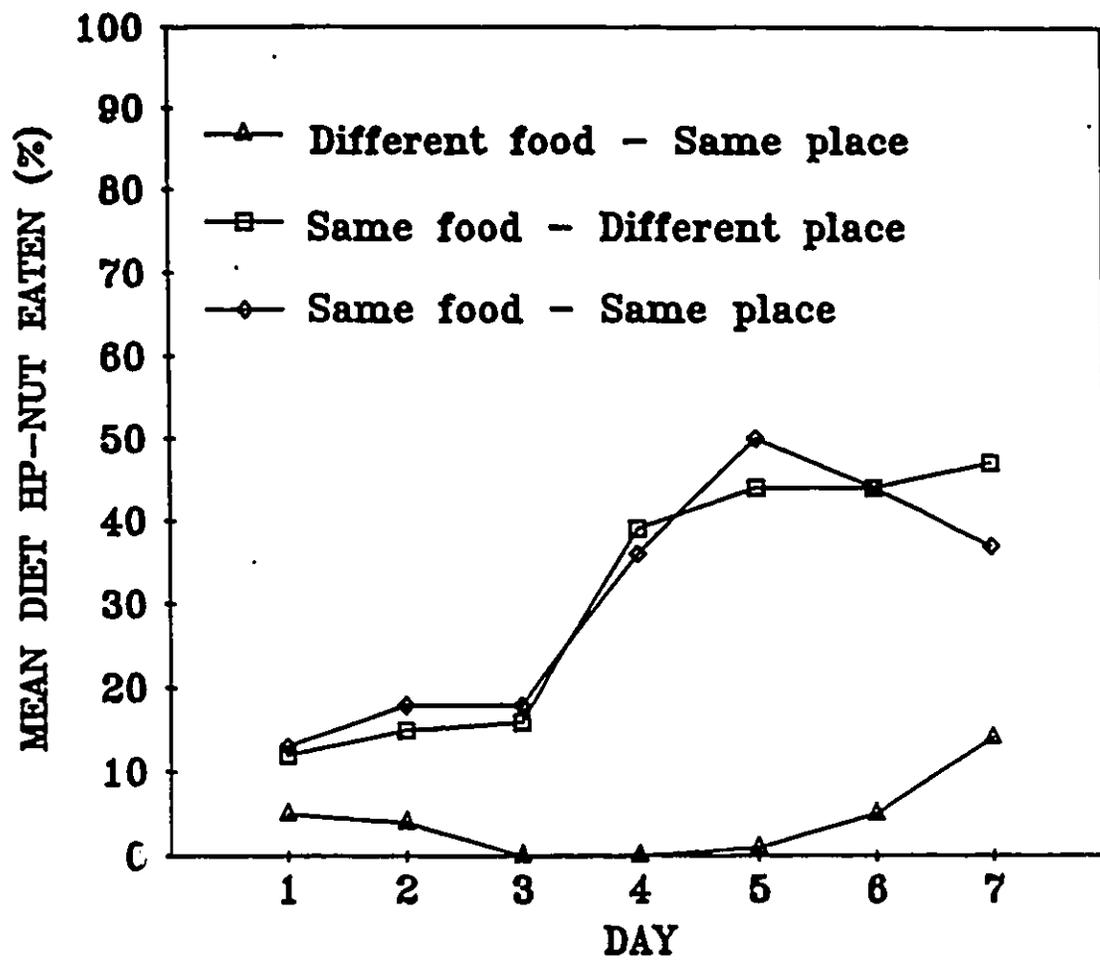


## Results and Discussion

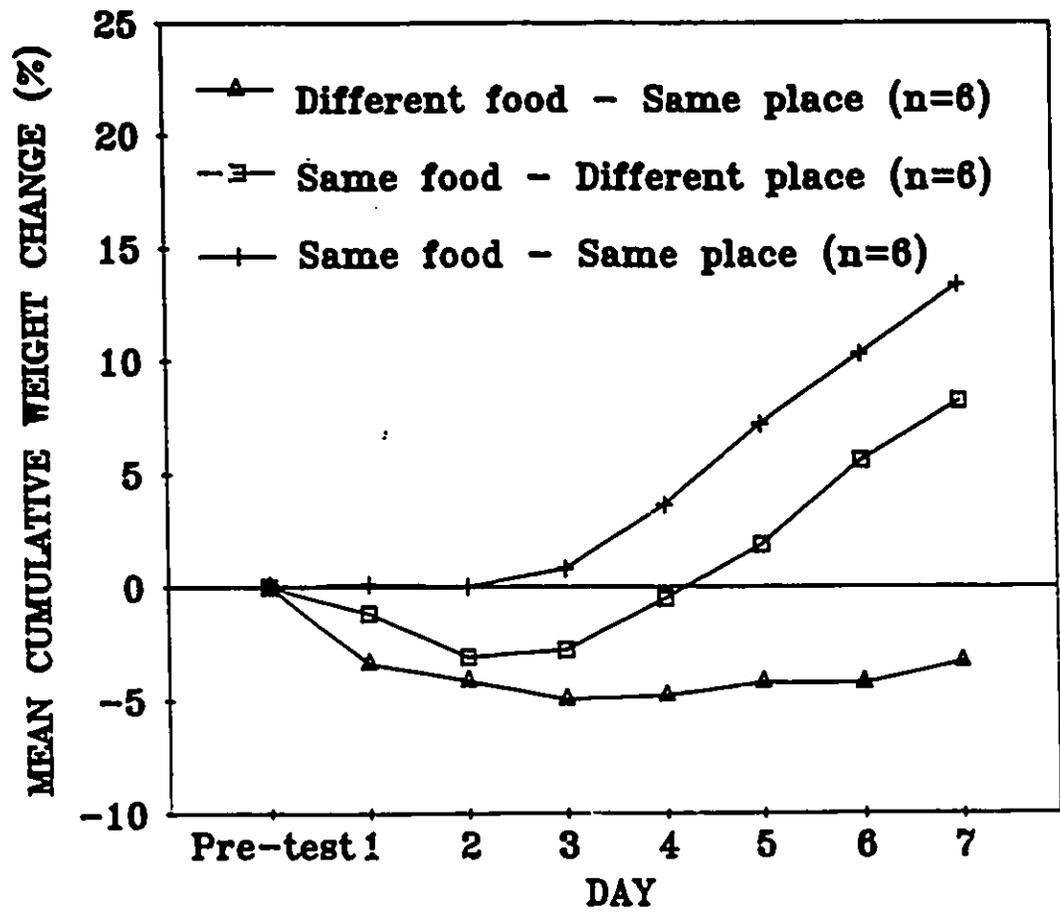
The main results of the present experiment are displayed in Figs. 13 and 14 which show respectively: (Fig. 13) the mean percentage of Diet HP-Nut eaten by subjects in each of the three groups during each day of testing and (Fig. 14) the mean percentage cumulative weight gain of subjects in each of the three groups during testing. 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. There was a significant effect of treatment on the percentage 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 a significantly lower proportion of Diet HP-Nut during testing than did subjects in the Same-Food/Same-Place group ( $[LSD]=.42, p<.01$ ), 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.

An ANOVA of percentage weight gain also showed a significant difference among the three groups ( $F[2,15]=3.85, p<.05$ ). Taken together, these results indicate that under the experimental conditions used in this research the type of food eaten by a demonstrator was a more potent social influence than was the location at which a demonstrator ate.

**Fig. 13. Mean amount of Diet HP-Nut ingested, as a percentage of total intake, by subjects in the Same-Food/Same-Place, Same-Food/Different-Place, and Different-Food/Same-Place conditions.**



**Fig. 14. Mean cumulative percent weight change of subjects in the Same-Food/Same-Place, Same-Food/Different-Place, and Different-Food/Same-Place conditions.**

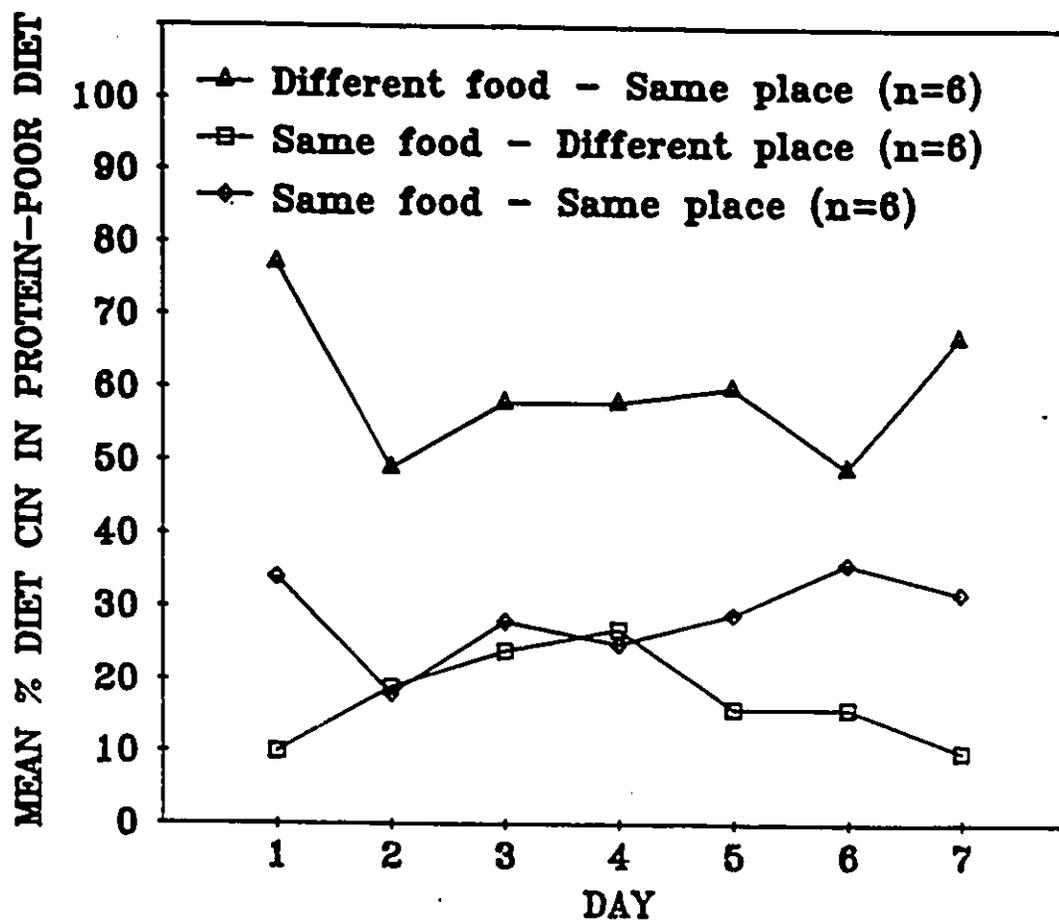


There are two possible explanations for the inability of subjects in the Different-Food/Same-Place condition to find the protein-rich HP-Nut diet. Either subjects in the Different-Food/Same-Place condition were influenced by the type of food eaten by their respective demonstrators (Diet Cin), or they were simply not influenced by the feeding behaviour of their respective demonstrators. If these subjects were influenced by the type of food eaten by their respective demonstrators, then subjects in the Different-Food/Same-Place condition should show a strong bias towards eating Diet Cin; if subjects in the Different-Food/Same-Place condition were simply not responsive to social cues, then they should not have shown an enhanced preference for Diet Cin. These two explanations for the poor diet selections made by subjects in the Different-Food/Same-Place condition cannot be discriminated simply by comparing the mean percentage of Diet Cin eaten by rats in the Different-Food/Same-Place condition, because Diet Cin intake is not independent of Diet HP-Nut intake. This problem can be avoided by comparing the amount of Diet Cin eaten, as a percentage of total protein-poor diet eaten, by subjects in the three conditions (see Fig. 15). Subjects in the Different-Food/Same-Place condition ate more Diet Cin, as a percentage of total protein-poor diet eaten, than did subjects in the Same-Food/Same-Place condition (Newman-Keuls post-hoc test,  $\underline{W}_T=.51$ ,  $p<.01$ ) and subjects in the Same-Food/Different-Place condition (Newman-Keuls post-hoc test,  $\underline{W}_T=.52$ ,  $p<.01$ ). It can therefore be concluded that subjects in the Different-Food/Same-Place condition were induced to eat Diet Cin by their demonstrator, and, as a result, avoided the HP-Nut diet.

Further research is required to gain a complete insight into how rats use information about what foods others feed upon and where others feed to make beneficial diet selections. One might speculate, for example, that in a natural setting information about where others feed is of greater importance than it was in the laboratory environment used in the present series of experiments. Wild rats that have been unsuccessful at finding a source of a

needed nutrient may follow others to a feeding site, and while at the feeding site obtain information about the type of food being eaten by others. If wild rats use information about where others feed in this fashion, then it may not be necessary for them to acquire precise information about where others feed in order to greatly benefit from such information. Thus, the close proximity of diets to one another may have prevented rats from using information about where others fed in order to find nutritious food.

**Fig. 15. Mean amount of Diet Cin ingested, as a percentage of total protein-poor diet intake, by subjects in the Same-Food/Same-Place, Same-Food/Different-Place, and Different-Food/Same-Place conditions.**



**Chapter IV: The effect of protein deprivation on the tendency of rats to match the diet choice of others.**

The advantage that rats could potentially derive from matching the diet choice of conspecifics that had already discovered sources of needed nutrients might lead one to expect that rats should always closely match the diet choices of others. However, an animal that uses high levels of social information when selecting diets would incur a cost if it adopted the diet preferences of another making poorer diet selections than its own. In general, the advantage that an animal would gain from using social information would depend upon how poor its own diet selections had been; the worse its diet choices, the more likely it is to benefit from adopting the choice pattern of another. One would, therefore, predict that a malnourished animal would be more likely to match the diet choices of others than would a well-nourished animal. The experiments reported in the present chapter were conducted to test this prediction.

**EXPERIMENT 7**

The present experiment tested the prediction that rats exposed to knowledgeable others are more likely to select diets which permit adequate growth when protein-deprived rather than protein-replete.

## Method

### *Subjects and Test diets*

Thirty-four experimentally-naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 16 rats, weighing 200-250g served as demonstrators. The four test diets described in Method of Experiment 1 were used.

### *Apparatus*

The open field test enclosure described in Method of Experiment 1 was used (see Fig. 1).

### *Procedure*

A 2x2 factorial design was used in which protein-deficiency state and presence or absence of demonstrators were the two independent variables.

The experiment was performed in four steps:

**Step 1. *Demonstrator training.*** Using the procedure described in Method of Experiment 1, demonstrators were trained to eat the protein-rich, Diet HP-Nut and to avoid the three protein-poor diets .

**Step 2. *Protein-deprivation.*** While demonstrators were being trained, 17 randomly chosen subjects were made protein-deficient by feeding them, for one week, a diet composed of equal parts powdered Purina Laboratory Rodent Chow (Diet P), solid Crisco oil, corn starch, and granulated sugar, supplemented with 2% vitamin-mineral mix (Teklad Diets : three parts Vitamin fortification mix, catalogue 40060, to one part mineral mix, usp XIV, catalogue 170880). All protein-deprived subjects lost weight during the protein-deprivation stage. The remaining 17 subjects were fed Diet P during the protein-

deprivation stage, and all 17 subjects gained weight. All subjects had ad lib access to their respective diets and water.

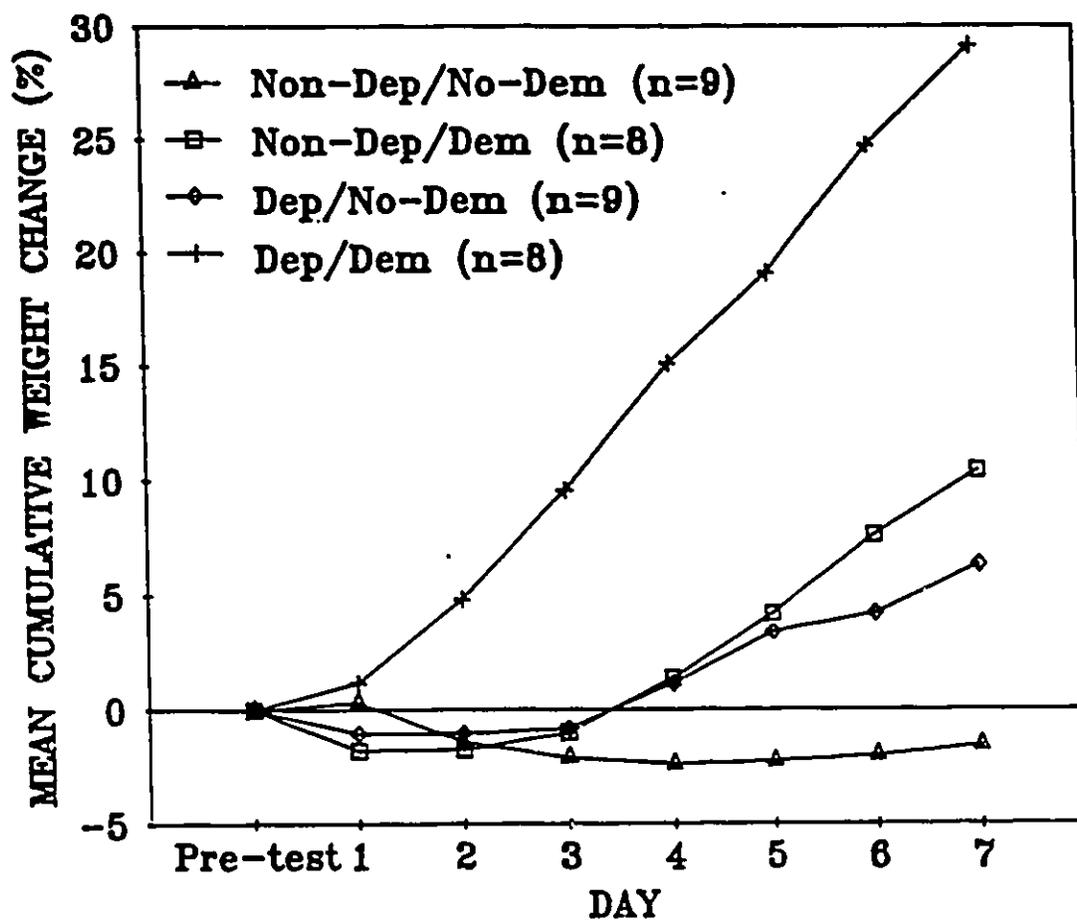
**Step 3. Habituation.** Both protein-deficient rats to be tested in isolation (Dep/No-Dem;  $n=9$ ), and non-deficient rats to be tested in isolation (Non-Dep/No-Dem;  $n=9$ ) were placed individually into a test enclosure and left undisturbed for 24 hr. Protein-deficient rats to be tested with a demonstrator present (Dep/Dem;  $n=8$ ), and non-deficient rats to be tested with a demonstrator (Non-Dep/Dem;  $n=8$ ) were placed in the test enclosure with a single demonstrator for the same period or time. During habituation all subjects in each of the four groups had ad lib access to water and to the diet they were fed in Step 2.

**Step 4. Testing.** Following habituation, the four test diets were placed in the test enclosure, one in each corner (see Fig. 1) and subjects were left undisturbed for one week except for daily weighing of food bowls and subjects.

## Results and Discussion

The results of Experiment 7 are presented in Fig. 16, which shows the mean cumulative percentage weight gain of subjects in the four conditions. A 2x2 ANOVA indicated that the growth rate of subjects, as measured by total percent weight gain, was significantly enhanced by both the presence of a demonstrator ( $F[1,30] = 30.5, p=.00002$ , one-tailed) and by protein deprivation ( $F[1,30] = 16.9, p=.00025$ , one-tailed). In addition, there was a statistically significant interaction between the presence of a demonstrator and protein deprivation ( $F[1,30] = 2.90, p=.047$ , one-tailed). Thus, presence of a demonstrator had a greater effect upon the growth of protein-deprived subjects than upon the growth of non-deprived subjects, an interaction which would be expected if protein-deprived rats matched the diet choices of their respective demonstrators more

**Fig. 16. Mean cumulative percent weight change of protein-deprived and non-deprived subjects choosing diets either in isolation, or in the presence of a demonstrator eating a protein-rich diet (Diet HP-Nut).**



closely than non-deprived rats. Post-hoc analysis revealed that Dep/Dem subjects gained significantly more weight, as a percentage of their initial weight, than did subjects in each of the three other groups (see Table 2 for significance levels). The greater growth exhibited by Dep/Dem subjects is consistent with the conclusion that protein deprivation caused rats to more closely match the diet choice of their respective demonstrators than they would otherwise have done.

While the present results were consistent with the hypothesis that protein deprivation caused rats to match the beneficial diet choices of demonstrators, there are three plausible alternative explanations. The most obvious explanation is that cumulative percentage weight gain is an inadequate measure of growth when protein-deprived and non-deprived animals are compared. At the beginning of testing protein-deprived rats weighed 25% less than non-deprived rats. It is therefore possible that the use of a measure of growth which is based upon the weight of animals just prior to testing may have artificially inflated the growth of protein-deprived rats. Because they entered testing at a lower weight, any given amount of growth on the part of protein-deprived rats would be reflected in a larger percentage weight gain than a comparable amount of growth in non-deprived rats

In fact, if one compares the actual amount of weight gained by deprived and non-deprived rats exposed to a demonstrator, the difference in their weight gain remains statistically significant (Newman-Keuls test  $W_r=33.25$ ,  $p<.01$ ), suggesting that this simple explanation cannot account for the observed difference in growth of these two groups.

It is also possible that Dep/Dem subjects gained more weight than Non-Dem/Dem subjects after eating the same quantity of protein, because protein deprivation resulted in physiological adaptations to increase the efficiency of protein use. Moreover, greater efficiency in protein usage by protein-deprived animals, coupled with the increase in

protein consumption caused by the presence of the demonstrator, could have yielded the significant interaction between protein deprivation and presence of a demonstrator.

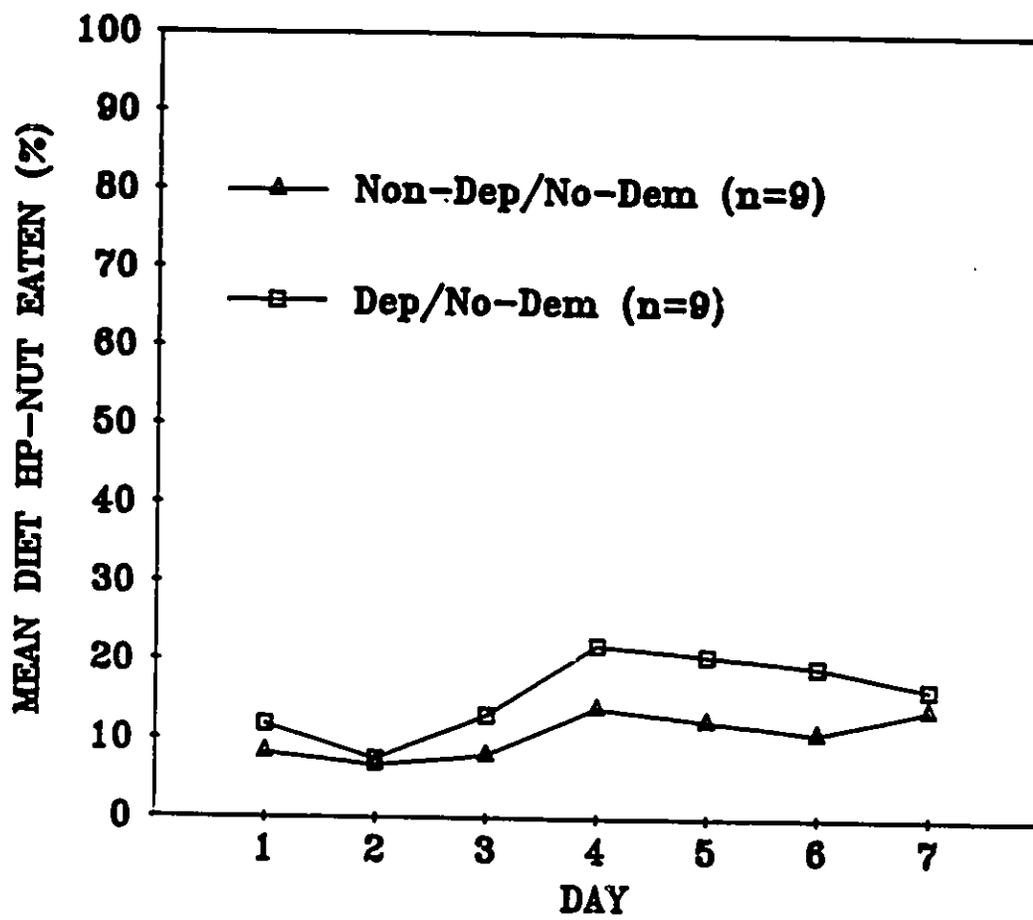
A final plausible explanation for the present results is that protein deprivation caused rats to have a lower threshold for detecting the consequences of protein ingestion. That is, a protein-deprived rat that ate a small quantity of Diet HP-Nut might have been more likely to detect and respond to its physiological effects than a non-deprived rat. If protein deprivation does increase sensitivity to the effects of protein ingestion, then a protein-deprived rat that was biased by a demonstrator to eat a small quantity of Diet HP-Nut would be more likely to develop a preference for that diet than would a non-deprived rat. Protein deprivation would, therefore, amplify the effect of a demonstrator on a subject's preference for Diet HP-Nut, and result in a significant interaction between protein deprivation and the presence of a demonstrator. If this second interpretation of the results is correct and protein deprivation does increase sensitivity to the effects of protein ingestion, then one would expect isolated protein-deprived subjects to eat more of Diet HP-Nut than did isolated non-deprived subjects. While Dep/No-Dem subjects did ingest a higher percentage of Diet HP-Nut during the 7 days of testing than Non-Dep/No-Dem subjects (see Fig. 17), this difference in percentage intake did not reach significance on any testing day. The failure of Dep/No-Dem subjects to ingest a significantly higher percentage of Diet HP-Nut than Non-Dep/No-Dem subjects might be taken as evidence that Dep/No-Dem subjects were no more sensitive to the effects of protein ingestion than were Non-Dep/No-Dem subjects. However, in order to detect the effects of the protein in Diet HP-Nut, rats must first eat a sufficient quantity of the diet. Because subjects in both isolated groups depicted in Fig. 17 ate very little of Diet HP-Nut on each testing day, one would not expect Dep/No-Dem subjects to eat a greater proportion of Diet HP-Nut than Non-Dep/No-

**Dem subjects, even if Dep/No-Dem subjects were better able to detect the effects of protein ingestion than were Non-Dep/No-Dem subjects.**

**Table 2. Results of Newman-Keuls pairwise comparisons of mean weight gain during the week of testing, as a percentage of initial weight, by subjects in the Dep/Dem, Non-Dem/Dem, Dep/No-Dem, and Non-Dem/No-Dem conditions.**

| Comparison      | W <sub>r</sub> | significance level |
|-----------------|----------------|--------------------|
| -----           |                |                    |
| Dep/Dem vs.     |                |                    |
| Non-Dep/Dem     | 26.16          | p<.01              |
| Dep/No-Dem      | 30.29          | p<.01              |
| Non-Dep/No-Dem  | 38.19          | p<.01              |
| -----           |                |                    |
| Non-Dep/Dem vs. |                |                    |
| Dep/No-Dem      |                | not significant    |
| Non-Dep/No-Dem  | 12.03          | p<.05              |
| -----           |                |                    |
| Dep/No-Dem vs.  |                |                    |
| Non-Dep/No-Dem  |                | not significant    |
| -----           |                |                    |

Fig. 17. Mean amount of Diet HP-Nut ingested, as a percentage of total intake, by protein-deprived and non-deprived isolated subjects.



## EXPERIMENT 8

The present experiment is a repetition of Experiment 7 using an apparatus which allowed the actual diet selections of subjects with demonstrators to be monitored.

### Method

#### *Subjects and Test diets*

Twenty-four experimentally naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 12 rats, weighing 200-250g, served as demonstrators. Rats chose among the four test diets described in Method of Experiment 1.

#### *Apparatus*

The divided test enclosure described in Method of Experiment 3 was used (see Fig. 4).

#### *Procedure*

The procedure used in the present experiment was identical to that used in Experiment 7, except for four minor changes resulting from the use of the divided enclosure: (1) Subjects and demonstrators were not housed together, but were instead placed in the subject and demonstrator compartments of the divided enclosure. (2) Metal semi-circular food bowls (10-cm-diam.) were used rather than glass dishes. The metal food bowls were attached to the hardware-cloth divider as in Experiment 3 (see Fig. 4). (3) All demonstrators were fed powdered Purina Laboratory Rodent Chow (Diet P) during

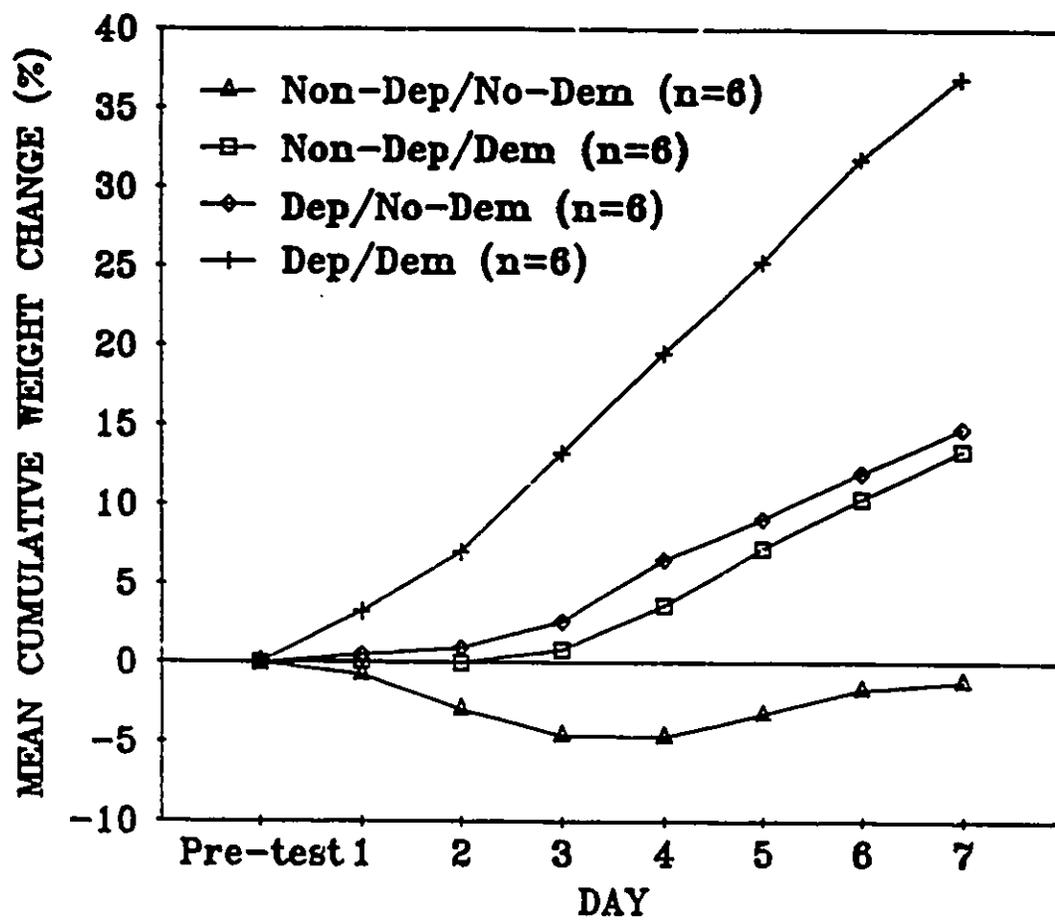
habituation, rather than the diet eaten by their respective subjects. (4) Demonstrators were not trained to eat the HP-Nut diet, but rather, as in Experiment 3, were fed this diet from a bowl attached to the divider opposite their subject's bowl containing Diet HP-Nut.

Six subjects were randomly assigned to each of four conditions: Dep/Dem (protein-deprived subjects with a demonstrator), Dep/No-Dem (protein-deprived subjects without a demonstrator), Non-Dep/Dem (non-deprived subjects with a demonstrator), Non-Dep/No-Dem (non-deprived subjects without a demonstrator).

## Results and Discussion

As can be seen in Fig. 18, the percentage weight change of subjects in the four conditions of the present experiment closely matched the percentage weight change of subjects in the corresponding conditions of Experiment 7 (see Fig. 13). However, an ANOVA of the percentage weight change of subjects in the four conditions yielded a somewhat different outcome than that obtained in Experiment 7. As in Experiment 7, both independent variables, protein deprivation and presence of a demonstrator, had statistically significant effects upon percent weight change during testing: protein deprivation ( $F[1,20]=16.07$ ,  $p=.00047$ , one-tailed), presence of a demonstrator ( $F[1,20]=14.06$ ,  $p=.00080$ , one-tailed). But in contrast to Experiment 7, in the present experiment the interaction between protein deprivation and presence of a demonstrator was not significant ( $F[1,20]=.188$ ,  $p=.33$ , one-tailed). Post-hoc comparisons of group means indicated that the lack of significance in the interaction between protein deprivation and presence of a demonstrator was not due to a failure of Dep/Dem subjects to gain a substantial percentage of their initial weight. In the present experiment, just as in Experiment 7, post-hoc analysis indicated that Dep/Dem subjects gained a significantly higher percentage of their initial

**Fig. 18. Mean cumulative percent weight change of protein-deprived and non-deprived subjects choosing diets either in isolation, or in the presence of a demonstrator eating a protein-rich diet (Diet HP-Nut).**



weight than subjects in each of the three other groups (see Table 3 for significance levels). The lack of significance in the interaction must therefore have been due to the fact that Dep/No-Dem subjects in the present experiment gained 16.0 percent more of their initial weight than Non-Dep/No-Dem subjects. The high rate of growth of Dep/No-Dem subjects relative to Non-Dep/No-Dem subjects suggests that protein deprivation rendered subjects better able to find the protein source. However, as Table 3 shows, this difference in the amount that Dep/No-Dem and Non-Dep/No-Dem subjects grew did not reach significance.

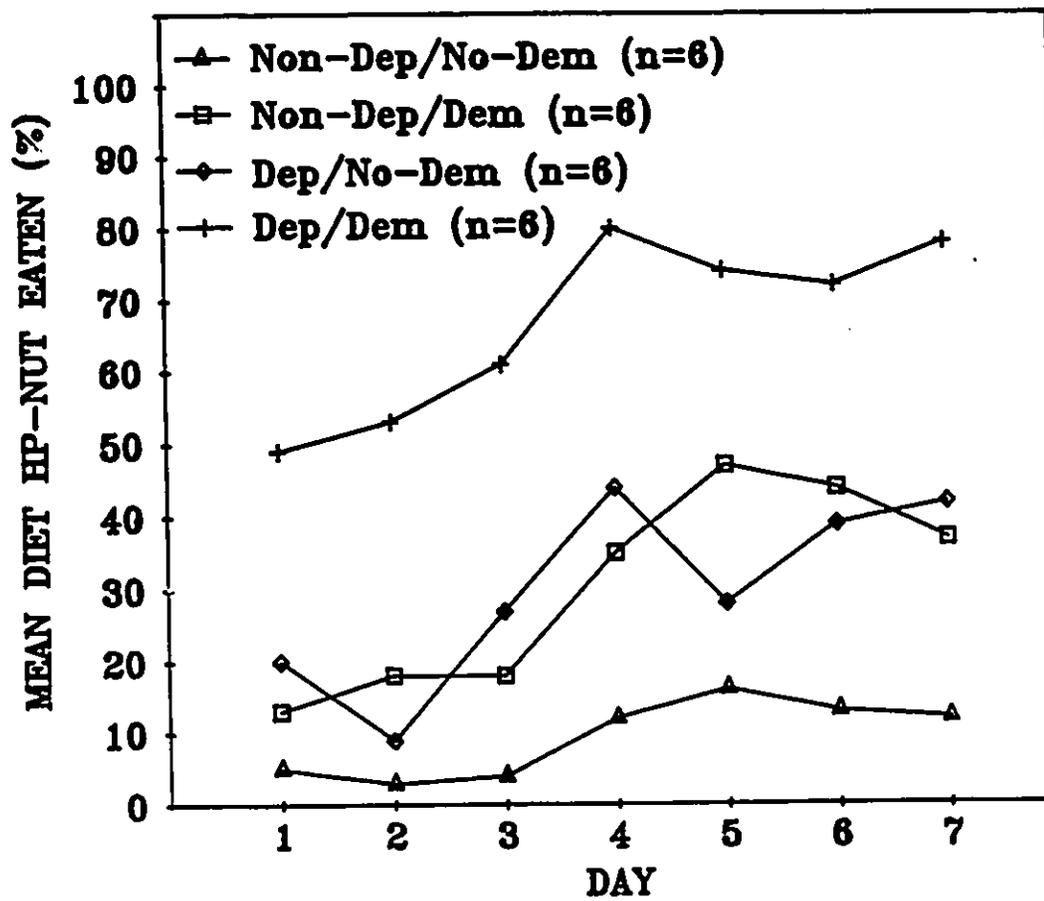
As shown in Fig. 19, percentage intake of Diet HP-Nut by the four groups corresponded to their respective growth during the 7 days of testing (Fig. 15). An ANOVA of Diet HP-Nut intake indicated that both independent variables significantly increased percentage intake of Diet HP-Nut: protein deprivation ( $F[1,20]=8.62, p=.0081$ ), presence of a demonstrator ( $F[1,20]=9.89, p=.005$ ). However, once again the interaction between protein deprivation and presence of a demonstrator was not significant ( $F[1,20]=.039, p=.522$ ).

The finding that the differential growth rate of the four groups corresponded to their relative Diet HP-Nut intake in the present experiment indicates that the substantial growth displayed by Dep/Dem subjects relative to Dep/No-Dem subjects in Experiment 7 was not simply a consequence of their enhanced ability to metabolize protein. However, the results do not allow one to discriminate between the remaining two possibilities discussed in Experiment 7: whether protein deprivation caused rats to be more sensitive to the effects of protein ingestion, or caused them to more closely match the diet choices of others, or both.

**Table 3. Results of Newman-Keuls pairwise comparisons of mean weight gain, as a percentage of initial weight, by subjects in the Dep/Dem, Non-Dep/Dem, Dep/No-Dem, and Non-Dep/No-Dem conditions.**

| Comparison      | W <sub>r</sub> | significance level |
|-----------------|----------------|--------------------|
| -----           |                |                    |
| Dep/Dem vs.     |                |                    |
| Non-Dep/Dem     | 19.78          | p<.05              |
| Dep/No-Dem      | 18.63          | p<.01              |
| Non-Dep/No-Dem  | 34.55          | p<.01              |
| -----           |                |                    |
| Non-Dep/Dem vs. |                |                    |
| Dep/No-Dem      |                | not significant    |
| Non-Dep/No-Dem  | 14.77          | p<.05              |
| -----           |                |                    |
| Dep/No-Dem vs.  |                |                    |
| Non-Dep/No-Dem  |                | not significant    |
| -----           |                |                    |

**Fig. 19. Mean amount of Diet HP-Nut ingested, as a percentage of total intake, by protein-deprived and non-deprived subjects choosing diets either in isolation, or in the presence of a demonstrator eating Diet HP-Nut in the demonstrator compartment of the divided enclosure.**



## EXPERIMENT 9

The failure to find an interaction between protein deprivation and the presence of a demonstrator, reported in Experiment 8, lends itself to two interpretations. Either protein deprivation does not increase the propensity of rats to match the diet choices of others, or the increase was masked by other effects of protein deprivation. More specifically, the fact that protein deprivation caused a marginal increase in intake of protein-rich diet, even in the absence of a demonstrator, might have overshadowed an effect of protein deprivation on social behaviour. In the present experiment, this possibility was explored by making the diet eaten by demonstrators low in protein. If protein-deprived rats continue to show an exaggerated preference for their demonstrator's diet when there are no positive consequences for doing so, it is difficult to escape the conclusion that protein-deprived rats are more prone to matching the diet choices of others than are non-deprived rats.

### Method

#### *Subjects and Test diets*

Thirty-six experimentally naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 16 rats, weighing 200-250g, served as demonstrators. Rats chose among four foods, the three protein-poor diets described in Method of Experiment 1 (Cin, Coc, and Thy), and a fourth low-protein diet composed of the same nutrients in the same proportions as the three other diets, but flavored with 1% Club House ground nutmeg (LP-Nut).

### *Apparatus*

The divided test enclosure described in Method of Experiment 3 was used (see Fig. 4).

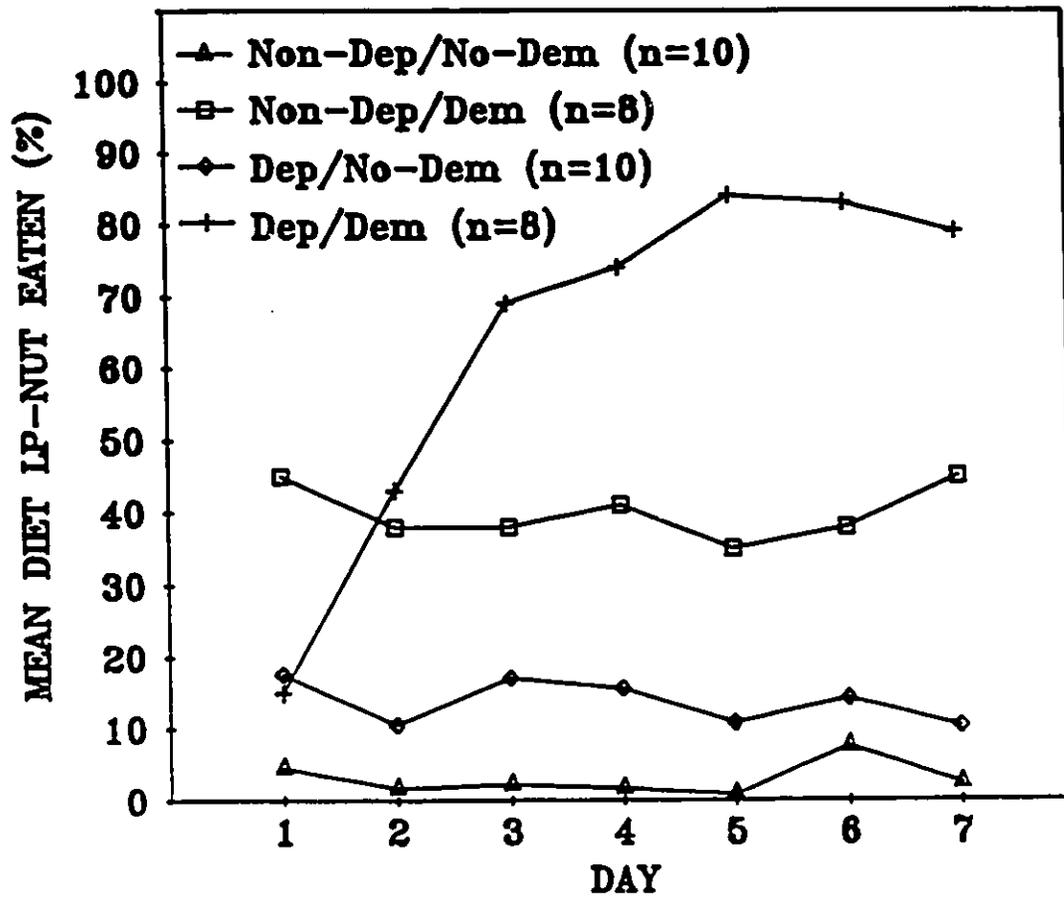
### *Procedure*

The procedure used was identical to that of Experiment 8. Ten subjects were randomly assigned to each of the two isolated conditions, Non-Dep/No-Dem and Dep/No-Dem, and eight rats were randomly assigned to each of Non-Dep/Dem, and Dep/Dem conditions.

## **Results and Discussion**

The main results of Experiment 9 are presented in Fig. 20, which shows the mean percentage of Diet LP-Nut ingested by subjects in each of the four conditions. An ANOVA of these results showed that both independent variables, protein-deprivation state and presence of a demonstrator, had significant effects upon preference for Diet LP-Nut : protein deprivation ( $F[1,32]=5.21, p=.027$ ), presence of a demonstrator ( $F[1,32]=39.65, p=.00001$ ). The fact that deprivation state had a significant effect upon Diet LP-Nut intake cannot be attributed to the superior ability of protein-deprived rats to detect protein sources because Diet LP-Nut was as low in protein as each of the other three test diets. The significant effect of protein deprivation upon preference for Diet LP-Nut therefore suggests that protein deprivation caused rats to more closely match the diet choice of their respective demonstrators than they would otherwise have done. This interpretation of the significant effect of protein deprivation is also supported by an analysis of the interactive effect of protein deprivation and presence of a demonstrator upon percentage of Diet LP-Nut eaten.

**Fig. 20. Mean amount of Diet LP-Nut ingested, as a percentage of total intake, by protein-deprived and non-deprived subjects choosing diets either in isolation, or in the presence of a demonstrator eating Diet LP-Nut in the demonstrator compartment of the divided enclosure.**



While the interaction was not statistically significant across all testing days ( $F[1,32]=.237$ ,  $p=.634$ ), it was significant in the predicted direction on testing days 5,6, and 7 (see Table 4). That is, on testing days 5,6, and 7, the combination of protein deprivation and presence of a demonstrator caused rats to eat significantly more Diet LP-Nut than would be expected given a simple additive effect of protein deprivation and presence of a demonstrator.

While these results seem to conclusively show that protein-deprived rats are more prone to matching the diet selections of others than are non-deprived rats, results obtained on testing day 1 are difficult to reconcile with this hypothesis. On Day 1 the interaction between deprivation state and presence of a demonstrator was significant, but in a direction opposite to that predicted by the hypothesis that protein deprivation increases level of matching (see Table 4). That is, on Day 1 the combination of protein deprivation and presence of a demonstrator caused subjects to eat significantly less Diet LP-Nut than would be expected given a simple additive effect between the two independent variables. Indeed, while Dep/Dem subjects ate a significantly higher proportion of Diet LP-Nut than Non-Dep/Dem on testing days 3,4,5,6, and 7, Dep/Dem subjects actually ate a significantly smaller proportion of Diet LP-Nut than Non-Dep/Dem subjects on testing day 1 (see Table 5).

It is difficult to draw a simple conclusion from these results. The results seem to indicate that protein deprivation does not merely increase the extent to which a rat matches the diet choices of others. The overall effect of protein deprivation was to cause subjects to ingest a greater percentage of their demonstrator's diet, yet on testing day 1 it had the opposite effect. The mechanism underlying this peculiar behaviour was examined in Part 2 of this thesis.

**Table 4. Results of ANOVA comparing the amount of Diet LP-Nut eaten, as a percentage of total intake, by protein-deprived and non-deprived subjects that chose diets either in isolation or in the presence of a demonstrator eating Diet LP-Nut.**

| Effect of<br>Deprivation | Day |     |      |       |       |      |      |
|--------------------------|-----|-----|------|-------|-------|------|------|
|                          | 1   | 2   | 3    | 4     | 5     | 6    | 7    |
| F[1,32]                  | .48 | .22 | 4.47 | 8.30  | 13.14 | 6.03 | 4.74 |
| p(one-tailed)            | .25 | .32 | .020 | .0035 | .0006 | .009 | .017 |

| Effect of<br>Demonstrator | Day  |       |        |        |       |        |       |
|---------------------------|------|-------|--------|--------|-------|--------|-------|
|                           | 1    | 2     | 3      | 4      | 5     | 6      | 7     |
| F[1,32]                   | 7.95 | 15.70 | 22.20  | 35.40  | 61.08 | 33.41  | 43.14 |
| p(one-tailed)             | .004 | .0003 | .00008 | .00001 | 0     | .00001 | 0     |

| Effect of<br>Interaction | Day   |     |     |     |      |      |      |
|--------------------------|-------|-----|-----|-----|------|------|------|
|                          | 1     | 2   | 3   | 4   | 5    | 6    | 7    |
| F[1,32]                  | 9.17  | .16 | .76 | .91 | 5.38 | 3.84 | 3.28 |
| p(one-tailed)            | .0025 | .35 | .20 | .17 | .012 | .028 | .038 |

**Table 5. Results of Newman-Keuls pairwise comparisons of LP-Nut intake, as a percentage of total intake, by subjects in the Dep/Dem and Non-Dem/Dem conditions.**

## Dep/Dem vs. Non-Dem/Dem

| Day | Wr   | significance level |
|-----|------|--------------------|
| 1   | .389 | p<.05              |
| 3   | .427 | p<.05              |
| 4   | .460 | p<.05              |
| 5   | .637 | p<.01              |
| 6   | .594 | p<.01              |
| 7   | .509 | p<.01              |

**Chapter V: The effects of thiamine deprivation, total food deprivation, and recovery from protein deprivation on the tendency of rats to match the diet choice of others.**

The results of Chapter IV show that protein deprivation caused rats to more closely match the diet choice of others. The purpose of the present chapter was to determine whether rats subjected to thiamine deprivation, to total food deprivation, or to protein deprivation followed by recovery, also display an enhanced tendency to match the diet choices of others.

## **EXPERIMENT 10**

The present experiment is an investigation of the effect of thiamine deficiency upon the tendency of rats to match the diet choices of demonstrators.

### **Method**

#### *Subjects and Test diets*

Eighteen experimentally naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 32 rats weighing 250-300g served as demonstrators.

Rats chose among four thiamine-deficient diets. These diets were composed of 100% Thiamine-Deficient Test Diet (Teklad Diets: TD 87352), flavored with one of the following flavorings: 1% McCormick's fancy ground cinnamon (Diet TD-Cin), 2% Hershey's cocoa (Diet TD-Coc), 1% McCormick's ground thyme (Diet TD-Thy), or 1%

McCormick's ground nutmeg (Diet TD-Nut). The TD- prefix indicates that the diets were thiamine-deficient.

### *Apparatus*

The divided test enclosure described in Method of Experiment 3 was used (see Fig. 4).

### *Procedure*

The experiment was conducted in three steps.

**Step 1. *Thiamine deprivation.*** Eight randomly chosen subjects were given ad lib access to a thiamine deficient diet (Teklad Diets, Madison, WI; catalogue number TD 85378) for three weeks. The remaining 10 subjects in the control group were given ad lib access to the same diet supplemented with .5% thiamine hydrochloride (Sigma Chemical Company; Catalog number T 1270). All subjects had ad lib access to water.

**Step 2. *Habituation.*** In order to familiarize subjects with their testing environment, they were placed individually into the subject compartments of the divided enclosures, and demonstrators were placed in the adjacent demonstrator compartments. Subjects were given ad lib access to the same diet they were fed during Step 1. Demonstrators were given ad lib access to powdered Purina Laboratory Rodent Chow (Diet P). All animals had ad lib access to water for the 24 hr habituation period.

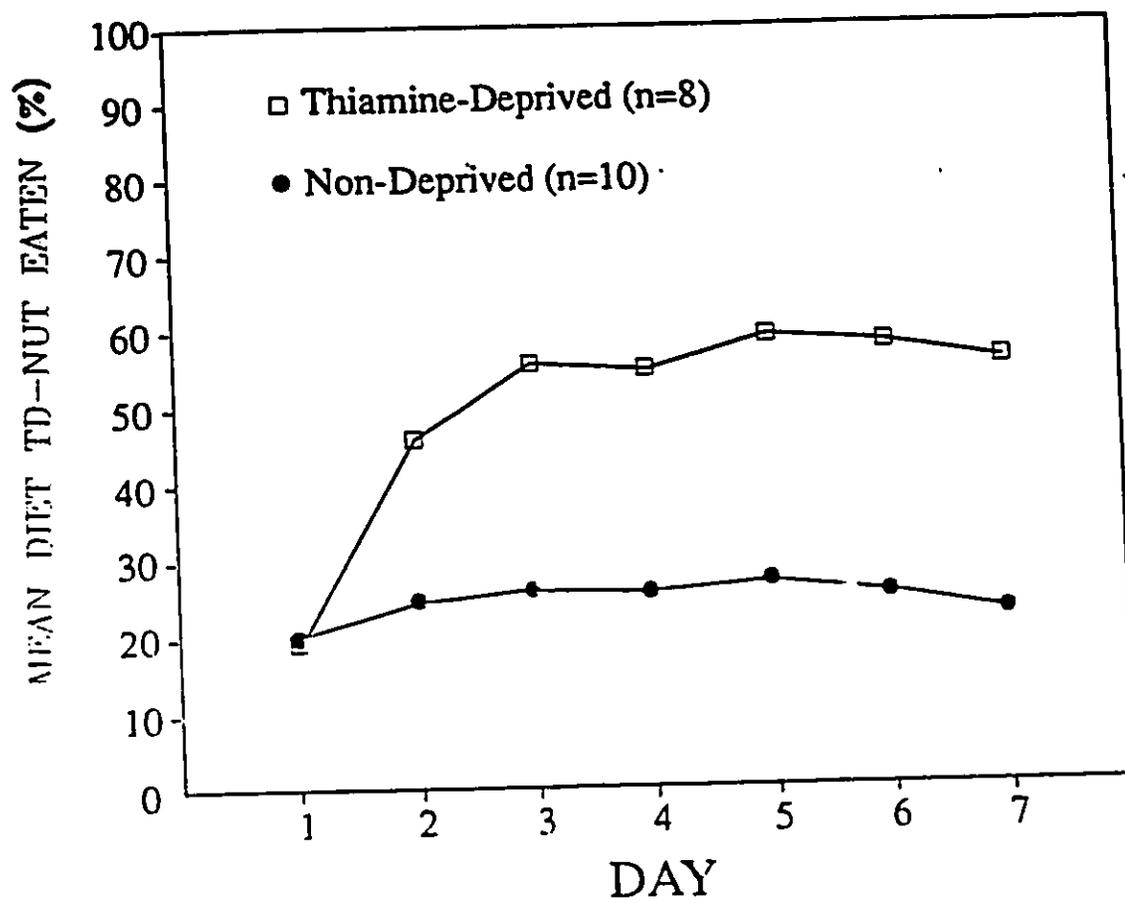
**Step 3. *Testing.*** Following habituation, all food bowls were removed and each subject was given four metal, semi-circular, 10-cm-diam. food bowls containing the test diets. These food bowls were attached to the divider and contained the test diets in the order Diet TD-Cin, TD-Coc, TD-Thy, and TD-Nut from the front of the cage to the back. A single food bowl containing Diet TD-Nut was placed into all demonstrator

compartments. This bowl was attached to the divider immediately opposite each observer's bowl of Diet TD-Nut (see Fig. 4). For the next week subjects were left undisturbed except for a daily weighing of food bowls and rats.

### Results and Discussion

The main results of the present experiment are shown in Fig. 21, which shows the mean percentage of Diet TD-Nut eaten by thiamine-deprived and non-deprived subjects. Thiamine-deprived subjects ate a higher percentage of Diet TD-Nut, the diet being eaten by their respective demonstrators, than non-deprived subjects (Student t-test,  $t(16)=1.72$ ,  $p<.05$ , one-tailed). The finding that thiamine-deprived rats, like protein-deprived rats (Experiments 7,8, and 9), displayed an enhanced tendency to match their respective demonstrator's diet choices suggests that enhanced matching is a general response to nutrient deprivation, rather than a specific response to protein deprivation.

**Fig. 21. Mean amount of Diet TD-Nut ingested, as a percentage of total intake, by thiamine-deprived and non-deprived subjects exposed to a demonstrator eating Diet TD-Nut.**



## EXPERIMENT 11

In the present experiment I examined the diet-selection behaviour of rats that had undergone successive periods of total food deprivation.

### Method

#### *Subjects and Test diets*

Twenty experimentally naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 40 rats weighing 300-350g served as demonstrators.

Rats chose among the four foods described in Method of Experiment 9: Diets Cin, Coc, Thy, and LP-Nut.

#### *Apparatus*

The divided test enclosure described in Method of Experiment 3 was used (see Fig. 4).

#### *Procedure*

The experiment was conducted in three steps.

**Step 1. Food deprivation.** Ten randomly chosen subjects were placed on a feeding schedule for one week in which they were fed powdered Purina Laboratory Rodent Chow (Diet P) for 1 hr at the same time each day. The remaining 10 subjects in the control group were given ad lib access to the same food for one week. All subjects had ad lib access to water.

**Step 2. Habituation.** In order to familiarize subjects with their testing environment, they were placed individually into the subject compartments of the divided enclosures, and a single demonstrator was placed into each adjacent demonstrator compartment. Those rats on a feeding schedule were maintained on this schedule during habituation. Control subjects and all demonstrators were fed ad lib Diet P. All animals had ad lib access to water for the 24 hr habituation period.

**Step 3. Testing.** Following habituation, bowls containing Diet P were removed and each subject was given four metal, semi-circular, 10-cm-diam. food bowls containing the test diets. These food cups were attached to the dividing screen and contained the test diets in the order Diet Cin, Coc, Thy, and LP-Nut from the front of the cage to the back. A single food bowl containing Diet LP-Nut was given to all demonstrators. This bowl was attached to the dividing screen immediately opposite their observers' Diet LP-Nut bowl (see Fig. 4). For the next week subjects were left undisturbed except for daily weighing of food bowls and rats.

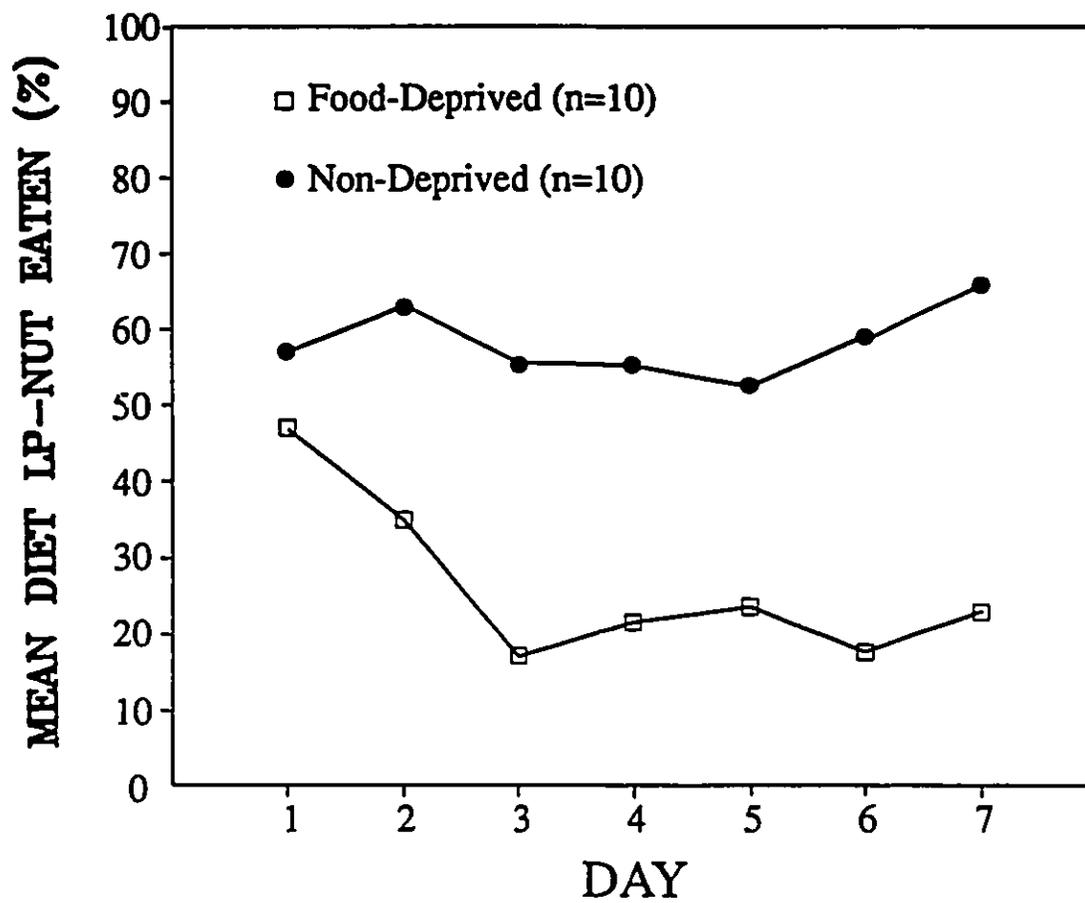
## Results and Discussion

In Experiments 9 and 10 respectively it was found that protein deprivation and thiamine deprivation caused rats to more closely match their demonstrator's diet. If nutrient deprivation was sufficient to cause such enhanced matching behaviour, then one might expect that animals which had undergone periodic total food deprivation, and were therefore nutrient deprived when given the diet-selection task, would show a similar tendency. Contrary to expectation, food-deprived rats ate a significantly smaller percentage

of their demonstrators' diet (Diet LP-Nut) during testing than did non-deprived rats (Student t-test,  $t(18)=2.94$ ,  $p=.0043$ , two-tailed) (see Fig. 22).

The difference in tendencies to match the diet choices of demonstrators expressed by protein- or thiamine-deprived rats and food-deprived rats may be due to a difference in the physiological state of subjects during testing. In Experiment 9 and 10, rats were made nutrient deficient during the deprivation phase and were kept nutrient deficient during testing by being fed four nutrient-poor diets. In the present experiment, the primary effect of food deprivation was to prevent rats from ingesting sufficient calories to maintain energy balance. Rats in the present experiment were then allowed to recover from their primary nutrient deficiency during testing by being fed four carbohydrate-rich foods. The behaviour of food-deprived rats may therefore be due to the fact that animals recovering or recovered from nutrient deficiency are less likely to match the diet selections of their demonstrators than rats that had not been nutrient deprived. That is, a history of nutrient deficiency is not sufficient to make rats more closely match the diet selections of their demonstrator. Rather, rats must be nutrient deficient when exposed to a demonstrator in order to display an enhanced tendency to match the diet selections of others.

Fig. 22. Mean amount of Diet LP-Nut ingested, as a percentage of total intake, by food-deprived and non-deprived subjects exposed to a demonstrator eating Diet LP-Nut.



## EXPERIMENT 12

The results of Experiment 11 suggested that rats must be nutrient deprived at the time of testing in order to show enhanced matching of their demonstrator's diet. If rats must indeed be nutrient deprived in order to show enhanced matching, then rats that have recovered from nutrient deprivation should be no more likely to match the diet selections of their demonstrator than rats without a history of deprivation. The present experiment directly tested this proposition.

### Method

#### *Subjects and Test diets*

Twelve experimentally naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 12 rats, weighing 200-250g, served as demonstrators.

Rats chose among same four foods described in Method of Experiment 9: Diets Cin, Coc, Thy, and LP-Nut.

#### *Apparatus*

The divided test enclosure described in Method of Experiment 3 was used (see Fig. 4).

### *Procedure*

The experiment was conducted in four steps.

**Step 1. *Protein deprivation.*** Six randomly chosen subjects were made protein deficient by being fed, for one week, a diet composed of equal parts powdered Purina Laboratory Rodent Chow (Diet P), solid Crisco oil, corn starch, and sugar, supplemented with 2% vitamin-mineral mix (Teklad Diets : three parts Vitamin fortification mix, catalogue 40060, to one part mineral mix, usp XIV, catalogue 170880). The remaining 6 subjects were fed Diet P for the same period of time. All subjects had ad lib access to their respective diets and water.

**Step 2. *Recovery.*** For the next two weeks all subjects were given ad lib access to Diet P and water.

**Step 3. *Habituation.*** Subjects were placed individually into the subject compartments of the divided enclosures, and the demonstrators were placed into the adjacent demonstrator compartments. Subjects and demonstrators were then given ad lib access to Diet P and water for 24 hr.

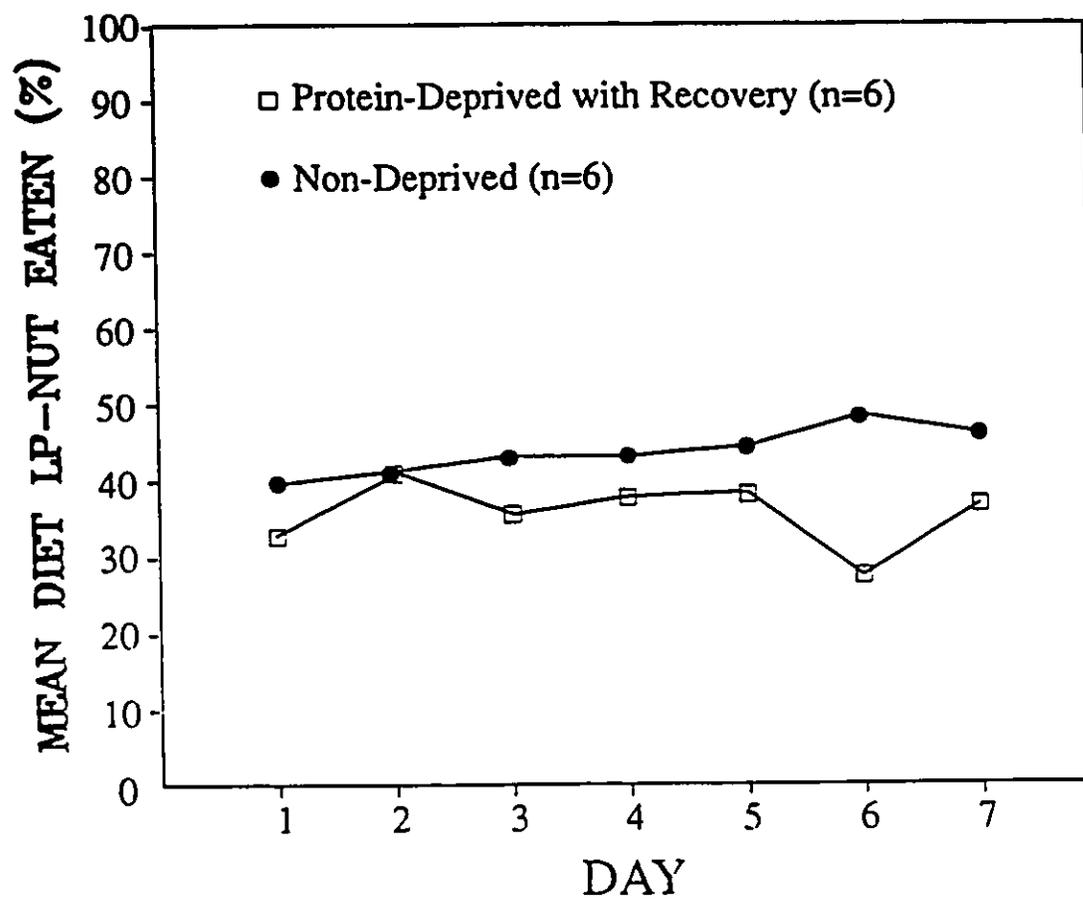
**Step 4. *Testing.*** Following habituation, bowls containing Diet P were removed and each subject was given four metal, semi-circular, 10-cm-diam. food bowls containing the test diets. These food cups were attached to the dividing screen and contained the test diets in the order Diet Cin, Coc, Thy, and LP-Nut from the front of the cage to the back. A single food bowl containing Diet LP-Nut was placed into the demonstrator compartment of both groups. This bowl was attached to the dividing screen immediately opposite their

observers' Diet LP-Nut bowl (see Fig. 4). For the next week subjects were left undisturbed except for a daily weighing of food bowls and rats.

### Results and Discussion

The main results of the present experiment are shown in Fig. 23, which depicts the mean percentage of Diet LP-Nut eaten by non-deprived subjects and by subjects that had recovered from protein deficiency. These results suggest that protein-deprived rats lose their enhanced predisposition to match the diet choices of others after they have recovered from deprivation. While protein-deficient subjects in other experiments (Experiments 7,8, and 9) consistently showed an enhanced preference for their demonstrator's diet, subjects in the present experiment that had recovered from protein deficiency did not significantly differ from non-deprived subjects in their preference for their demonstrator's diet (Student t-test,  $t(10)=1.46$ , N.S.).

**Fig. 23. Mean amount of Diet LP-Nut ingested, as a percentage of total intake, by non-deprived subjects and subjects that had recovered from protein-deprivation exposed to a demonstrator eating Diet LP-Nut.**



## Part 1: Summary

The results presented in Part 1 of this thesis indicate that rats were profoundly influenced in their diet-selections by the diet choices of others. Both weanling (Experiment 1) and adolescent rats (Experiments 2,3,7, and 8) were much more likely to develop a preference for a relatively unpalatable protein-rich food source when exposed to others feeding upon it. Rats matched the diet choices of others even when there were no positive consequences for doing so, and when there were several more palatable alternatives available (Experiment 9).

Under the conditions used in the present experiments, rats were primarily influenced by what others ate (Experiment 4), rather than by where others ate (Experiment 5). When these two types of social information were placed in opposition, only the type of food eaten by a demonstrator seemed to affect the diet-selections of subjects (Experiment 6).

The extent to which diet-selection was influenced by the feeding behavior of others varied across conditions. Diet-selections were under greater social control when three demonstrators were displaying the same diet-preference than when just one demonstrator did so (Experiment 2). Both protein-deprivation (Experiments 7,8,and 9) and thiamine-deprivation (Experiment 10) also enhanced the tendency of rats to match the diet choice of others. Results presented in Experiments 11 and 12 suggested that animals must be nutrient-deficient in order to exhibit an enhanced tendency to match the diet choice of others. A history of nutrient-deprivation is not sufficient to make rats more likely to match the diet choices of others than non-deprived rats.

## Part II

### Chapter I: A comparison of the "feeding-restriction" and the "social-responsiveness" mechanisms of enhanced matching during nutrient-deprivation.

The data presented in both Chapters IV and V indicate that both protein deprivation (Experiments 7,8, and 9) and thiamine deprivation (Experiment 10) enhanced the tendency of rats to match the diet choices of others. The benefit that a nutrient-deprived rat would derive from behaving in this manner seems clear: by accurately matching the diet selections of others a nutrient-deficient animal could increase its success at finding missing nutrients. The mechanism by which nutrient deficiency caused animals to more closely match the diet selections of others is less clear.

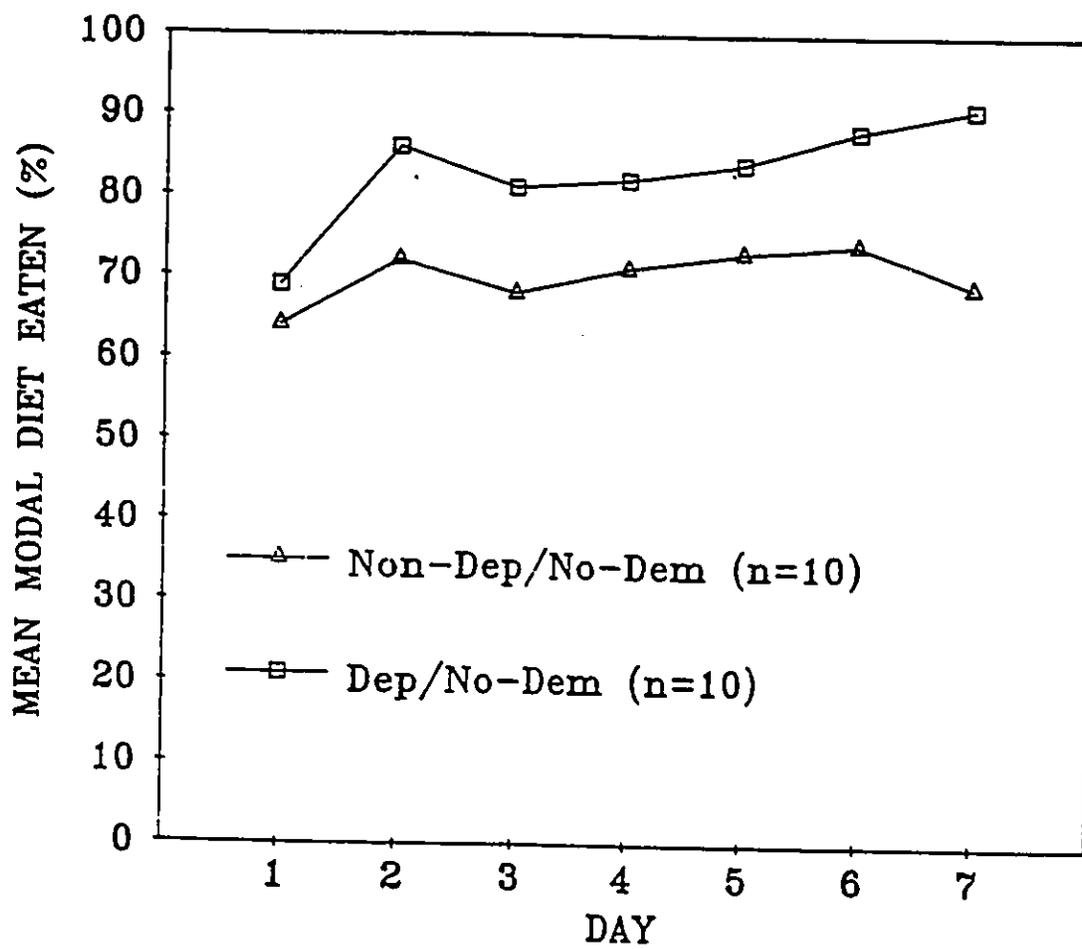
Consideration of the behaviour of nutrient-deprived animals suggests two possible mechanisms for their tendency to restrict feeding to the diet eaten by a demonstrator. One possibility is that nutrient-deprivation rendered rats more prone to restrict their feeding to a single diet (a feeding-restriction mechanism). Because rats, regardless of their deprivation state, showed a bias to select the diet eaten by their respective demonstrators, if nutrient-deprived rats showed the additional tendency to restrict feeding to a single diet, then nutrient-deprived rats would have displayed an enhanced tendency to feed upon their demonstrator's diet. Alternatively, nutrient-deprivation could have made rats more responsive to social influence, thereby causing them to eat a higher proportion of their respective demonstrators' diet (a social-responsiveness mechanism).

One means of discriminating between the social-responsiveness and the feeding-restriction mechanisms is to examine the diet choices of isolated, nutrient-deprived

subjects. If the enhanced tendency of nutrient-deprived animals to match the diet choices of others was mediated by the feeding-restriction mechanism, then one would expect isolated, nutrient-deprived rats to restrict feeding to a single diet. In contrast, if the social-responsiveness mechanism was responsible for the enhanced diet-matching behaviour of nutrient-deprived rats, then isolated nutrient-deprived rats would not be expected to restrict feeding to a single diet.

Unfortunately, it is not obvious what measure to use to quantify a tendency to restrict feeding to a single food. The most obvious measure is the proportion eaten by rats of their most preferred food during testing. Using this measure, a high proportion would indicate that rats had restricted feeding to a single food throughout testing. However, an examination of the diet selections of isolated animals in Experiment 9 showed that although isolated subjects displayed strong preferences for a certain food on each testing day, most isolated subjects did not consistently prefer the same food across testing days. Thus, if one uses the proportions of foods eaten over the entire week of testing to derive a measure of feeding restriction, a strong tendency to restrict feeding to a single diet on each testing day may be obscured. In order to avoid this problem, one may quantify a rat's tendency to restrict its feeding to a single diet by computing the amount it ate of its most preferred diet on each testing day (its "modal" diet), and use the average of these computations as a measure of tendency to restrict feeding to a single food. Applying this measure of restriction of feeding to the diet-selection data obtained from protein-deprived and non-deprived isolated animals in Experiment 9, one finds that relative to Non-Dep/No-Dem subjects, Dep/No-Dem subjects did indeed show an enhanced tendency to restrict feeding to a single food. As suggested by an examination of Fig. 24 and confirmed by statistical test, Dep/No-Dem subjects ate a significantly greater amount of their modal diet, as a proportion of total intake, than Non-Dep/No-Dem subjects on each day of testing

Fig. 24. Mean percentage of "modal" diet (the diet making up the largest proportion of each subject's total intake) eaten by protein-deprived and non-deprived isolated subjects.



(Student t-test,  $t(18)=2.62, p=.008$ , one-tailed\* ). The enhanced intake of modal diet by Dep/No-Dem subjects suggests that the strong preference shown by protein- and thiamine-deprived subjects for their respective demonstrators' diets was a consequence of their deprivation-induced tendency to restrict feeding to a single diet; the demonstrator may have only directed this tendency towards its own diet.

The feeding behaviour of Dep/Dem subjects in Experiment 9 also suggests that the feeding-restriction mechanism was responsible for their behaviour. As discussed in Experiment 9, Dep/Dem subjects actually ate significantly less of their respective demonstrators' diet than did Non-Dep/Dem subjects on the first testing day. Such an outcome is not expected if the effect of protein deprivation was to render rats more responsive to social cues, yet is expected if protein deprivation caused rats to restrict feeding to a single food. If nutrient-deprived rats tend to restrict feeding to a single diet, then nutrient-deprived rats should only show an enhanced tendency to feed upon their respective demonstrators' diet when the strength of social influence is sufficient to make this diet preferred over available alternatives. Dep/Dem subjects might have indirectly avoided their respective demonstrators' diet on the first day of testing because social influences were not sufficient to make this relatively unpalatable diet the preferred alternative. Dep/Dem subjects might have restricted their feeding to another diet, causing them to actually eat significantly less of their respective demonstrators' diet than Non-Dep/Dem subjects.

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\* Because percentage scores were used, scores were transformed using an Arcsin Transform ( $Y' = \text{Arcsin } \sqrt{Y}$  )

### EXPERIMENT 13

The purpose of the present experiment was to determine whether the feeding-restriction mechanism or the social-responsiveness mechanism was responsible for the feeding behaviour of nutrient-deprived rats. If nutrient-deprived subjects ate a high proportion of their respective demonstrators' diet because nutrient deficiency caused them to become more responsive to social cues when selecting diets, then one would expect them to show a strong preference for their respective demonstrators' diet under all conditions. If, on the other hand, nutrient-deprived subjects ate a high proportion of their respective demonstrators' diet because nutrient deficiency caused them to restrict their feeding to a single diet (their modal diet), then nutrient deprivation should actually make subjects avoid their respective demonstrators' diet under two conditions. First, if the diet eaten by a demonstrator is highly unpalatable, then it is likely that the social influence of the demonstrator will be insufficient to make the diet the demonstrator is eating into a subject's modal diet. A nutrient-deprived subject, exposed to a demonstrator eating a highly unpalatable diet, would therefore be expected to show an enhanced tendency to restrict its feeding to a diet other than its demonstrator's diet. Second, if a demonstrator provided only a weak social influence on diet choice, then it is again unlikely that the demonstrator's influence would be sufficient to make the diet it is eating into a subject's modal diet. A nutrient-deprived subject exposed to a demonstrator that exerts only a weak social influence on diet choice would therefore be expected to show an enhanced tendency to restrict its feeding to a diet other than the one eaten by its demonstrator.

Pilot studies indicated that the capacity of a rat to act as a demonstrator depends upon its size; large rats seemed, for some as-yet-unknown reason, to be more effective demonstrators than small rats. Thus, if the feeding-restriction mechanism were operating,

nutrient-deprived subjects would be expected to show an enhanced avoidance of their respective demonstrators' diet when: (a) the demonstrator's diet is highly unpalatable, or (b) a small demonstrator is used.

In the present experiment, subjects were exposed to either a small or a large demonstrator feeding upon an unpalatable diet. According to the feeding-restriction mechanism, exposing nutrient-deprived subjects to a small or large demonstrator feeding upon an unpalatable diet should yield opposite results. If a small demonstrator were used, its social influence may be insufficient to make the unpalatable diet it fed upon the modal diet of subjects. In this case, the feeding-restriction mechanism predicts that nutrient-deprived rats should show an enhanced tendency to avoid an unpalatable diet eaten by a small demonstrator. In contrast, if a large demonstrator were used, its social influence is likely to make the unpalatable diet it is eating into the modal diet of subjects. The feeding-restriction mechanism therefore predicts that nutrient-deprived rats should show an enhanced tendency to feed upon an unpalatable diet eaten by a large demonstrator, and an enhanced tendency to avoid an unpalatable diet eaten by a small demonstrator.

The social-responsiveness mechanism makes very different predictions about the diet choices of nutrient-deprived rats exposed to either small or large demonstrators feeding upon an unpalatable diet. If nutrient deprivation rendered rats more susceptible to social influence, then one would expect nutrient-deprived subjects to show an enhanced tendency to feed upon an unpalatable diet eaten by a demonstrator regardless of the size of that demonstrator.

## Method

### *Subjects and Test diets*

Twenty-six experimentally naive rats of the same weight, sex, and strain as those used in Experiment 2 served as subjects. An additional 26 rats, 14 of them weighing 75-125g and 12 weighing 250-300g, served as demonstrators.

Rats chose among four foods, the three relatively-palatable, protein-poor diets described in Experiment 1 (Cin, Coc, and Thy), and an unpalatable protein-poor diet flavored with nutmeg, Diet UPLP-Nut (abbreviated form of unpalatable, low-protein, nutmeg-flavored diet). This diet was composed of 80% basal mix, a nutritionally complete mixture except for its lack of protein (Teklad Diets, catalogue TD86146), 15% corn starch, and 5% casein (Teklad Diets, catalogue 160030), flavored with 1% Club House ground nutmeg.

### *Apparatus*

The divided test enclosure described in Method of Experiment 3 was used (see Fig. 4).

### *Procedure*

A 2x2 factorial design was used in which protein deficiency state and size of demonstrator were the two independent variables. The experiment was conducted in three steps:

**Step 1. Protein-deprivation.** Eighteen randomly chosen subjects were made protein deficient by feeding them, for one week, a diet composed of equal parts powdered Purina Laboratory Rodent Chow (Diet P), solid crisco oil, corn starch, and sugar, supplemented

with 2% vitamin-mineral mix (Teklad Diets : three parts Vitamin fortification mix, catalogue 40060, to one part mineral mix, usp XIV, catalogue 170880). The remaining 12 subjects were fed Diet P for the same period of time. All subjects had ad lib access to their respective diets and water.

**Step 2. Habituation.** Subjects were randomly assigned to four conditions, Dep/Small-Dem condition (protein-deprived subjects with one small demonstrator,  $n=7$ ), Dep/Large-Dem (protein-deprived subjects with one large demonstrator,  $n=6$ ), Non-Dep/Small-Dem (non-deprived subjects with one small demonstrator,  $n=7$ ), and Non-Dep/Large-Dem (non-deprived subjects with one large demonstrator,  $n=6$ ). Subjects were placed individually into the subject compartments of the divided enclosures, and their demonstrators were placed into their adjacent demonstrator compartments. Subjects and demonstrators were then given ad lib access to the diet they were given in Step 1 and water for 24 hr.

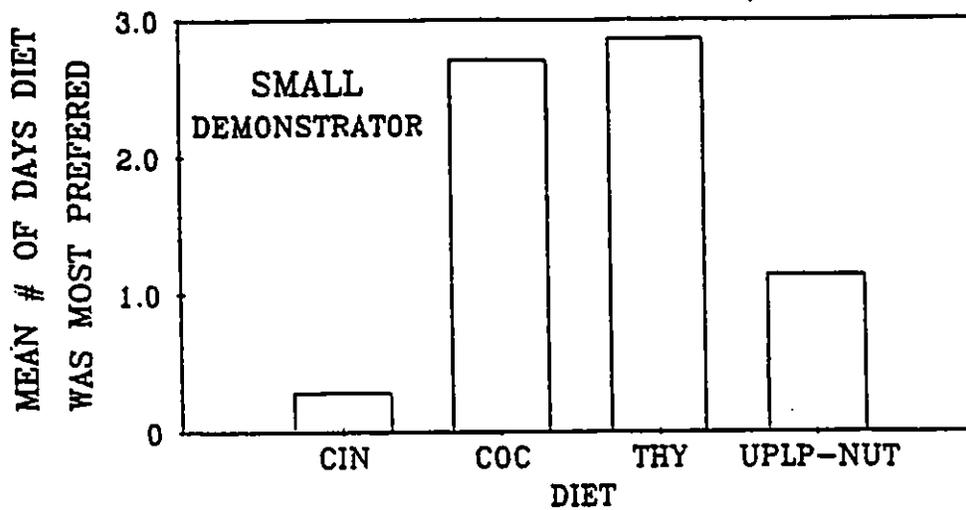
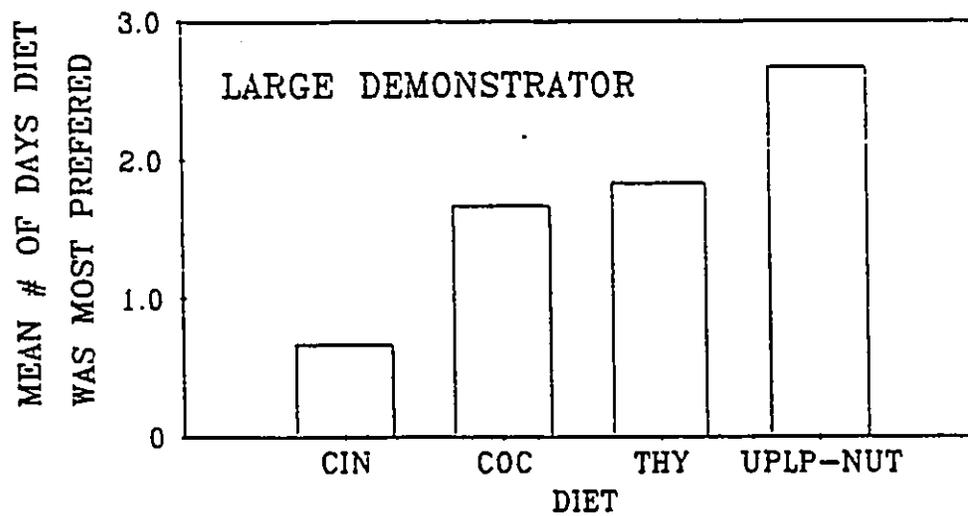
**Step 3. Testing.** Following habituation, all food bowls were removed and each subject was given four metal, semi-circular, 10-cm-diam. food bowls containing the test diets. These food cups were attached to the dividing screen and contained the test diets in the order Diet Cin, Coc, Thy, and UPLP-Nut from the front of the cage to the back. A single food bowl containing Diet UPLP-Nut was given to each demonstrator. This bowl was attached to the dividing screen immediately opposite their subjects' Diet UPLP-Nut bowl (see Fig. 4). For the next week subjects were left undisturbed except for daily weighing of food bowls and subjects.

## Results and Discussion

In the present experiment, the strength of preference of subjects for their respective demonstrators' diet was manipulated by using two sizes of demonstrator. Size of demonstrator had the expected effect upon the preference shown by subjects for the diet eaten by their respective demonstrators (Diet UPLP-Nut). As shown in Fig. 25a, which presents the mean number of days that non-deprived subjects exposed to a large demonstrator preferred Diet UPLP-Nut, those subjects exposed to a large demonstrator (Non-Dep/Large-Dem) favored Diet UPLP-Nut over the three alternative diets on most testing days. In contrast, as shown in Fig. 25b, when a small demonstrator was used (Non-Dep/Small-Dem) Diet UPLP-Nut was only the third most preferred diet.

This difference between the strength of social influence exerted by small and large demonstrators over subject diet choice was used to discriminate between the feeding-restriction mechanism and the social-responsiveness mechanism. If nutrient-deprived rats show an enhanced tendency to feed upon their demonstrators' diet because they are more responsive to social influence (the social-responsiveness mechanism), then one would expect protein-deprived subjects to show a stronger preference for their demonstrator's diet than non-deprived subjects regardless of size of demonstrator. In contrast, if nutrient-deprived rats show an enhanced tendency to feed upon their demonstrators' diet because nutrient-deprivation caused them to restrict their feeding to a single diet (the feeding-restriction mechanism), then the effect of protein deprivation should not have been independent of demonstrator size. Because Non-Dep/Large-Dem subjects preferred Diet UPLP-Nut on most testing days (their modal diet), the feeding-restriction mechanism should have made rats exposed to a large demonstrator restrict their feeding to Diet UPLP-Nut when protein-deprived. Non-Dep/Small-Dem subjects did not prefer Diet UPLP-Nut

**Fig. 25 a,b. Mean number of days on which each of the four test diets is most preferred by non-deprived subjects exposed to a large demonstrator eating Diet UPLP-Nut or a small demonstrator eating Diet UPLP-Nut.**

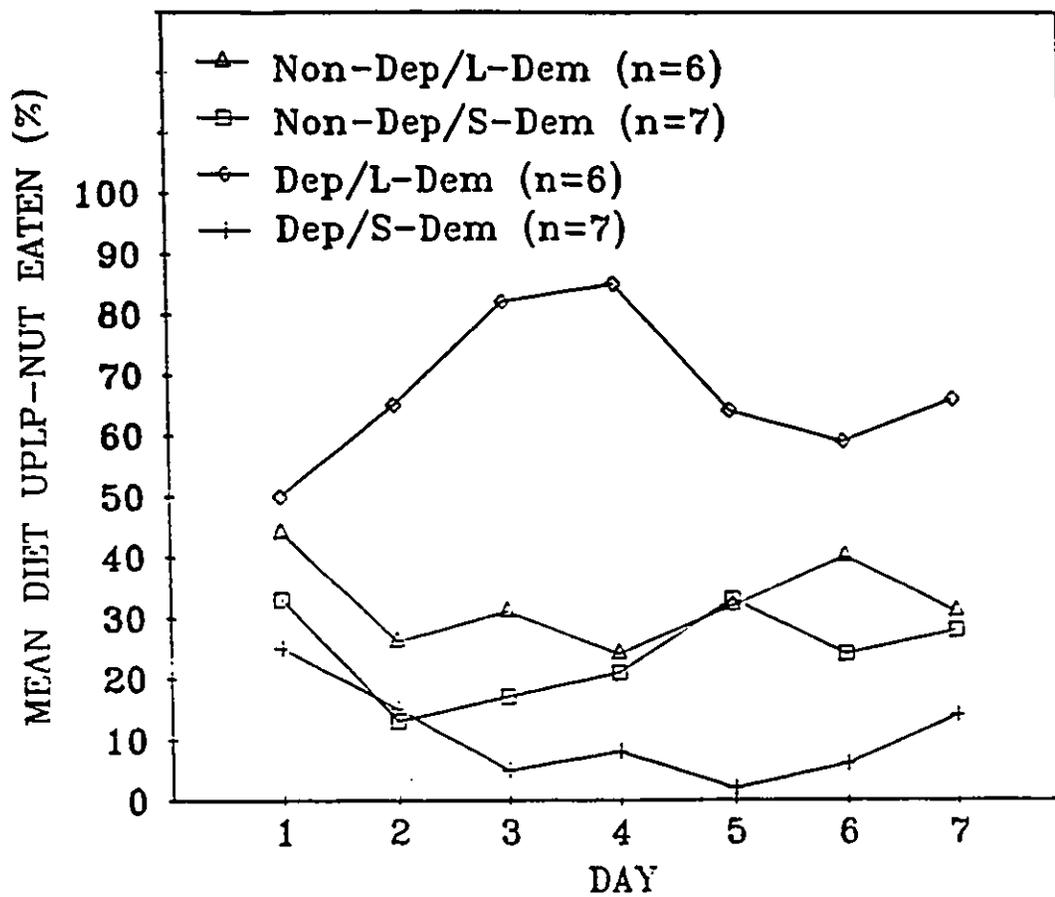
**B:****A:**

on most testing days. The feeding-restriction mechanism should, therefore, have made rats exposed to a small demonstrator restrict their feeding to a diet other than Diet UPLP-Nut when protein-deprived, causing them to avoid their demonstrators' diet.

An analysis of diet-selection data indicates that the enhanced tendency of protein-deprived subjects to match their demonstrators' diet choice was indeed contingent upon demonstrator size, an outcome that is consistent with the feeding-restriction mechanism, but not with the social-responsiveness mechanism. As Fig. 26 suggests, and as post-hoc analysis confirmed, protein deprivation enhanced the tendency of subjects exposed to a large demonstrator to match their demonstrators' diet. Dep/Large-Dem subjects ate significantly more Diet UPLP-Nut than Non-Dep/Large-Dem subjects (Newman-Keuls post-hoc analysis,  $\underline{W}_T=.406$ ,  $p<.01$ ). However, protein deprivation had the opposite effect upon the diet choice of subjects exposed to small demonstrators. Dep/Small-Dem subjects actually ate less Diet UPLP-Nut than Non-Dep/Small-Dem subjects (Newman-Keuls post-hoc analysis,  $\underline{W}_T=.627$ ,  $p<.05$ ). This interaction between deprivation state and effect of demonstrator size was statistically significant ( $F[1,22]=11.80$ ,  $p=.00265$ ). Thus, the feeding behaviour of protein-deprived subjects suggests that protein deprivation increases the tendency of rats to restrict their feeding to a single diet, rather than increasing their responsiveness to social influence.

While the present results are consistent with the feeding-restriction mechanism, it should be noted that another explanation can also account for the present results. It is possible that protein deprivation has a complex effect upon the behaviour of rats, making them more responsive to social cues emitted by large demonstrators, and less responsive to those emitted by small demonstrators. This interpretation does not, however, account for the fact that isolated protein-deprived subjects in Experiment 9 showed a stronger tendency than isolated non-deprived subjects to restrict their feeding to a single diet. Nor does this

**Fig. 26. Mean amount of Diet UPLP-Nut ingested, as a percentage of total intake, by protein-deprived and non-deprived subjects exposed to either a large or a small demonstrator eating Diet UPLP-Nut.**



interpretation explain the fact that on the first testing day protein-deprived subjects in Experiment 9 actually ate a smaller percentage of their demonstrators' diet than non-deprived subjects. Taken together, the results presented in this chapter indicate that protein deprivation predisposes rats to feed upon a single food, and that this behavioural mechanism alone was responsible for the enhanced tendency of nutrient-deprived subjects to match the diet choices of others (Chapters IV and V).

The finding that subjects were more likely to match the diet selections of large demonstrators than small demonstrators raises the question of whether such behaviour has any adaptive significance. This possibility will be addressed in the General Discussion of this thesis

## Part 2: Summary

Part II of this thesis examined two behavioural mechanisms that might be responsible for the tendency of protein-deprived rats to match more closely than do non-deprived rats the diet choices of their respective demonstrators. According to the social-responsiveness mechanism, protein deprivation renders animals more responsive to social influence when choosing diets. In contrast, the feeding-restriction mechanism holds that protein deprivation does not effect the responsiveness of rats to social influence directly, but rather increases the tendency of rats to restrict their feeding to a single diet. According to the feeding-restriction mechanism, a protein-deprived rat shows an enhanced preference for their demonstrator's diet not because it is more susceptible to social influence, but because its enhanced tendency to feed upon a single diet is directed by social influence towards its demonstrator's diet.

Three classes of evidence presented in the present chapter suggested that the feeding-restriction mechanism, rather than the social-responsiveness mechanism, was operating: (a) In the absence of a demonstrator, protein-deprived subjects tended to restrict feeding to a single diet to a greater extent than did non-deprived subjects. (b) On the first test day of testing, protein-deprived subjects actually ate a significantly smaller proportion of their demonstrators' diets than did non-deprived subjects. (c) When exposed to a small demonstrator eating an unpalatable diet, protein-deprived subjects ate a smaller proportion of their demonstrators' diets than did non-deprived subjects. Because all three of these findings were more consistent with the feeding-restriction mechanism than the social-responsiveness mechanism, the findings presented in Part II suggest that protein-deprived

rats show an enhanced tendency to match the diet choice of others because protein deprivation renders them more likely to feed upon a single diet.

## GENERAL DISCUSSION

### I. The cause of diet-selection failures.

#### 1. Historical view of failures to select adequate diets.

The emphasis early investigators placed on inherited mechanisms of diet selection led them to overlook the importance of environmental factors in food choice (e.g. Richter et al., 1938; Osborne and Mendel, 1918). With few exceptions (Dove, 1935; Kon, 1931), early investigators conceived of the environment as an unimportant aspect of a diet-selection task, an aspect that could be modified without affecting the ability of animals to find adequate nutrients. As a consequence, these investigators could not explain why animals often failed to compose adequate diets when nutrient-rich foods were made available to them. Because such failures could not be reconciled with the belief held by early investigators that the ability to select adequate diets is an inherited trait, they chose to ignore failures, or to interpret them creatively, as examples of successful diet selection (e.g. Osborne and Mendel, 1918; Richter et al., 1938).

When it was unequivocally demonstrated in the 1960s that animals learn to prefer nutritious foods by responding to consequences of ingestion (e.g. Rozin, 1965; Garcia et al. 1967), there was a shift in the perceived role of the nutrient environment in diet selection. Rather than being a superficial aspect of diet-selection tasks, the nutrient environment was now acknowledged to be a crucial determinant of successful diet selection. During the 1960s it was recognized that animals typically fail to find adequate nutrients when: (a) more than two or three alternative diets are available, (b) a needed

nutrient is present only in a relatively unpalatable diet, or (c) ingestion of a nutrient-rich food does not result in an immediate positive physiological effect (see Westoby (1974) for a review). Thus, the environment came to be viewed as a factor that could mask the ability of animals to solve diet-selection problems, and failures on the part of animals to solve diet-selection problems were attributed to characteristics of the nutrient environment (e.g. Lat, 1967; Overmann, 1976).

## **2. The importance of the social environment for successful diet selection.**

The present research indicates that it was incorrect to attribute diet-selection failures to characteristics of the nutrient environment alone. Results obtained in Experiments 6,7, and 8 indicated that rats, allowed to interact with others feeding upon a protein-rich diet, readily developed a preference for that diet, even though three alternative diets were available and the protein-rich food was relatively unpalatable. Under these same conditions, most isolated rats failed to ingest sufficient protein to grow. Results obtained in Experiments 9, 10 and 13 indicated that rats matched the diet choices of others for at least one week, even when such matching did not result in positive, internal consequences. Social influences could, therefore, allow animals to find sources of slow-acting nutrients. Taken together, these results suggest that failures on the part of isolated laboratory rats to find adequate nutrients were due to the inadequacy of their social environment in combination with the challenge posed by their nutrient environment.

That rats should rely upon social information to find nutritious foods does not seem surprising if one considers the advantages to be gained from utilizing this source of dietary information. In comparison with a rat that used social information to guide its diet choices, an asocial rat would face a prolonged period of nutrient deprivation before it could compose an adequate diet. Such prolonged nutrient deprivation could potentially lead to death or

permanent disability from malnutrition or consequent disease, and might also reduce a rat's likelihood of surviving encounters with predators, aggressive conspecifics, and parasites.

An asocial rat is also at risk of ingesting toxins. Indeed, exposure to toxins is a direct consequence of an asocial rat's strategy of searching for nutritious food by personally sampling novel, potentially-toxic foods. A rat could greatly reduce its exposure to toxins by allowing the proven diet choices of others to guide its own selection of foods.

Given that an asocial wild rat would have to incur the costs associated with prolonged nutrient deprivation and toxicosis, it seems likely that natural selection would favor wild rats that rely heavily upon social information when choosing diets. As discussed above, the present research is consistent with this argument; rats readily matched the diet choices of others and thereby enhanced their ability to choose nutritious foods. Considered together, the obvious benefits rats would derive from using social information to make diet choices in the wild, and the present empirical confirmation that rats make use of social information when choosing diets, strongly suggest that the social environment plays a central role in diet selection in the wild.

If this argument is accepted, then one must conclude that our current understanding of how wild animals find adequate nutrients, based as it is upon the diet-selection behaviour of isolated rats, is to some degree inaccurate and in need of revision. The amount of revision that is required is not altogether clear at this early stage of research. Empirical support for the hypothesis that the social environment plays a crucial role in diet selection has been obtained under artificial laboratory conditions, leaving open the possibility that under natural conditions the social environment plays a lesser role in this process.

## **II. Potential methodological exaggeration of the importance of social information for successful diet selection.**

### **1. The difficulty of diet-selection tasks.**

There are several ways that the artificial conditions used in the present research might possibly have elicited diet-selection behavior that is unlike that expressed by rats in a wild setting, thereby making social influences appear to be more important for successful diet selection than they truly are under natural conditions. It is possible, for example, that the difficult diet-selection tasks that were used in the laboratory gave socially-housed rats an artificial advantage over rats that chose diets in isolation. If rats had been presented with a simple diet-selection problem, then animals exposed to demonstrators might not have had as great an advantage over isolated animals.

There is no indication, however, that the diet-selection tasks used in the present research were unnaturally difficult. Indeed, the selection problems used in the present research were probably more like those encountered in nature than were those used in previous research. For example, Rozin (1965), in his studies of vitamin B selection, used equipalatable diets, he presented rats with only two alternatives, and he made rats deficient in vitamin B, ingestion of which leads to an extremely rapid onset of recovery. It must surely be rare for rats in a natural setting to be confronted with a selection problem that so strongly biases them towards successful diet choice.

Rozin's (1965) study is an extreme case, yet most studies in the diet-selection literature have, similarly, used experimental conditions which strongly bias animals toward successful diet selection. The majority of diet-selection studies have investigated selection of the fast-acting B vitamins (see Rozin, 1976 for a review). In addition, a high proportion of studies have made animals choose among three or fewer diets, selected to be similar in palatability.

## 2. The use of artificially-constrained demonstrators.

The importance of the social environment for successful diet selection might also have been exaggerated in the present research by the use of demonstrators that were artificially constrained, either by aversion training or by physical means, to eat only the nutrient-rich diet. In a natural environment, such artificial constraints would not exist, allowing individual animals to eat several different diets in one feeding bout. An analysis of the stomach contents of wild Black rats (*R. rattus*) living on the Galapagos islands showed that the rats had been eating as many as 12 different foods (Clark, 1982). Given this dietary range, it is possible that some social, dietary information could be lost in transmission. The mechanisms by which rats communicate dietary information do not preclude such a possibility. For example, Galef and Wigmore (1983) found that rats prefer novel foods they have previously smelled on the breath of others. It seems quite likely that the scent of some foods on the breath of a demonstrator would obscure the scent of others, limiting the ability of animals to use scent on the breath of others as a source of dietary information.

Clark (1982) also found that some foods eaten by wild rats made up only a very small proportion of their total intake. Such minor food items might have contained important micro-nutrients, yet left virtually no scent on a demonstrator's breath. Thus, it is possible that an unconstrained demonstrator could not transmit information about nutritious foods that comprise only a small proportion of its diet. Further research is required to determine the extent to which free-feeding rats can act as demonstrators.

### 3. The use of synthetic diets.

Assuming for the moment that neither the difficulty of the diet-selection task used in the present research, nor the use of constrained demonstrators, resulted in unnatural diet-selection behavior, it is still possible that the importance of social information for successful diet-selection was exaggerated by the artificial laboratory conditions used. It is possible, for example, that unlearned preferences for nutritious foods are a better source of dietary information than they have appeared to be in the laboratory. If unlearned preferences are an accurate guide to nutritious foods in the natural environment, then rats would be better able to choose nutritious diets in the absence of social information.

Richter et al.'s (1938) suggestion that unlearned preferences for nutritious foods is an important diet-selection mechanism was discredited after it was shown that laboratory animals are unable to find many nutrients by taste alone. However, these negative findings were obtained in studies in which animals were offered synthetic foods, rather than foods found in the natural environments of rats. It is possible that, in natural environments, there is a strong correlation between the palatability of foods and their nutritional value. For example, rats may possess an unlearned preference for the complex pattern of gustatory qualities that are associated with meat. Or alternatively, rats may learn to prefer the taste of meat more rapidly than the taste of a synthetic food of the same nutritional value. As far as I am aware, such possibilities have not been investigated.

The seemingly arbitrary flavors associated with nutritious natural foods found in the vicinity of a wild population might also be exploited by animals as a source of dietary information. Indeed, one could argue that natural selection should ensure that animals in a closed population evolve to prefer the taste of local foods that contain needed nutrients. Assuming that: (a) the diet preferences of wild animals are sufficiently variable to allow

some animals to prefer local, nutritious foods, (b) diet preference is heritable (there is a correlation between diet preference and genotype), (c) well-nourished individuals produce more offspring than do poorly-nourished individuals, and (d) the types of foods available in a given locale remain the same over many generations, then the proportion of individuals in the population that prefer local, nutritious foods will increase due to natural selection. By this mechanism, seemingly arbitrary flavors of local, nutritious foods can become reliable signals for nutrient sources.

Empirical evidence supports both assumptions (a) and (b) above. In support of assumption (a), Dove (1935) found chickens to be highly variable in their diet preferences. Indeed, the variability in the preferences of chickens in a cafeteria-feeding situation was so marked that, although some chickens made poor diet selections and lost weight, others made diet selections resulting in better growth than chickens fed a commercial diet. Similarly, Kon (1931) found that rats differed greatly in their immediate preference for the protein, casein. In a diet-selection task, those rats that displayed an unlearned preference for casein rapidly gained weight, those that did not prefer casein lost weight and died. Kon's (1931) finding, that the preference shown by rats for protein sources is highly variable, was replicated by Scott and Quint (1946). Scott and Quint (1946) presented rats with a variety of different protein sources and found that while no rat preferred all the protein sources, a proportion of rats preferred each of the different protein sources. In support of assumption (b), Scott (1946) found that there is a stronger correspondence between the diet-preferences of rat litter mates than between those of non-relatives. Scott's (1946) finding can not be explained in terms of acquired preferences passed from mother to offspring because all mothers were maintained on the same laboratory diet. Assumption (c) does not require empirical verification; at some level of malnutrition an animal's capacity to successfully reproduce must be compromised. Assumption (d) is likely to be true as well;

there is every reason to suppose that many of the foods animals exploit are stable over a duration sufficient for natural selection to occur.

Because all four assumptions are at least tentatively confirmed, it is possible that inherited preferences for local-nutrient sources could be present in wild populations. If wild animals do prefer nutritious foods in their local environment, then they would not require much assistance from their social environment in order to make successful diet choices. It is, therefore, possible that the present study inflated the importance of social influences by blocking the use of unlearned preferences through the use of synthetic foods.

Additional research using diet-selection problems actually found in nature is required to test the possibility that have unlearned preferences for specific nutritious foods found in a local habitat, or a more general set of unlearned preferences for natural nutritious foods. Natural diet-selection task could be prepared by presenting rats both with natural foods that are found in the stomachs of trapped wild rats, and a variety of other potential foods also found in the natural environment. If laboratory-reared, wild rats were only able to compose an adequate diet from natural foods when in the presence of knowledgeable others, it would unequivocally confirm that the social environment plays a major role in diet selection in the wild. If, however, laboratory-reared wild rats from a specific location were better able to compose an adequate diet from foods taken from that location than are rats from another location, then it would suggest that rats have inherited preferences for local, nutritious foods. Finally, if rats were better able to compose an adequate diet from among natural foods taken from any arbitrary locale than from synthetic foods, then it would suggest that rats possess general unlearned preferences for nutritious natural foods. The presence of such unlearned preferences for natural foods would indicate that rats require less assistance from their social environment to find nutritious foods than is suggested by the present research.

### **III. Revising current theories of diet selection to incorporate the role of the social environment.**

Although a complete picture of the specific role the social environment plays in diet selection in the wild must await further research, it seems likely that a revision of our current understanding of diet selection will be necessary in order to give sufficient weight to social aspects of diet selection. The extent of revision that will be necessary depends not only upon how important the social environment is for successful diet selection, but also upon the specific ways in which the social environment facilitates diet selection. For example, if the social environment acts simply to restrict diet sampling to foods most likely to contain needed nutrients, then only a small revision of our current conception of diet selection in the wild would be required: it would merely be necessary to acknowledge that social influences simplify diet-selection by reducing the number of alternative diets a rat must sample to find needed nutrients.

Although the present research does, indeed, indicate that the basic role of the social environment is to direct diet sampling towards nutritious foods, the diet choices of rats were not completely governed by the diet choices of others. Rather, the extent to which one rat matched the diet choice of another depended upon the situation. In general, the present research suggests that rats show a greater tendency to match the diet choices of others only when such matching is likely to lead to superior diet choices.

#### **1. Effect of nutrient deprivation on tendency to match the diet choice of others.**

Results presented in Chapters IV and V indicated that the extent to which a rat matches the diet choice of others is enhanced by nutrient deprivation (Experiments 7,8,9,10), and reduced by nutrient repletion (Experiment 11). The advantage of such a

modifiable response to social influence seems clear. A nutrient-deprived animal would benefit from showing an increased tendency to match, because by so doing it would increase its chances of matching the diet choices of successful others. Indeed, the benefit an animal would accrue from matching the diet choices of others would be proportional to its degree of nutrient deprivation. In contrast, a nutrient-replete animal would benefit from resisting social influences which could cause it to deviate from its own adequate diet choice. Thus, the findings presented in Chapters IV and V suggest that rats match the diet choice of others to a degree which, given their state of nutrient deprivation, is most likely to yield superior diet choices.

## **2. Effect of number of demonstrators on tendency to match the diet choice of others.**

The present research provided other examples of rats modifying the extent to which they matched the diet choices of others according to the situation. Results presented in Experiment 2 showed that rats were more likely to feed upon a protein-rich diet when three demonstrators expressed a preference for this diet than when only one demonstrator did so. Such graded responses to social influence could increase the likelihood that a rat would adopt only beneficial diet preferences. If only a single rat preferred a certain food, then that rat might be expressing an idiosyncratic, maladaptive preference for a nutrient-poor food. On the other hand, if several rats prefer the same food, then it is less likely that they have all developed a maladaptive preference for a nutrient-poor food, and more likely that the food provides a needed nutrient.

### **3. Effect of demonstrator size on tendency to match the diet choice of others.**

Rats may also respond to the size of a demonstrator in order to ensure that they match a beneficial diet choice. Protein-deprived rats that chose among four protein-poor diets were much more likely to match the diet choice of a large demonstrator than they were to match the diet choice of a small demonstrator (Experiment 13). Non-deprived rats showed a much weaker discriminative response to large and small demonstrators. One might speculate that the conditional response shown by protein-deprived rats to large and small demonstrators solves a problem inherent in using social information. The problem arises when an animal uses social information, but does not experience immediate reinforcement for doing so. In such a situation, is it in the best interests of a rat to persist in eating the food another is eating "on the assumption" that the food that another is eating contains a slow-acting nutrient, or should the rat abandon the food in order to sample other foods "on the assumption" that the other rat has a maladaptive preference for the food? The best strategy may depend upon the source of the social information. If a large rat is eating a diet, then it is unlikely that it is showing a maladaptive preference. The fact that the rat has grown to its large size indicates its diet selections have been adequate. If, however, the source of social information is a small rat, it is more likely that it is displaying a maladaptive diet preference; a small rat has not proven itself capable of choosing nutritious food. Thus, if a large conspecific is feeding on the diet, the best strategy is to adopt the diet preference; if a small conspecific is feeding upon it, the best strategy is to sample other diets.

These examples suggest that the ways in which rats utilize their social environment in order to make beneficial diet selections may be quite complex. Rats do not simply allow

the diet choices of others to govern their own diet choices. Rather, their use of social information is determined by aspects of their internal and external environments, in a manner that facilitates successful diet selection. If future research confirms this conclusion, then it would suggest that our current conception of animals as passive recipients of dietary information may not be the most advantageous paradigm for advancing our understanding of diet selection. More progress might be made by viewing animals as actively seeking accurate dietary information from the available information sources.

#### **IV. The direction of future research.**

##### **1. Studying the process of diet selection under more natural conditions.**

Given the early state of research on the social aspects of diet selection, it is difficult to know what direction future research should take to best illuminate the role of the social environment in diet selection. It is clear, however, that it is necessary to study animals in nutrient and social environments which simulate those present in nature. Only by so doing will it be possible to gain an unbiased understanding of how wild animals use various sources of dietary information to make beneficial diet selections.

A very important and virtually unstudied area is the feeding behaviour of groups of animals. Very basic questions about the feeding behaviour of rats choosing foods in a group have yet to be answered. For example, it is not known which rats in the group sample novel foods, or the extent to which they do so. Nor is it known how rapidly dietary information is transmitted through a group, or what conditions control the rate at which it spreads.

## **2. Inherent limits in the amount of dietary information that can be obtained from the social environment.**

Another basic question that must be answered about the role of the social information in diet selection is how precise such information is. Can rats use social information to learn about foods that make up only a small proportion of the diet of others? Can rats learn the proportion of foods to eat by attending to the diet choices of others? It seems improbable that rats could obtain precise information about the types of foods to eat by attending to the scent of diets on the breathe of others. However, rats might obtain such precise information by attending closely to the diet choices made by others at feeding sites. It is even possible that rats possess the ability to combine information obtained from several others to reduce the noise inherent in socially-acquired dietary information. Given our present state of knowledge about how rats use social information to make beneficial diet selections, few possibilities should be ruled out.

## **3. How do demonstrators arise in wild populations?**

Learning how demonstrators originally arise in a wild population of recent immigrants is also necessary in order to better understand the role of the social environment in diet selection. One might argue that the only way that demonstrators could arise is for rats to have the ability to find adequate nutrients by individually sampling novel foods, because rats penetrating a new territory that contains a variety of novel foods could not use social information to compose a nutritious diet. If such immigrants survive, then the social environment must not be necessary for the development of beneficial diet preferences.

From this conclusion, one might go on to argue that the social environment provides only an auxiliary source of dietary information, rather than an indispensable source.

This argument contains the erroneous assumption that an animal which makes beneficial diet selections must possess mechanisms for selecting an adequate diet. In fact, if the diet preferences of wild rats are sufficiently variable, then a proportion of immigrants should prefer nutritious food in their new environment simply by chance. As those rats that prefer nutrient-poor foods expire, the proportion of the population that prefers nutritious foods would increase. Thus, a population of recent immigrants with sufficiently diverse diet preferences would rapidly come to be dominated by animals with beneficial diet preferences, even if the immigrants do not possess mechanisms to find nutrient sources. Survivors could act as demonstrators for weanling rats in the next generation. I am not, of course, suggesting that animals have no mechanisms to select nutritional diets without help from their social environment, but rather that it is not necessary for animals to have such mechanisms in order for demonstrators to arise within a population.

It should be noted that the first few generations of demonstrators in an immigrant population may compose diets that are adequate, yet far from optimal for their nutrient environment. However, superior demonstrators would soon arise as those animals that make serendipitous discoveries of previously unexploited nutrient sources out-survive their peers, and therefore act as demonstrators for an extended period of time. If this process continued, then one would expect demonstrators that prefer the most nutritious foods available to eventually arise.

## CONCLUSION

The social environment provides rats with a source of dietary information with which to solve a variety of problems inherent in the process of diet selection. The present research indicates that rats may utilize social information to increase their likelihood of finding a relatively unpalatable nutrient source among several alternative foods, a diet-selection task that most isolated rats fail to solve. In addition, the present research suggests that rats could potentially use social information to find sources of slow-acting nutrients, even those nutrients that have a beneficial effect a week following ingestion.

The manner in which rats used social information to select adequate diets may be interpreted as evidence for the presence of evolved mechanisms to abstract accurate dietary information from their social environment. Rats were more likely to match the diet choice of others when nutrient deprived, when exposed to large demonstrators, or when exposed to several demonstrators all choosing the same diet. As discussed above, these variable responses to the social environment might be used in a natural environment to reduce the likelihood that rats would develop preferences for nutrient-poor foods.

The need for behavioral mechanisms for abstracting accurate dietary information from the social environment becomes clear if one considers the problems facing wild animals that uses social information to find nutritious foods. Wild rats must sift through the enormous quantity of noisy and potentially ambiguous dietary information provided by the tens or even hundreds of individuals in their respective social environments in order to select a diet that is not only adequate for growth, but will also allow them to successfully compete for food and mates. It would seem that researchers intent on discovering how wild animals select nutritious foods face a difficult challenge.

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