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response components, and hierarchical and sequential control states making up a behavior system. For example, periodic presentation of a reward entrains an appetitive structure while allowing relatively free expression of the underlying elements. Manipulation of CS characteristics can be added to engage specific perceptual-motor modules. The techniques of operant conditioning can be used to explore, differentiate, and link modules and motivational states.

The application of the behavior system approach to the study of natural learning in the laboratory requires knowledge of the subject's behavior and ecology and an ability to establish and tune laboratory circumstances to engage elements of the underlying appetitive structure. To a biologically oriented researcher, attempting to tune a laboratory setting may seem like trying to draw a picture in the dark, but it can have impressive results. The fact that the three major instrumental responses of laboratory learning (maze running, lever pressing, and key pecking) can be produced reliably by simple pairings or stimulus exposure speaks well of the ability of experimenters to produce a good fit between the animal and the environment. However, the fact that most researchers have not explored this fit experimentally, nor have even appeared to recognize the ecological significance of these responses, shows that tuning alone is inadequate to drive the analysis of learning.

An important remaining issue is how to treat the mechanistic and quantitative models of modern laboratory learning research. I find overstated Kuo's comment (1967, p. 7), that "if many learning theorists have apparently succeeded in their mathematical predictions, that can be explained by the fact that they have ignored the great complexity and variability of behavior." But the point is well taken that all learning involves more complexity than is currently accounted for by these models. To clarify the nature of laboratory and natural learning, as well as the relations between them, an account of the subject's appetitive structure is essential.

AN ADAPTATIONIST PERSPECTIVE ON SOCIAL LEARNING, SOCIAL FEEDING, AND SOCIAL FORAGING IN NORWAY RATS

Bennett G. Galef, Jr.

For 20 years, my coworkers and I have been engaged in the study of social learning in animals. During most of that time, those working in my laboratory have been analyzing several ways in which social interactions among Norway rats (*Rattus norvegicus*) can affect their selection of both foods and foraging sites.

There are a number of reasons to believe that social learning is important to young rats struggling to compose a safe, yet balanced, diet. First, we have identified four ways in which social interaction among rats can influence their food choices (see Galef, 1976, 1986a for reviews), and Gemberling (1984) has described a fifth. Such redundancy in itself suggests that information about what and where others are eating can be of considerable use to rats. Second, as we shall see below, there is direct evidence that, even in the laboratory, social interactions can be crucial to the survival of young rats as they make the potentially perilous transition from nutritional dependence on their mother's milk to independent foraging and feeding.

This chapter reviews data collected in my laboratory since 1983. It is more explicitly Darwinian in its approach than is usually the case in discussions of

behavior acquisition by animals. First, in a brief introduction, I discuss my view of the relationship between the study of social learning in animals and what Lewontin and Gould have referred to, albeit unsympathetically, as the "adaptationist program" (Gould & Lewontin, 1979; Lewontin, 1978). In a second, longer section, I describe in some detail recently completed laboratory analyses of one type of social learning: olfactory communication of information about foods among Norway rats. Last, I discuss the possible implications of our laboratory findings for understanding the ways in which Norway rats may find food and avoid poisons in their natural habitat. Thus, in this chapter, analytic laboratory studies of the causes of behavior are sandwiched between an adaptationist introduction and adaptationist extrapolations to more evolutionarily relevant situations. This organization reflects the way I think about my laboratory research.

SOCIAL LEARNING FROM AN ADAPTATIONIST PERSPECTIVE

In a characteristically elegant passage, Ernst Mayr (1973, p. 651) described two rather different types of "genetic program" (I prefer to think of them as two types of "developmental program") which are translated into phenotypic characteristics during ontogeny:

We can ask what differences exist between genetic programs responsible for behaviors formerly called innate and those regarded as experientially acquired. A genetic program that does not allow appreciable modifications during the process of translation into the phenotype I call a *closed program*—closed because nothing can be inserted in it through experience. Such closed programs are widespread among the so-called lower animals. A genetic program that allows for additional input during the lifespan of its owner I call an *open program*.

I will use Mayr's dichotomy between open and closed programs as a starting point to discuss the extent to which one might expect an adaptive "fit" between the phenotype of an organism and the demands of the particular environment in which it lives.

Closed developmental programs.

By definition, the ontogeny of a behavioral phenotype that develops from the transcription of a closed developmental program is unaffected by the vagaries of the environment in which it matures. Although there are circumstances in which a closed program would be more fit than any open program that could produce similar behavior, the inability of closed programs to produce different phenotypes, each appropriate to a particular environment, constrains the perfection of design (Williams, 1966, p. 12) of phenotypic characteristics that result from translation of closed programs.

As Williams has indicated, "Favorable selection of a gene is inevitable if [that

gene] has favorable mean effects compared to available alternatives of the moment" (1966, p. 27). Genes contributing to closed programs have been selected for their favorable mean effects on survival and reproduction. Consequently, the phenotypic features produced by transcription of closed developmental programs, unmodified by experience, can be adaptive only with respect to the mean properties of the range of environments in which the members of a species have evolved. Hence, closed programs cannot produce phenotypes that are matched to each of the range of conditions that contributes to the mean environment, and the fit between an individual and its environment that results from transcription of a closed program is likely to be relatively crude.

Open developmental programs.

Open developmental programs, which are sensitive to experience in their translation from genotype to phenotype, provide a way in which individual phenotypes can, in principle, achieve a greater degree of accommodation to the idiosyncrasies of the particular locales in which they mature than can phenotypes produced by transcription of closed programs. Although open programs might sometimes respond to environments experienced during ontogeny by producing phenotypes less, rather than more, able to cope with the demands of that environment, open developmental programs, like closed programs, are products of natural selection: those open programs that respond to environments by producing poorly adapted phenotypes will be selected against; those that respond by producing well-adapted phenotypes will be favorably selected. The result, in many circumstances, should be an increase in the frequency of open programs able to respond adaptively to the environments in which individuals mature.

Individual and social learning.

Although there are exceptions (e.g., Marler & Tamura, 1964; West, King, & Harrocks, 1983), most investigators of the role of experience in the modification of phenotypes during ontogeny have studied interactions between a developing organism and its physical environment, since the physical environment in which an open program is translated into a phenotype contains many useful cues as to the developmental end points appropriate to that environment. However, the physical features of an environment are not the only useful sources of information available to an open program about the path its translation to phenotype should follow.

The behaviors of adults that interact with a developing individual are, not infrequently, valuable indicators of behavioral end points towards which development should proceed. Adults with whom a developing individual interacts have phenotypes adequate for survival in the particular environment in which the

interactions occur. If open programs could incorporate the behavior of those adults into the phenotype of the developing individual, production of a phenotype matched to the idiosyncratic demands of the environment would be all but assured. Open developmental programs that accepted behavior of adult conspecifics as inputs could, in effect, provide a nongenetic means for the transmission of acquired, adaptive phenotypic characteristics either between or within generations.

That it might be useful in theory for naive individuals to incorporate into their own phenotypes behavioral features exhibited by conspecifics does not, of course, prove that naive individuals actually can or do use the behavior of knowledgeable others to guide their own development. Determining whether individuals make use of conspecifics as guides in development, and, if so, describing the processes by which the behavior of conspecifics can bias the translation of open programs towards particular phenotypic end points, are empirical, rather than theoretical, enterprises.

Accordingly, for 20 years, my coworkers and I have been using the development of diet choice by rats as a model system to explore the ways in which developing individuals can incorporate the behavior of others into their own behavioral phenotypes. In the next section, I review recent findings from that research program.

RATTUS NORVEGICUS: A SOCIAL, CENTRAL-PLACE FORAGING SPECIES

Many behavioral ecologists have suggested that in environments where the distribution of foods is unpredictable and patchy, social animals foraging from a central place (for example, birds foraging from a roost) could exchange useful information at the central place concerning the availability of foods in the larger environment (Bertram, 1978; DeGroot, 1980; Erwin, 1977; Waltz, 1982; Ward & Zahavi, 1973). For example, an unsuccessful forager might spot a successful forager at an aggregation site, then follow the successful individual when it left on its next foraging trip.

Although the use of aggregation sites as information centers was originally proposed to explain the evolution of bird roosts (Ward & Zahavi), aggregations other than roosts could serve this function, and organisms other than birds could benefit from their use. For example, it has long been known that the hives of honeybees act as information centers where returning foragers provide nestmates with both olfactory information (Wenner, 1971) and visual (dance) information (von Frisch, 1967) that directs nestmates to the patchy, ephemeral sources of nectar and pollen on which honeybees feed.

Outside the laboratory, Norway rats are social central-place foragers. Each rat is a member of a colony that inhabits a burrow. When foraging, colony members

disperse from the burrow, feed, and then return to the burrow (Calhoun, 1962; Telle, 1966). Thus, the burrows of Norway rats, like the roosts of some species of birds, could, in principle, function as information centers, and Norway rats are an appropriate species to use in laboratory experiments examining ways in which social interactions may facilitate food finding by members of social central-place foraging species.

The basic experiment

The laboratory studies described below were intended to simulate natural situations in which a foraging rat eats a food at some distance from its burrow, returns to its burrow, and then interacts with a burrowmate. Our initial purpose was to discover whether, as a result of such interaction, a rat could acquire information concerning the food another rat had eaten and, if so, whether it would make use of this information when it had to select a food to eat.

The subjects were housed in same-sex pairs, each pair in a cage divided in two by a screen partition. To simplify exposition, I refer below to the "successful forager" in each pair as the "demonstrator," and to the other member of the pair as the "observer." The basic experiment, illustrated in Figure 1, was carried out in five steps. In Step 1, a demonstrator and an observer with unlimited access to Purina Laboratory Rodent Chow and water were housed together for a 2-day period of familiarization with their enclosure and with each other. In Step 2, the demonstrator and the observer were placed on opposite sides of the cage and separated by the screen partition, and the demonstrator was deprived of food for 24 hours to ensure that it ate when given the opportunity to do so. In Step 3, the Rodent Chow was removed from the observer's side of the cage to prepare the observer for testing. The demonstrator was moved to a cage in a separate room and, for 30 minutes, was allowed to eat one of two different diets: a cinnamon-

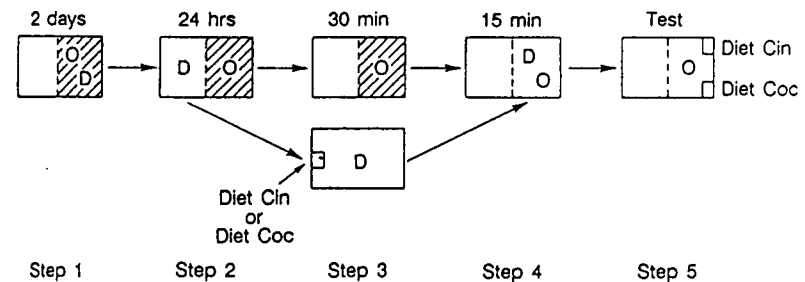


FIGURE 1. Schematic diagram of the procedure of the basic experiment. O = observer; D = demonstrator; hatching indicates maintenance diet present in cage. (After Galef & Wigmore, 1983.)

flavored diet (Diet Cin) or a cocoa-flavored diet (Diet Coc). In Step 4, immediately after the demonstrator finished eating, it was placed with the observer, and the two rats were allowed to interact freely for 15 minutes. Finally, in Step 5, the demonstrator was removed from the experiment, and for 60 hours, the observer was offered an opportunity to eat from either of two weighed food cups, one containing Diet Cin and the other containing Diet Coc.

Figure 2 shows the mean percentage of Diet Coc eaten by observers whose demonstrators had eaten either Diet Coc or Diet Cin during the experiment. As can be seen in Figure 2, (1) those observers whose demonstrators ate Diet Coc ate a much greater percentage of Diet Coc than did those observers whose demonstrators ate Diet Cin, and (2) the effects of the diet eaten by demonstrators on the diet preference of their respective observers were still apparent 48–60 hours after the interaction between the two rats had occurred. The results of this first experiment show: (1) that an observer rat can extract information from its demonstrator that is sufficient to identify the diet the demonstrator has previously eaten, and (2) that this socially acquired information is sufficient to bias observers' subsequent selection of diets.

Variations on a theme. We have performed different versions of this basic experiment many times, using a variety of different diets (Galef, in press; Galef,

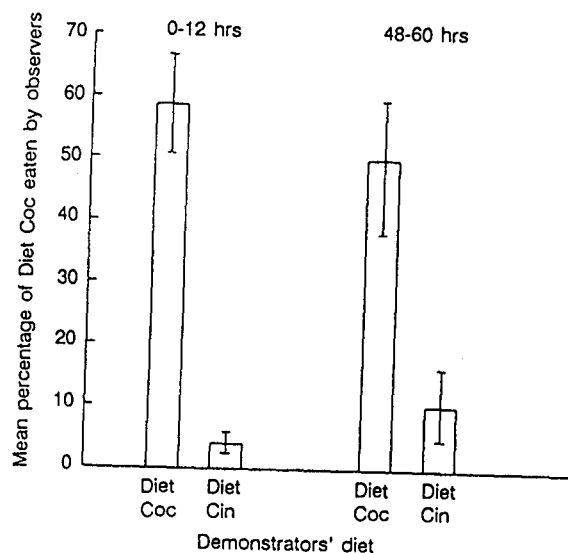


FIGURE 2. Mean amount of cocoa-flavored diet (Diet Coc) ingested, as a percentage of total amount of food eaten, by observers whose demonstrators ate either Diet Coc or cinnamon-flavored diet (Diet Cin). (From Galef & Wigmore, 1983.)

Kennett, & Wigmore, 1984; Galef & Wigmore, 1983), with both hungry and replete observers, with both male and female demonstrator-observer pairs, and with both wild and domesticated Norway rats. We have also performed versions of the experiment with demonstrator-observer pairs that were familiar with one another beforehand, and with pairs that never met each other prior to the interaction described in Step 4 of the basic experiment. We have repeated the basic experiment with old demonstrators and observers and young ones (Galef, Kennett, & Wigmore, 1984). In every case, we have seen robust enhancement of the preferences of observers for their respective demonstrators' diets. Similarly, Posadas-Andrews and Roper (1983) and Strupp and Levitsky (1984), using rather different laboratory situations, have repeatedly observed demonstrator influence on later diet selection by observers. Apparently, demonstrator rats will influence their observers' diet preferences under a broad range of conditions.

Duration of effects. Although the effects of exposure to a demonstrator fed a certain diet on its observer's subsequent food choice can be substantial, one might expect such effects to be transitory. Long-lasting learned preferences for foods have proven to be difficult to induce in mammals other than humans (Capretta & Rawls, 1974; Rozin, 1984; Rozin, Gruss, & Berk, 1979; Warren & Pfaffmann, 1959). However, in recent experiments, we have found that by the simple expedient of exposing rats to demonstrators that had eaten a diet, rather than to the diet itself, it is possible to induce preferences of indefinite duration for both palatable and unpalatable foods (Galef, in press). In these experiments, observers interacted for 30 minutes once every 2 or 3 days with demonstrators that were fed one of two roughly equipalatable diets (Diet Cin or Diet Coc) and were then allowed to choose between Diet Cin and Diet Coc for 23 hours per day. As Figure 3 shows, the observers exhibited preferences for their respective demonstrators' diets that were maintained for weeks. Similarly, observers briefly exposed on several occasions to demonstrators that had been fed an inherently unpalatable cayenne pepper-flavored diet exhibited a substantially enhanced preference for that diet (Galef, in press). In sum, socially induced enhancement of food preferences occurs under a broad range of conditions, is of substantial magnitude, can last for considerable periods of time, and can mitigate effects of other major determinants of diet selection, such as palatability (Galef, 1986b; Galef, in press).

THE NATURE OF MESSAGES PASSING FROM DEMONSTRATORS TO OBSERVERS

Implication of olfactory signals

One obvious question arising from the results described above is, How does an observer rat acquire information from a demonstrator that allows it to identify the diet its demonstrator has eaten? We have developed several converging lines of

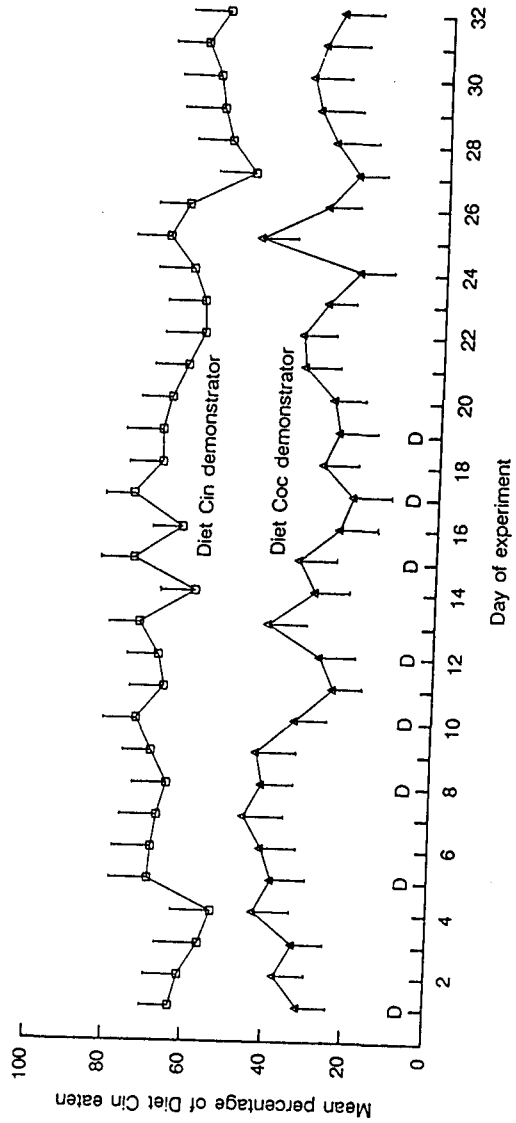


FIGURE 3. Mean amount of Diet Cin eaten daily by observers interacting with demonstrators fed either Diet Cin or Diet Coc, as a percentage of the total amount of food ingested. D = 30-minute exposure to a demonstrator. Flags = ± 1 SEM. (From Galef, in press.)

evidence, each consistent with the hypothesis that olfactory cues passing from demonstrator to observer suffice to allow observers to identify their respective demonstrators' diets.

To examine the mode of communication of information from demonstrator to observer, we had to gain some control over their interaction. We performed three experiments using a procedure similar to that illustrated in Figure 1, but with one important modification: during the part of the experiment in which the demonstrator and observer interact after the demonstrator has eaten (Step 4) they were held on opposite sides of the screen partition. As can be seen in Figure 4, the observers nevertheless developed a preference for their respective demonstrators' diets. However, as can also be seen in Figure 4, when the screen barrier separating demonstrator and observer was replaced by a Plexiglas barrier, the

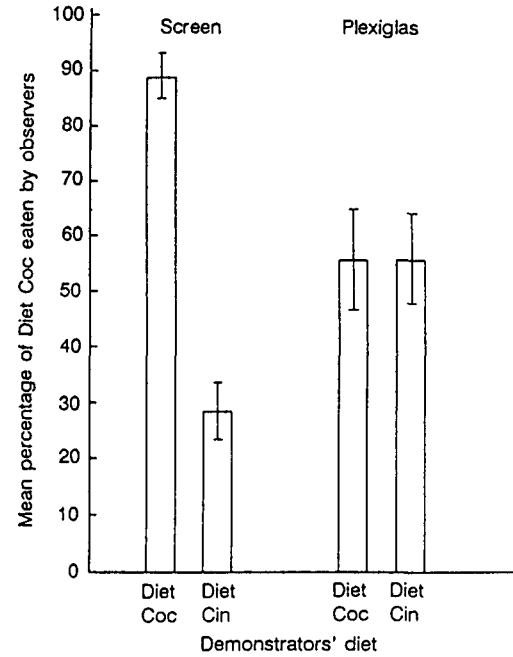


FIGURE 4. Mean amount of Diet Coc ingested, as a percentage of the total amount of food eaten by observers whose demonstrators ate Diet Coc or Diet Cin. Left: Observer and demonstrator separated by a screen barrier during interaction. Right: Observer and demonstrator separated by a Plexiglas partition during interaction. (From Galef & Wigmore, 1983.)

influence of demonstrators on the later diet preference of their respective observers was completely abolished (Galef & Wigmore, 1983). Thus, it was concluded that some sort of nonvisual contact between demonstrator and observer is necessary for successful communication to occur.

We conducted another experiment in which each demonstrator, after eating either Diet Cin or Diet Coc, was anesthetized and placed 2 centimeters from and facing the screen partition dividing the cage, with its observer on the other side of the screen. During the subsequent preference test (Figure 5), observers still exhibited a robust preference for their respective demonstrators' diets (Galef & Wigmore, 1983). Clearly, the signal passing from demonstrator to observer did not require physical contact between them.

On the other hand, as one would expect if olfactory cues play an important role in information transfer between demonstrator and observer, observers rendered anosmic by passing zinc sulfate solution through their nares (Alberts & Galef, 1971) failed to exhibit a preference for their demonstrators' diets (Galef & Wigmore, 1983). Control rats, whose nasal passages had been rinsed with saline solution, continued to exhibit a preference for their demonstrators' diets (Figure 6).

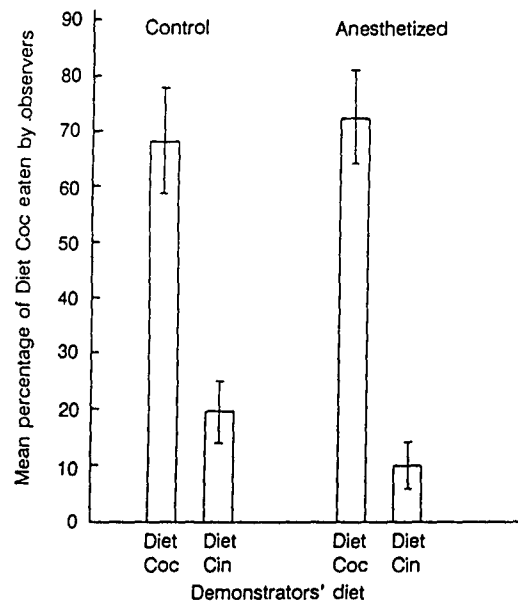


FIGURE 5. Mean amount of Diet Coc eaten by observers as a percentage of the total amount of food ingested. Left: Observers interacting with intact demonstrators. Right: Observers interacting with anesthetized demonstrators. (From Galef & Wigmore, 1983.)

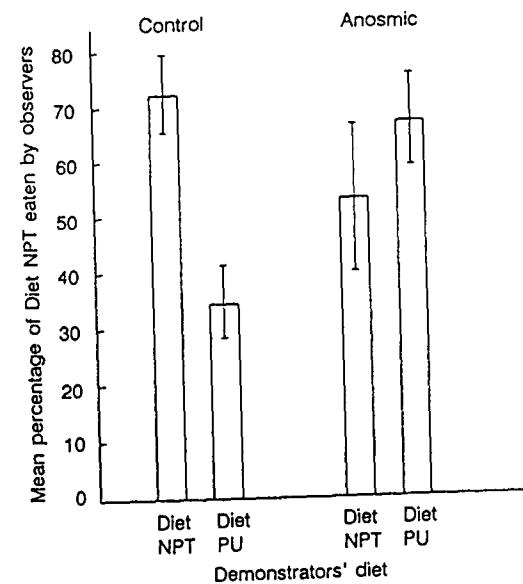


FIGURE 6. Mean amount of normal protein test diet (Diet NPT) ingested, as a percentage of total amount of food eaten, by observers whose demonstrators ate either Diet NPT or Diet Pu (Purina Laboratory Rodent Chow). Left: Observers' nasal cavities rinsed with saline. Right: Observers' nasal cavities rinsed with $ZnSO_4$, i.e., anosmic observers. (From Galef and Wigmore, 1983.)

Last, but not least, we found that humans can use olfactory cues emitted by a recently fed rat to determine which diet a rat has recently eaten. A human observer presented with a dozen rats in random order, half previously fed Diet Coc and half previously fed Diet Cin, could, by sniffing their breath, tell with better than 85 percent accuracy which rat had eaten which diet (Galef & Wigmore, 1983). The above results are all consistent with the view that olfactory cues passing from demonstrator to observer play an important role in communication between them.

CAUSES OF DEMONSTRATOR INFLUENCE ON OBSERVER DIET PREFERENCE

The simple familiarity hypothesis

One simple explanation of the influence of demonstrator rats on their respective observers' diet choices derives from the observation that rats are often somewhat hesitant to ingest an unfamiliar food (Barnett, 1958b; Galef, 1970). During

interaction with a demonstrator rat that has eaten an unfamiliar food, an observer rat is exposed to olfactory cues associated with the food, and should, subsequently, be at least slightly familiar with it. Consequently, an observer rat that has interacted with a demonstrator fed an unfamiliar food should eat that food in preference to an equipalatable, but totally unfamiliar, diet. Demonstrator influence on observer diet preference could thus be explained as the result of a simple increase in the familiarity of observers with the odor of diets fed to their respective demonstrators.

We have carried out a number of experiments designed to test the adequacy of explanations of demonstrator influence on observer diet preference in terms of demonstrator-induced diet familiarity of the sort described above (Galef, in press; Galef, Kennett, & Stein, 1985; Galef & Stein, 1985). In every case, the results of our studies have been contrary to the most straightforward predictions made on the basis of the simple familiarity hypothesis.

For example, I recently completed a study (Galef, in press) in which individual rats were given access to bowls containing either Diet Cin or Diet Coc for 30 minutes per day for 5 consecutive days (Days 1–5 in Figure 7). For the remaining 23½ hours of each day, each subject was offered a choice between Diet Cin and Diet Coc. As Figure 7 shows, five 30-minute periods of simple exposure to either Diet Cin or Diet Coc had no effect on subjects' diet preferences. Next, following two days on which all subjects were simply offered the choice of Diets Cin and Coc (Days 6 and 7 of the experiment), each subject was exposed to a demonstrator that had eaten either Diet Cin or Diet Coc. On each of the final three days of the experiment (Days 8, 9, and 10), each subject that had previously been exposed to Diet Cin for 30 minutes per day was allowed to interact for 30 minutes per day with a demonstrator that had just eaten Diet Coc. Conversely, each subject that had been exposed to Diet Coc was allowed to interact for 30 minutes per day with a demonstrator that had eaten Diet Cin. All subjects continued to be tested for their preferences between Diets Cin and Coc for the remaining 23½ hours of each day. As can be seen in Figure 7, interaction with a demonstrator that had eaten a diet profoundly affected the food preferences of subjects, even after they had been eating both diets offered in the preference test for 7 days. Clearly, simple exposure to a diet and exposure to conspecifics that have eaten a diet can have very different effects on diet preference.

The contextual hypothesis

An obvious alternative to the "simple familiarity hypothesis" is the hypothesis that observers' exposure to diet-related cues within a context provided by the presence of a demonstrator is necessary if brief olfactory exposure to diet-related cues is to alter an observer's subsequent diet preference. It is this "contextual hypothesis" that has been guiding our recent research:

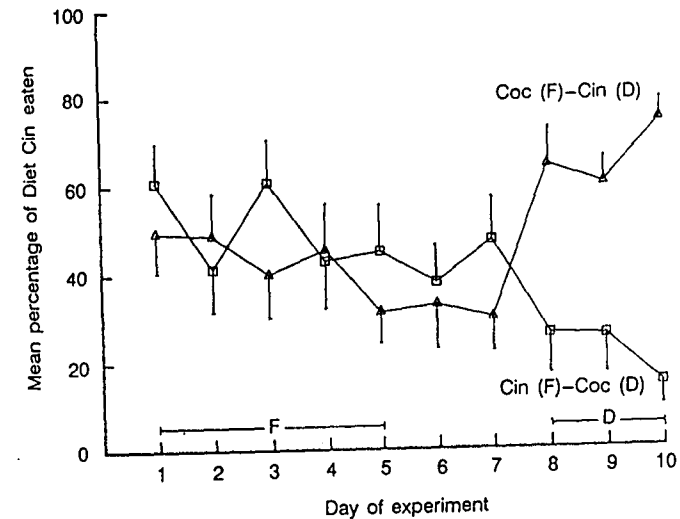


FIGURE 7. Mean amount of Diet Cin eaten daily by subjects during the 23½-hour period of choice as a percentage of total amount of food they ate each day during the choice test. Cin F–Coc D = Subjects first exposed to Diet Cin, then allowed to interact with a demonstrator fed Diet Coc. Coc F–Cin D = Subjects first exposed to Diet Coc, then allowed to interact with a demonstrator fed Diet Cin. F = 30-minute daily exposure to food. D = 30-minute daily exposure to a demonstrator. Flags = ± 1 SEM. (From Galef, in press.)

Let us assume, for the sake of argument, that I am correct in suggesting that the effects of demonstrator rats on the subsequent food preferences of observers are the result of the observers experiencing the smell of the diet within an olfactory context provided by the presence of the demonstrator. If so, then analysis of the olfactory message passing from demonstrator to observer can be treated as two separate questions: (1) What are the sources of the diet-related cues emitted by a demonstrator that permit an observer to identify its demonstrator's diet? (2) What are the contextual cues, also emitted by a demonstrator, that act in concert with the diet-related cues to alter an observer's subsequent diet preferences?

We have found (Galef & Stein, 1985) that both particles of food clinging to the fur and vibrissae of a rat and olfactory cues escaping from the digestive system of a rat are sufficient to permit observers to identify a food their respective demonstrators have eaten (Galef, Kennett, & Stein, 1985; Galef & Stein, 1985). We have been able to exploit the first of these findings to investigate both the

source and the chemistry of the contextual cues that cause observers to prefer a diet.

To look more closely at the contextual cues involved in demonstrator influence on observer diet preference, we again changed our experimental procedure slightly. The new procedure was similar to the basic experiment described above, but differed both in the way demonstrators were made to emit diet-related cues and in the treatment of demonstrators and observers during the period of their interaction. Rather than feeding the demonstrators, as is done in Step 3 of the basic procedure, we anesthetized them and dusted them with either Diet Cin or Diet Coc, and, instead of permitting demonstrator and observer to interact freely, as during Step 4 of the basic experiment, each anesthetized demonstrator was placed in the screen tube of the apparatus depicted in Figure 8. The observer was then introduced into the bucket-shaped portion of the apparatus, left there for 30 minutes, then moved back to its home cage for testing.

We allowed observers to interact in the apparatus illustrated in Figure 8 with demonstrators treated in four ways. Observers in the *powdered-face group* interacted with anesthetized demonstrators whose faces had been rolled in either Diet Cin or Diet Coc. Observers in the *dead powdered-face group* interacted with demonstrators that had been sacrificed by anesthetic overdose and had then had their faces rolled in either Diet Cin or Diet Coc. Observers in the *powdered-rear group* interacted with anesthetized demonstrators whose rear ends had been powdered with either Diet Cin or Diet Coc and that were then introduced into the screen tube with their rear ends inside the bucket and their heads outside of it. Last, observers in the *surrogate group* interacted with a rat-sized, cotton batting-stuffed length of tubular gauze, one end of which had been rolled in either Diet Cin or Diet Coc, and which was then placed in the screen tube.

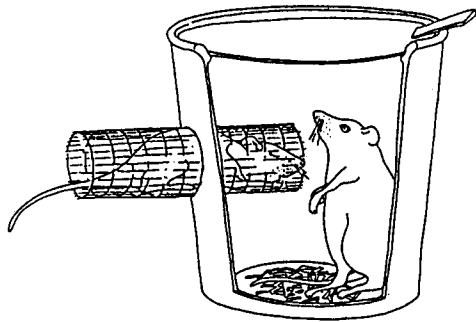


FIGURE 8. Apparatus used to investigate contextual olfactory cues. (From Galef & Stein, 1985.)

Figure 9 presents a measure of the degree of influence of the various sorts of demonstrators on their respective observers' subsequent diet preferences during testing. The greater the Coc-demonstrator:Cin-demonstrator ratio of a group in Figure 9, the greater the influence of demonstrators' diets on their observers' subsequent diet preferences (see Galef & Stein, 1985, for a detailed explanation of the calculation of Coc-demonstrator:Cin-demonstrator ratios).

To summarize the results of a series of statistical analyses presented in detail elsewhere (Galef & Stein, 1985), we found that observers in the powdered-face group preferred to eat the diet applied to the faces of their respective demonstrators, while observers in the surrogate group exhibited no tendency to select the diet with which their "demonstrators" had been powdered. The diet choices of observers in both the dead powdered-face and powdered-rear groups were significantly less affected by their demonstrators than were the diet choices of observers in the powdered-face group, and were significantly more affected by their demon-

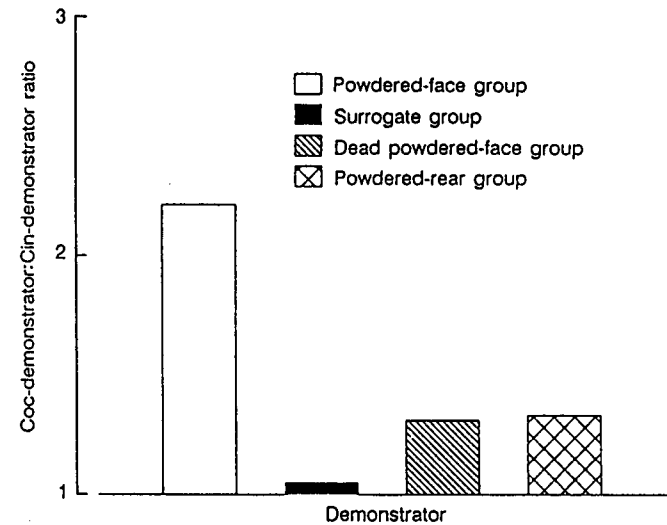


FIGURE 9. Diet Coc demonstrator:Diet Cin demonstrator ratios of groups of observers interacting with demonstrators and surrogates in the apparatus illustrated in Figure 8. Demonstrators were: powdered-face group = anesthetized rats with faces rolled in Diet Cin or Diet Coc; dead powdered-face group = dead rats with faces rolled in Diet Cin or Diet Coc; powdered-rear group = anesthetized rats with rear ends powdered with Diet Cin or Diet Coc and introduced into the screen tube with rear ends inside the bucket; surrogate group = rat-sized, cotton batting-stuffed gauze rolled in Diet Cin or Diet Coc. (After Galef & Stein, 1985.)

strators than were the diet choices of observers in the surrogate group. Taken together, these findings suggest: (1) that simple exposure of an observer rat to the smell of a particular diet is not sufficient to enhance its preference for that diet, and (2) that the contextual cues emitted by demonstrator rats that produce a preference for a diet in their observers are probably emitted most strongly from the anterior end of live rats.

Identification of the contextual semiochemical

One of the more obvious differences between live, anesthetized rats, which emit contextual cues that alter their observers' diet choices, and dead rats, which do not emit very effective contextual cues, is that the live rats are breathing and the dead rats are not. Similarly, the anterior end of a demonstrator, shown to be effective as a context, emits breath, while the posterior end of a demonstrator, which is relatively ineffective as a context, does not. Therefore, it seemed reasonable to ask whether there might be substances present in rat breath that provide the contextual cues that our data suggest cause the diets eaten by conspecifics to become attractive to observer rats.

Because rats breathe only through their noses, a comparison of the chemical contents of air samples taken from the noses of rats with similar samples taken from the throats of rats should reveal those substances that are unique to rat breath. One could then test the efficacy of substances found in rat breath as contexts. Because volatile sulfur compounds have been implicated as semiochemicals (i.e., chemical signals) in several mammalian species (Albone, Blazquez, French, Long, & Perry, 1986; Bailey, Bunyan, & Page, 1980; Pedersen & Blass, 1981; Singer, Macrides, & Agosta, 1980), we focused our chemical analyses on such compounds. Using mass spectrometric and gas chromatographic techniques (described in detail in Galef, Mason, Preti, & Bean, 1988), we found two volatile sulfur compounds, carbon disulfide (CS_2) and carbonyl sulfide (COS), at concentrations of about 1 part per million, in all samples of air taken from the nasal cavities of rats. We found neither sulfur compound in samples of air taken from the throats of rats.

Of course, the presence of CS_2 and COS in rat breath is not in itself evidence that these substances are semiochemicals playing a role in social influence on diet selection in rats. Our investigations of the efficacy of COS and CS_2 in inducing preference for odors with which they are associated are still few in number, but the results we have in hand are consistent with the hypothesis that CS_2 can play a significant role in altering diet preference in rodents. Because COS is a gas at room temperature, it is a difficult substance to work with, so we have concentrated on examining the possible role of CS_2 , which is a liquid, in guiding diet choice in rodents.

Bean, Galef, and Mason (1988) have reported that, in a simple choice

situation, pellets of laboratory chow moistened with a dilute CS_2 solution were preferred by mice to control pellets moistened with distilled water. Mice ate more CS_2 -moistened pellets than control pellets, and they entered chambers containing CS_2 -moistened pellets more frequently, and spent more time in them, than they did with similar chambers containing water-moistened pellets. The finding that a dilute solution of CS_2 increases the attractiveness of a food to which it is added, though of potential practical importance (Galef & Mason, 1986), is not directly relevant to the question of whether CS_2 played a role in enhancing diet preference in our basic experiment and its variants. In the experiments described in preceding sections, exposure to a food in an appropriate social context increased preference for the food when it was subsequently presented without a social context.

As mentioned in the preceding section, observer rats that interacted with an anesthetized demonstrator whose face had been powdered with a diet subsequently exhibited a preference for that diet. Rats that interacted with a piece of cotton batting powdered with the same diet did not exhibit a preference for it. If CS_2 is a semiochemical able to provide a context within which exposure to a diet enhances subsequent preference for that diet, then observer rats interacting with a piece of cotton batting both powdered with a diet and smelling of CS_2 should exhibit a subsequent preference for the diet with which the piece of cotton batting was powdered. The experiment we conducted to examine this possibility is a bit more elaborate than necessary, but the results are exceptionally clear (Galef, Mason, Preti, & Bean, 1988). Observer rats interacted with one of the following demonstrators: anesthetized rats whose faces were powdered with either Diet Cin or Diet Coc; pieces of cotton batting powdered with either Diet Cin or Diet Coc and moistened with six drops of distilled water; or pieces of cotton batting powdered with either Diet Cin or Diet Coc and moistened with six drops of CS_2 diluted to 1 part per million in distilled water. Each observer was next fed clean samples of Diet Cin and Diet Coc, then poisoned by intraperitoneal injection of 1 percent of body weight 1 percent weight/volume lithium chloride solution (see below for a discussion of the effects of poisoning on food preference). Following a 24-hour period of recovery from toxicosis, each observer was offered a choice between Diets Cin and Coc for 23 hours.

As Figure 10 shows, we found that observers that interacted either with anesthetized demonstrators or with pieces of cotton batting moistened with CS_2 chose to eat the diet with which their demonstrators had been powdered. Observers that interacted with surrogates moistened with water were not influenced by the diet placed on their demonstrators when subsequently choosing between Diets Cin and Coc. Apparently, CS_2 can act, as does the presence of a demonstrator rat, to enhance an observer's subsequent preference for a diet (Galef, Mason, Preti & Bean, 1988). Although not conclusive, the finding that CS_2 exists in rat breath and the finding that CS_2 enhances preference for diets previ-

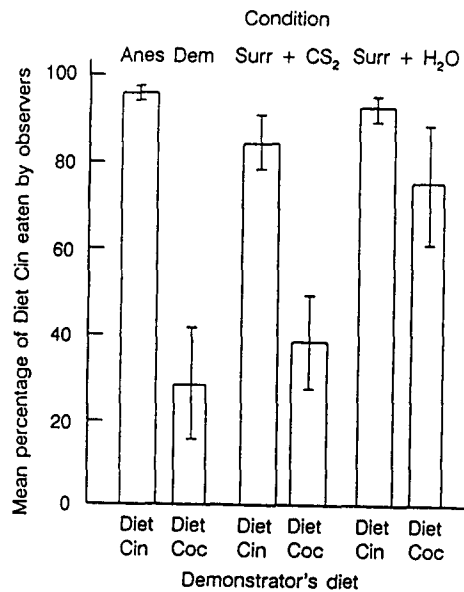


FIGURE 10. Mean amount of Diet Cin eaten, as a percentage of total amount of food ingested during testing, by observers exposed to three types of demonstrators powdered with Diet Cin or Diet Coc. Anes Dem = anaesthetized conspecific; Surr + CS₂ = cotton-batting surrogate moistened with CS₂ solution; Surr + H₂O = cotton-batting surrogate moistened with water. (From Galef, Mason, Preti, & Bean, 1988.)

ously experienced in contiguity with it surely suggest that CS₂ is a semiochemical involved in the social transmission of diet preference in rats.

RELEVANCE TO THE WORLD OUTSIDE THE LABORATORY

In this section, I use data from the laboratory to speculate about how social learning might help rats living outside the laboratory cope with the demands of their environment. Unfortunately, we know relatively little about the characteristics of the environments in which wild Norway rats live today; we know even less about the habitat in which Norway rats evolved. Consequently, the best I can do is to consider environments that appear to be reasonable ones for rats—environments with patchy, unpredictable distribution of foods, a few poisons, some nutrients in short supply, and a large number of ingestible, but non-nutritive, substances present—then speculate about how the behavioral proclivities we have demonstrated in the laboratory might help rats to thrive in such hypothetical environments. Below, I consider three ways in which socially acquired informa-

tion might be used by naive individual rats to increase their feeding efficiency: first, by providing information about where to eat; second, by providing information about what to eat; and third, providing information about what not to eat.

Where to eat?

In introducing our studies on social learning about foods by rats, I mentioned the possibility that the burrow systems of rats might serve as information centers where unsuccessful rats could extract information from their more successful fellows about where to go to find food. A successfully functioning information center, as described by Ward and Zahavi (1973), requires that unsuccessful individuals be able not only to discriminate successful from unsuccessful conspecifics (otherwise it might be a misinformation center), but also to exploit successful conspecifics as sources of information about where food is to be found. In a recent study (Galef, Mischinger, & Malenfant, 1987), we found that rats that were familiar with a maze would reliably, and without special training, follow other rats through the maze to food. We also found that rats trained to follow conspecifics through a maze were more likely to follow those conspecifics that had just eaten a safe food than to follow those conspecifics that had just eaten a food known to the potential followers to be poisonous. Thus, rats in the laboratory exhibit both an eagerness to follow conspecifics to feeding sites and an ability to select conspecifics to follow on the basis of the desirability of the foods those conspecifics have been eating. If successfully foraging rats in the wild behave appropriately (i.e., eat one food at a time, return to a burrow system and interact with conspecifics in the midst of feeding bouts, and allow other rats to follow them), then unsuccessful foragers could use their successful fellows as guides to the foods that both are seeking.

If the distribution of foods in natural circumstances were appropriate, a less complex interaction among individuals might also suffice to establish an information center. Imagine that foods were available intermittently at fixed locations around a rat burrow: table scraps occasionally appeared on a compost heap, chicken scratch was sometimes to be found in a henhouse, oats appeared in a stable. Over time, individual resident rats could learn where each of these foods was sometimes to be found. However, before leaving on its first foraging trip of an evening, an individual rat would not know whether it would find food on a visit to the henhouse or to the stable. If a rat learned from its fellows that they were eating oats, it might be able to figure out where to go to find food.

We introduced our subjects into the environment depicted in Figure 11. Each of three discriminable foods was available at a different, fixed location: cheese-flavored diet (Diet Ch) in the central arm of the maze, cocoa-flavored diet (Diet Coc) in the right arm, and cinnamon-flavored diet (Diet Cin) in the left arm. Only one of the three diets was available to a subject on any given day, and

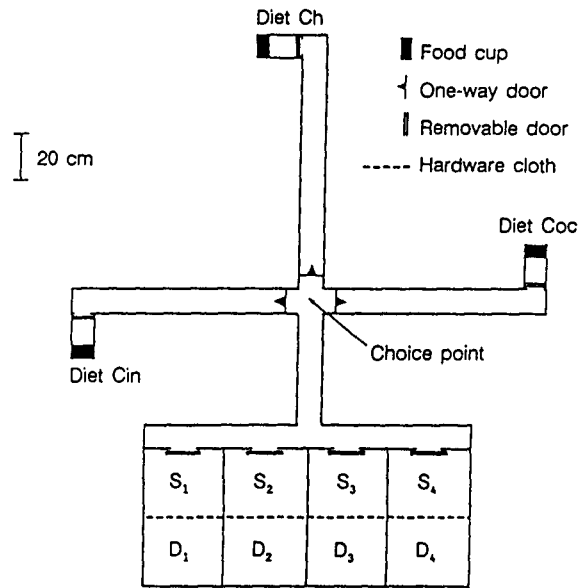


FIGURE 11. Plan of apparatus used in food location experiment. Diet Ch = cheese-flavored diet; Diet Cin = cinnamon-flavored diet; Diet Coc = cocoa-flavored diet. S = subject; D = demonstrator. (From Galef & Wigmore, 1983.)

the particular diet available to a subject on any day was selected randomly. Each subject (S_n in Figure 11) was given four trials per day in the maze using a correction procedure. On the first trial of each day, the subject had no information as to which food was available, and therefore had only one chance in three of selecting the correct arm of the maze. If it chose the correct arm, it was allowed to eat for a few minutes. If it didn't, it was locked in the arm it had chosen for a few minutes, and the trial was repeated until the subject found the food. Trials 2, 3, and 4 of each day were run in the same fashion. Each subject could, in effect, tell us when it understood this little world by exhibiting near-perfect performance in its first choices on trials 2, 3, and 4 of each day.

Once a given subject had reached the necessary criterion of near-perfect performance on trials 2, 3, and 4, we started testing that subject. On each test day, for 15 minutes prior to Trial 1 of that day, each subject was allowed to interact with a demonstrator rat (D_n in Figure 11) that had eaten the diet that was going to be available to that subject on that day. That is, if Diet Ch was going to be available to S_3 on a given day, S_3 's demonstrator, D_3 , was fed Diet Ch for 30 minutes, then allowed to interact with S_3 for 15 minutes prior to Trial 1 of S_3 's testing.

In order to determine whether subjects were capable of using information acquired from demonstrators to enhance their foraging efficiency, we compared the probability of a correct first response on the first trial of each day of testing (when information from a demonstrator was available to subjects) with the probability of a correct first response on the first trial of each of the last days of training (when no information from a demonstrator was available to subjects). As Figure 12 shows, four of our seven subjects were able to use the information provided by their respective demonstrators to facilitate location of unpredictable foods (Galef & Wigmore, 1983). Thus, we can conclude that rats that know where to find food can use their fellows to find out what food is available and can then orient their feeding trips in the appropriate direction. Whether conditions in natural environments are often appropriate for use of this ability to enhance foraging efficiency, I do not know.

What to eat?

A classic problem in experimental psychology concerns how omnivorous mammals can select a nutritionally adequate diet from among the myriad of available substances that they might try to eat. Based on some not very convincing evi-

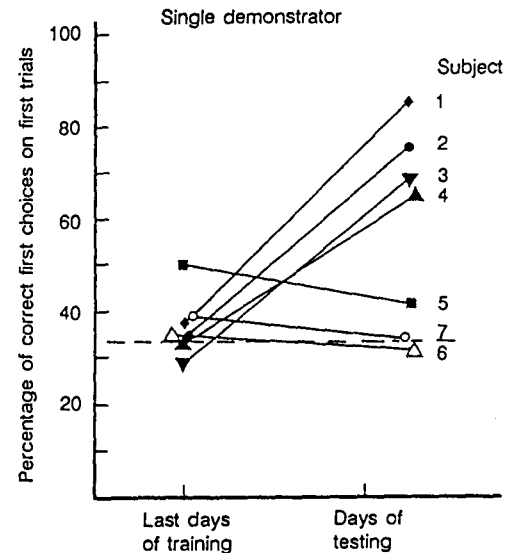


FIGURE 12. Percentage of correct first choices on first trials by subjects at the end of training and during testing in the apparatus illustrated in Figure 11. (After Galef & Wigmore, 1983.)

dence (see Galef & Beck, in press, for discussion), there seems to be a general belief that omnivores such as rats have an almost mystical ability to select foods containing needed nutrients. The fact is, however, that although rats in special situations can find a nutritionally adequate diet if one is available, the ability of rats to do so is actually quite limited (Epstein, 1967). Rats do quite poorly in choosing an adequate food if the number of foods to choose among is more than two or three, if the adequate diet is less palatable than deficient alternatives, or if relief of a deficiency state is considerably delayed after eating an adequate diet.

In a recent experiment, Matthew Beck (Beck & Galef, in press) presented individual weanling rats with a choice among four distinctively flavored diets. Three of these diets contained inadequate levels of protein (5 percent), and one diet (the least palatable of the four) had ample protein to support normal growth (20 percent). We found, as others had before us (Kon, 1931; Scott, Smith, & Verney, 1948; Scott & Quint, 1946; Tribe, 1954, 1955), that our subjects did poorly in this situation. None was able to develop a preference for the diet with adequate protein; in fact, the pups would have been well on their way to a premature demise if we had not stopped the experiment. However, weanling rats faced with the same diet selection problem while in the presence of adults that had been trained to eat the protein-rich alternative grew rapidly in the experimental situation. As can be seen in Figure 13, which shows the rate of weight gain of weanling rats with and without adult demonstrators, the learned patterns of diet selection of adults served as a useful source of information to naive juveniles.

What not to eat?

New recruits to a population, whether recent immigrants or naive juveniles, must not only select adequate foods, but must also avoid ingesting toxic foods present in the area in which they are learning to forage. A new recruit could "assume" that any living conspecifics it might encounter had not eaten a lethal quantity of any poisonous food present in their shared environment. Naive individuals could also assume that senior colony members had already learned to avoid eating any noxious nonlethal substances found in the vicinity. The same tendency to eat what others of one's social group are eating that we have found to facilitate the selection of a nutritionally adequate diet could also lower the probability of eating toxins.

Information acquired from conspecifics as to which foods they were eating could also be used in other, more sophisticated ways to facilitate poison avoidance. For example, a naive rat that ate two unfamiliar foods in rapid succession and then became ill might be well advised to act as though its illness was attributable to whichever of the two unfamiliar foods it had eaten that others of its social group were not eating. As was shown by the behavior of observers interacting with anesthetized demonstrators (see Figure 10), that is just how naive

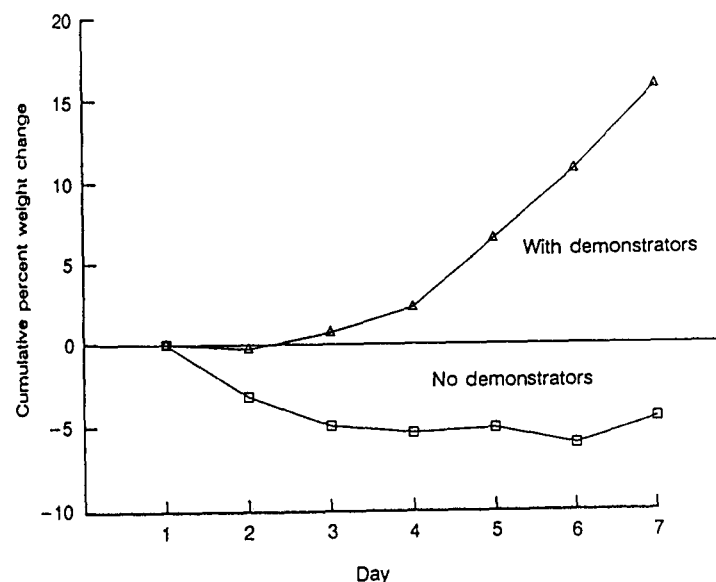


FIGURE 13. Mean cumulative weight gain of pups choosing among four diets in isolation and in the presence of trained demonstrators, as a percentage of the pup's body weight at the start of the experiment. (After Beck & Galef, in press.)

rats do behave (see also Galef, 1986b, 1986c). Naive rats that fall ill are less likely to acquire or maintain an aversion to an unfamiliar food if they have interacted with other rats that have eaten that unfamiliar food than if they have not. Thus, social learning might contribute to the development of adaptive dietary repertoires by guiding the learning of aversions. Of course, such a process would only be useful if rats encounter palatable, toxic foods in their natural habitat (Domjan & Galef, 1983), if they tend to ingest several palatable, toxic foods in rapid succession (a matter of some controversy), and if the dietary habits of others really are a reliable guide to safe and nutritious foods.

CONCLUSIONS

The results of the studies described above indicate that interactions among Norway rats can have important influences on both diet selection and foraging. In the laboratory, olfactory cues emitted by recently fed demonstrator rats permit observer rats to identify the foods that the demonstrators have eaten and cause the observers to increase their later intake of the food that their respective demonstra-

