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Social Factors in Diet Selection and Poison Avoidance by Norway Rats: A Brief Review

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I. INTRODUCTION

Study of the behavior of individual omnivores as they choose among foods of differing nutritive value has been an active area of research in psychobiology for more than 50 years. During that half-century, considerable progress has been made in identifying behavioral processes that contribute to an individual's ability to compose a nutritionally balanced, safe diet by choosing appropriately among a number of different substances. Congenital flavor preferences (Young, 1959, 1968), specific hungers (Richter, 1956), learning about the positive and negative consequences of eating various foods (Garcia and Koelling, 1966; Zahorik and Maier, 1969; Rozin, 1976; Booth, 1985), patterned sampling of foods (Rozin, 1969), and hesitancy to eat unfamiliar foods (Barnett, 1958) have all been implicated in adaptive diet selection by animals.

   In general, redundancy in the processes that can lead to the accomplishment of a goal indicates that success in achieving that goal makes an important contribution to fitness, and animals are usually very proficient at achieving those goals that increase their probability of survival and reproduction. Hence, the observed

redundancy in the behavioral processes that influence individual omnivores to choose adaptively among potential foods suggests, in itself, that such choices tend to be made wisely. It is, consequently, not surprising to find that many psychobiologists, not specialists in the study of diet selection, have formed the general impression that individual omnivores are very good at deciding which foods to eat and which to avoid eating.

This generally held view, that animals acting independently are proficient at selecting appropriate substances to eat, poses a problem for discussions of the role of social influence in diet choice by animals. If, as the literature suggests, the development of adaptive patterns of diet choice by animals can be understood fully in terms of the responses of individuals acting in isolation, then discussion of social influences on diet selection is an unnecessary elaboration. That is, there is little point in talking about social contributions to the development of adequate feeding repertoires in omnivores if each omnivore is perfectly capable of deciding for itself what to eat.

The main argument of the present chapter is that animals acting individually are, in fact, not nearly so good at selecting nutritionally balanced, safe diets as most discussions of food choice published during the past half-century would lead the unwary to conclude. Because individuals are far from perfect in their choice of substances to eat, socially acquired information can often play a critical role both in permitting naive rats to identify nutritive substances and in allowing the naive to determine which, if any, of the substances that they have eaten are toxic and should not be eaten again.

In Sections II and III I focus on data that suggest that individual animals have considerably greater difficulty than generally is appreciated both in selecting balanced diets and in avoiding ingestion of lethal quantities of toxins. In Section IV, I review briefly some of the evidence that indicates that interaction of naive individuals with more experienced others can help the naive both to select nutritive foods and to identify potential toxins.

The discussion of the literature on diet choice that comprises Sections II and III is not intended to suggest that earlier explanations of food choice by free-living animals are in any sense wrong. Congenital flavor preferences (Young, 1959, 1968), responses to novelty (Barnett, 1958), specific hungers (Richter, 1956), and learning about the positive or negative consequences of eating various substances (Garcia and Koelling, 1966; Zahorik and Maier, 1969; Rozin, 1976; Booth, 1985) are each important contributors to the making of adaptive food choices. Rather, it is my view that previous discussions of how free-living omnivores come to select the foods they eat are incomplete. These discussions are incomplete because they fail to take sufficiently into account the effects of social influence on diet choice, though, of course, passing mention of possible social influences on adaptive patterns of food selection is as old as the field itself (see, e.g., Dove, 1935; Richter, 1942–1943).

II. HOW GOOD ARE ANIMALS AT SELECTING A NUTRITIONALLY ADEQUATE DIET?

In a series of classic studies conducted in the 1930s and 1940s, Curt Richter (1942–1943) introduced naive, nondeprived, adult rats into a "cafeteria" setting in which each subject was presented with an array of relatively pure nutrients from which to compose a diet. Richter found that subjects in his cafeteria feeding situation selected substances to eat and drink with great efficiency. His subjects grew both faster and with lower caloric intake than did control subjects eating the McCullum diet (a nutritionally adequate diet compounded by nutritionists). The efficiency of Richter's subjects in self-selecting foods in a cafeteria led Richter (1942–1943) to speak of a "total self-regulatory" capacity, allowing rats to precisely control their intake of various micro- and macronutrients so as to optimize their efficiency of resource utilization.

The observed ability of animals to select a balanced diet by self-selecting from an array of relatively pure constituents in a laboratory cafeteria came as no surprise. Richter argued that the result was predictable from the simple observation that omnivores survive in natural habitat: "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 [to make dietary selections which are conducive to normal growth and reproduction]" (Richter et al., 1938, p. 734).

Unfortunately, Richter's assertion is too broad. The observation that omnivores survive outside the laboratory provides no evidence that they can construct nutritionally adequate diets from purified dietary components. In fact, survival outside the laboratory tells one little about the ability of omnivores to select the foods they need. Perhaps free-living omnivores can survive only in a relatively restricted range of environments where palatable, nutrient-rich foods are abundant. One cannot deduce a general ability to select foods with great efficiency from the fact of survival in nature.

Whether logically compelling or not, the success of Richter's subjects in his cafeteria feeding situation, taken together with the suggestion that this success was only a limited demonstration of the ability of omnivores to select appropriate substances to ingest in natural environments (after all, Richter's cafeteria contained no useless or harmful substances), had profound influence. For decades, the notion that both animals and humans had the ability to totally self-regulate their nutrient intake guided both the design of experiments and the interpretation of data.

The power of Richter's conception of total self-regulatory behavior to hold the scientific imagination is illustrated by publication, as recently as 1987, in the prestigious *New England Journal of Medicine,* of a paper (Story and Brown, 1987) that simply states that 50 years ago, Clara Davis, an early nutritionist,

neither showed nor claimed to show that children could self-select a well-balanced diet from a cafeteria of purified nutrients. Davis (1928, 1939) presented children with an array of highly nutritious foods among which to choose. Her subjects could hardly have failed to select adequate diets so long as they showed some variability in their food choices. As Davis stated explicitly in 1939 (and Richter seems to have failed to appreciate), the success or failure of subjects in a cafeteria feeding situation depends on the particular array of foods offered to them to choose among (Galef and Beck, 1990).

Even in the 1940s, when Richter was completing his studies of diet selection by rats in cafeteria feeding situations, there was reason to question the generality of his finding of efficient diet choice by rats faced with a cafeteria of foods. The majority of early studies of diet selection failed to confirm Richter's observation of efficient self-selection by rats (Lát, 1967). Richter attributed the negative findings in the literature of his day to "the complex nature of the natural foods or food mixtures offered for choice" (Richter et al., 1938, p. 176); it might have been more accurate to attribute the relatively infrequent, great success of rats in some cafeteria situations to the provision of particularly felicitous combinations of foods for rats to choose among. Epstein (1967), for example, has suggested that availability of multiple sources of protein and the presence of a carbohydrate of low palatability were responsible for the success of rats in the particular cafeteria Richter used in his studies of total self-selection.

The range of environments in which individual omnivores can succeed in self-selecting adequate diets was and is far more restricted than Richter realized. If the number of foods among which rats must choose is greater than two or three (Harris et al., 1933), if the consequences of eating particular substances are not felt for many hours (Harris et al., 1933), if important nutrients (particularly proteins) are available only in a relatively unpalatable form (Kon, 1931; Scott, 1946), then the ability of individual rats to self-select a balanced diet from among "a great variety of beneficial, useless, and even harmful substances" is not impressive. The data are not presently and have never been consistent with the view that individual adult animals are exceptionally capable of composing nutritionally adequate diets by choosing among an array of foods.

One might wish to argue that, although not perfect at composing balanced diets, adult rats are still pretty good at choosing foods to eat. It's really a matter of opinion as to whether the performance of a subject surviving in a cafeteria situation is "good" or "bad," since no a priori probability of success has ever been calculated. There can be no question, however, that weanling rats perform abysmally in cafeteria feeding situations. Weanlings fail to choose adequate diets even in situations where adults do reasonably well. For example, Tribe (1954, 1955) presented fifteen 100 g, female rats with seven foods. Thirteen solved the problem and grew almost normally; only 2 of 10 weanling rat pups survived in the same situation. Scott et al. (1948) offered twenty 12- to 15-week-old rats a choice among but four foods. Thirteen of these 20 sexually mature individuals gained

weight, and all lived; only 9 of 31 weanlings survived in the same situation. Kon (1931) offered four 28-day-old rats three foods to choose among, supplemented by hand-fed vitamins; two of the four weanlings died and one gained no weight for 7 weeks.

Such failures of weanlings to self-select adequate diets in situations far simpler than those one might expect them to face outside the laboratory seem to me to be of particular importance in understanding the behavioral processes responsible for the development of adequate feeding repertoires in natural circumstances. It is at weaning that young rats, or other young mammalian omnivores, must undertake the potentially arduous task of developing de novo a diet of independently acquired foods adequate to support growth and development. An adult may be challenged from time to time by failure of one or another of the resources on which it has come to depend. Every weanling must respond to the withdrawal of its major source of sustenance and the need rapidly to develop a nutritionally adequate, safe diet composed of substances selected from among a plethora of available ingestables. Yet, rat pups consistently fail to solve diet-selection problems in the laboratory that must be considerably simpler than those they face in natural circumstances. This failure of weanling rats to self-select a balanced diet suggests that the cafeteria feeding experiment, the presumed laboratory analogue of diet selection in nature, fails to capture some important aspect of the process of learning to select a balanced diet as such learning occurs outside the laboratory.

III. CAN INDIVIDUAL RATS AVOID TAKING LETHAL QUANTITIES OF TOXIC BAITS?

Rats selectively associate tastes with gastrointestinal malaise (Garcia and Koelling, 1967). They tolerate very considerable delays between tasting a novel substance and experiencing illness and still form an aversion to the taste of the novel substance (Garcia et al., 1966). In the literature, both these proclivities have been discussed frequently as adaptive specializations of general Pavlovian conditioning processes modified in the service of poison avoidance (Seligman, 1970; Rozin and Kalat, 1971; Shettleworth, 1983; but see Logue, 1979; Revusky, 1977; Domjan, 1980; Domjan and Galef, 1983).

If rats are adaptively specialized to learn to associate tastes with toxicosis, then by implication rats should be good at avoiding ingestion of lethal quantities of any toxic substances they encounter. Indeed, review of the psychological literature suggests that because each rat has available a variety of behavioral tactics that can decrease its probability of ingesting lethal quantities of poisons, killing free-living rats by poisoning them is a formidable task. Consequently, it was somewhat surprising to me to find that although total extermination of a rat population by poisoning is difficult, it is not unusual for professional exterminators to kill 80–90% of a target population by introducing a poison bait into a rat-infested area (Meehan, 1984). Often, even quite unsophisticated application of a poison bait

will suffice to kill the majority of a target population of rodents. For example, Chitty (1954), working during the war years at Oxford, found that poison baits that were introduced without prebaiting into the home ranges of censused colonies of wild rats typically caused the death of 75% of colony members. Chitty had no evidence that surviving rats in his studies had learned to avoid the poison bait; perhaps some individuals found the bait unpalatable, were exceptionally reluctant to eat unfamiliar food, or simply failed to encounter the poison. Poison-avoidance learning may be even less successful in protecting rats against introduced poisons than Chitty's (1954) data suggest.

By increasing the probability that rodents will consume a lethal quantity of poison before toxicosis is experienced (e.g., by using palatable poison baits, by using rodenticides that are both lethal in small amounts and have delayed onset of symptoms, by "prebaiting," etc.), it is possible to create an environment in which individual rodents have low probabilities of survival. Of course, if one's goal is complete extermination of a population, escape of even one pregnant female means failure of the extermination effort.

Ingestion of lethal doses of toxins by animals is also observed in the case of poisons other than those specifically composed by humans to kill pests. Naturally occurring toxins, like man-made poisons, kill large numbers of mammals. For example, each year the American cattle industry loses an estimated 3–5% of its total herd to poisonous plants, particularly halogeton, larkspur, lupine, and loco-weed (James, 1978). Naturally occurring poison baits, like their man-made counterparts, are not easily avoided by animals that encounter them.

In sum, the abilities of animals either to self-select a balanced diet or to avoid eating toxins are not so highly evolved as to preclude a meaningful contribution of socially acquired information to decisions about what to eat and what to avoid eating. There exists, at the least, the logical possibility of important social contributions to the development of adaptive patterns of selection and rejection of foods by animals foraging outside the laboratory.

IV. SOCIAL SOLUTIONS TO THE PROBLEM OF SELECTING NUTRITIONALLY ADEQUATE, SAFE DIETS

One invariant feature of the environment in which each mammal develops, if it survives to weaning age, is the presence of a conspecific adult, a dam, who by her very existence and reproductive success has demonstrated both the nutritional adequacy and safety of her diet. No matter how slow or inefficient individual adults might be at learning either to avoid toxins or to identify sources of requisite nutrients, a juvenile could be reasonably sure that its dam (or any other surviving adult it encountered) had not eaten seriously injurious quantities of debilitating substances and had located sources of all those nutrients necessary for growth and survival. Most important, a juvenile could be reasonably sure that sympatric adults had composed a nutritionally adequate, safe diet in the same geographical

area in which the juvenile had to achieve nutritional independence. "Eat what adults are eating, do not eat what adults are not eating" could serve as a useful rule of thumb to juvenile members of any species living in a reasonably stable environment (Boyd and Richerson, 1985).

Of course, the fact that young omnivores could benefit from using adult conspecifics as guides to what to eat and what not to eat does not mean that they do so. It is an empirical question whether young mammals can, in fact, exploit their elders as sources of information about foods.

For 20 years, my students, co-workers, and I have been studying the ways in which naive, developing individuals can incorporate the behavior of more knowledgeable others into their own behavioral repertoires. We have found, in a broad range of circumstances, that the food choices of young rats are profoundly influenced by the food choices of the adults with whom the young interact. In the present section, I review briefly some of the major findings of this research program to illustrate the many ways in which social interactions can facilitate the development of adaptive dietary repertoires by weanlings (for more complete reviews see Galef, 1977, 1982, 1985a, 1986a, 1989a, 1989b; Galef and Beck, 1990).

The original impetus for examining the possibility that weanling Norway rats might use information garnered from adult conspecifics in developing their own feeding repertoires arose from field observations made by Fritz Steiniger, an expert in the control of rodent pests. Steiniger (1950) reported that if he continued to use one poison bait in an area for several months, acceptance of that bait declined dramatically. He observed, in particular, that young rats, born to adults that had learned to avoid a bait, rejected the bait without even sampling it themselves. The young fed exclusively on alternative, safe foods available to their respective colonies.

This avoidance by young wild rats of a food that the adults of their colony had learned to avoid turned out to be a very robust phenomenon, easily captured in the laboratory. In our first experiments (Galef and Clark, 1971a), we established groups of male and female, adult, wild rats (Rattus norvegicus) in 1 × 2 m enclosures. Water was continuously available in the enclosure, and food was present for 3 hours/day in two food bowls placed about 1 m apart. Each food bowl contained one of two, nutritionally adequate diets, discriminable from the other in taste, smell, texture, and appearance.

Adults of each colony were trained to eat one of the foods presented each day and to avoid the other by the simple expedient of introducing a nausea-inducing agent (LiCl) into samples of one of the two foods. The adults rapidly learned not to eat the poisoned food and, most important, for several weeks thereafter, avoided eating the previously poisoned food when offered uncontaminated samples of it.

Our experiments began when litters of pups, born to our trained colonies, left their nest sites to feed on solid food for the first time. We observed both adults and pups throughout daily 3-hour feeding periods on closed-circuit television and

recorded the number of times pups in each colony ate from each food bowl. After members of a litter of pups had fed on solid food for 2 weeks, we transferred them to new enclosures where, now without the adults of their colony, the pups were again offered a choice between uncontaminated samples of the two diets. In this second situation, we could directly measure the amount of each diet eaten by pups during daily feeding periods simply by weighing each of the two food bowls offered to the pups before and after each feeding period.

The results of our manipulations were exceptionally clear. Only 1 of 247 rat pups we watched feed for 2 weeks with adults trained to avoid one diet and eat another ever ate even a single bite of the food that the adults of its colony had been trained to avoid. The other 246 pups fed exclusively on whichever diet the adults of their colony were eating. Furthermore, after transfer to enclosures separate from the adults of their colony, pups continued, for several days, to eat only the food that the adults of their colony had eaten and to avoid the alternative that the adults of their colony had learned to avoid. Taken together, these results demonstrate, as Steiniger's (1950) field observations suggested, that juvenile rats can and will use adults with whom they interact as sources of information about which foods to eat and which to avoid.

My co-workers and I have spent much of the past 20 years identifying and describing four independent ways in which the behavior of adult rats can influence diet selection by their young. Below, I review each of these four modes of social influence briefly before turning to consideration of evidence that such social influence can lead rats in complex environments away from toxins and toward nutritionally balanced, safe diets.

A. Modes of Social Influence of Adult Rats on Their Young

1. Presence of Adults at a Feeding Site

One of the simplest and, perhaps, less interesting ways in which adult rats can induce naive young to eat one food rather than another is for the adults to eat at one location rather than at another. The presence of adults at a feeding site attracts young to that site and causes them to feed on whatever food is present there. For example, four times as much food was eaten by both 19- and 25-day-old, domesticated rat pups from a food bowl with an anesthetized female rat draped over its rim than from an identical bowl 1 m away (Galef, 1981). Similarly, Clark and I observed each of nine, individually marked, wild rat pups eat their very first meal of solid food in a large enclosure; the young animals ate that meal both while an adult was eating and at the same food bowl from which the adult was eating, not from a second food bowl 1.5 m away (Galef and Clark, 1971b).

2. Deposition of Residual Olfactory Cues

The results of a number of studies indicate that adult rats mark both the area around a food source and a food that they are eating with residual olfactory cues that make the marked site or marked food more attractive to juveniles seeking

food than identical unmarked foods or sites. Galef and Heiber (1976) restricted either mothers and their young or groups of virgin female rats to one end of a 2 × 1 m cage for several days. Then, while these stimulus animals were absent from the cage, food-deprived juveniles were tested individually for 1-hour periods with identical bowls of food at each end of the cage. The young took 70–90% of the food they ate from the end of the enclosure that had been soiled by other rats. Young rats also ate more food from a bowl that an experimenter had surrounded with rat excreta than from a clean food bowl in an unsoiled area (see also Galef, 1981). Galef and Beck (1985), similarly, showed that rats spontaneously mark a feeding site they are visiting, making it more attractive to other rats than an identical, unmarked site.

Though effective in biasing the diet preferences of young in adaptive directions, indirect behavioral mechanisms for communication of food selection such as those described above and in Section IV.A.1 are not very sophisticated. Instances in which adult rats communicate directly to their young information as to what foods should be eaten and avoided are, perhaps, of greater interest.

3. Flavor Cues in Mother's Milk

The results of two sets of studies (Galef and Henderson, 1971; Galef and Sherry, 1973) in my laboratory, as well as a variety of findings from other laboratories (see, e.g., Martin and Alberts, 1979) are consistent with the hypotheses (a) that the milk of a lactating rat contains cues reflecting the flavor of her diet, and (b) that flavor cues in mother's milk influence weanlings' selection of solid foods to eat.

Some of the most convincing evidence of the existence of flavor cues in mother's milk that reflect the flavor of mother's diet came from studies in which rat pups nursing from a female rat fed one diet were made ill by injection of LiCl after having been hand-fed a small quantity of milk that had been expressed manually from a second lactating female eating a different diet. Tests at weaning showed that pups treated in this way had developed a substantial aversion to the diet fed to the lactating female from which the manually expressed milk had been taken (Galef and Sherry, 1973). In the other studies, Galef and Henderson (1972) found that rat pups raised by mothers eating diet B and fostered for 6 hours/day for 18 days to a lactating female eating diet A showed an enhanced preference for diet A at weaning, relative to pups fostered daily to maternal, nonlactating females. Further evidence of transmission of diet cues through mother's milk has been provided by artificially introducing a flavor into the milk of a mother rat (e.g., by intraperitoneal injection) and, thus, causing her pups to exhibit an enhanced preference at weaning for foods of the introduced flavor (Le Magnen and Tallon, 1968; Martin and Alberts, 1979).

4. Olfactory Cues on the Breath of Adult Rats

Galef and Wigmore (1983) and Posadas-Andrews and Roper (1983) discovered independently that after a naive rat (an observer) interacted for a few minutes with

a conspecific that had previously eaten some food (a demonstrator), the observer would show a substantially enhanced preference for the food that its demonstrator had previously eaten. We have made considerable progress in understanding the messages passing from demonstrator to observer that allow demonstrators to influence their respective observers' food choices.

To summarize the results of a complex series of studies, the data suggest that both olfactory cues (Galef and Wigmore, 1983) escaping from the digestive tract of demonstrator rats and the smell of bits of food clinging to their fur are sufficient to allow observers to identify the foods that their respective demonstrators ate (Galef and Stein, 1985). However, simple exposure of observers to the smell or taste of a food is not, in itself, sufficient to enhance an observer's preference for that food (Galef et al., 1985). Observers' preferences for foods are altered by experience of the smell of a food in combination with olfactory cues emerging from the anterior end of a living demonstrator rat (Galef and Stein, 1985). These demonstrator-produced semiochemicals, when experienced by a naive rat at the same time that it experiences the smell of a food, alter the subsequent diet preference of the observer. The semiochemicals produced by demonstrators that increase the preference of observers for a food are probably volatile sulfur compounds (e.g., carbon disulfide, a chemical present on rat breath) that, when added to a food, increase the preference of both rats and mice for that food (Bean et al., 1988; Galef et al., 1988; Mason et al., 1988).

B. Uses of Socially Acquired Information

The evidence reviewed briefly above indicates that rats can be influenced in their choices of either feeding sites or foods by the feeding behavior of other rats. Below, I am concerned with evidence that information garnered by naive rats from more knowledgeable conspecifics can be used by the naive to find nutritionally adequate foods, to avoid toxins, and to forage more efficiently than would be possible in the absence of socially-acquired information.

1. What to Eat

In a recent experiment, Beck and Galef (1988) presented individual weanling rats with a choice among four distinctively flavored foods. Three of these foods contained inadequate levels of protein (4.4%) and one, the least palatable of the four, had ample protein (17.5%) to support normal growth. We found, as had others before us (Kon, 1931; Scott and Quint; 1946; Scott et al., 1948; Tribe, 1954, 1955), that young subjects performed poorly in such a situation. None of our juvenile subjects was able to develop a preference for the protein-adequate food in 6 days; each pup lost weight, and if we had not terminated the experiment when we did, all probably would have died. Weanling rats faced with the same diet selection problem while in the presence of adults previously trained to eat the protein-rich alternative, grew rapidly in the experimental situation.

Analyses of the ways in which trained rats influenced the food preferences of naive, adolescent rats (150–175 g) juveniles showed that the naive rats were

influenced in their food choices by the foods eaten by their respective demonstrators, not by the place where their respective demonstrators ate. In one experiment, we separated naive rats from their demonstrators with a screen partition and, choosing among four food cups (one of which contained the protein-rich diet that the demonstrator was eating and the other three of which each contained a different protein poor diet), allowed each naive rat to interact through the partition with a demonstrator that was given protein-rich diet to eat from a food cup placed adjacent to its observer's food cup, containing a protein-poor diet. The observers ate as much protein-rich diet as did observers whose demonstrators ate protein-rich diet from a food cup placed adjacent to the observer's food cup containing protein-rich diet.

In a situation in which individual, naive rats found it impossible to select a nutritionally adequate diet from among more palatable, but inadequate, alternative diets, the naive rats used information acquired from more knowledgeable conspecifics to identify the adequate diet.

2. Identification and Avoidance of Toxins

New recruits to a population (recent immigrants or naive juveniles) not only must find and ingest nutritionally adequate diets, they also must avoid ingesting any toxic substances they encounter. In the search for needed nutrients, a naive individual might have to sample broadly among unfamiliar, ingestible substances. By sampling one unfamiliar substance at a time and waiting long enough between meals of unfamiliar foods to evaluate independently the postingestional consequences of each (Rozin and Kalat, 1971), a naive individual could evaluate the toxicity of each unfamiliar substance it ingested. There is, however, little evidence that rats actually sample among several unfamiliar foods to permit their independent evaluation. A growing body of evidence suggests, to the contrary, that even wild rats offered several unfamiliar foods to eat often sample most of them during a single, initial bout of feeding on the unfamiliar foods (Barnett, 1956; Beck et al., 1988). Use of information about the foods that others are eating could provide an alternative route for identification of toxic substances by naive individuals, even if the naive individual had eaten more than one unfamiliar substance before falling ill.

Galef (1986b, c, 1987), found that naive rats were less likely to form aversions to foods that other rats had eaten than they were to form aversions to totally unfamiliar foods. Naive "observer" rats, which had the opportunity to interact with a recently fed "demonstrator" rat before eating two unfamiliar foods and becoming ill, learned an aversion to whichever food their respective demonstrators had not eaten (Galef, 1986b, 1987). Furthermore, a substantial portion of rats that had formed an aversion to a diet, as a result of association of that diet with toxicosis, abandoned their aversions following exposure to other rats that had eaten the averted diet (Galef, 1985; 1986c). If, as seems likely, it is usually the case that an unfamiliar substance that others are eating is less likely to be toxic than an unfamiliar substance that others are not eating, then social influences on

taste-aversion learning could be an important source of information as to whether illness was food related and which of several recently eaten foods was most probably illness inducing (Domjan and Galef, 1983, Galef, 1986b, 1987).

3. Where to Eat

Galef et al. (1987) found that rats that were familiar with a maze would spontaneously follow trained rats through the maze to food. They also found that rats trained to follow leader rats through a maze were more likely to follow leaders that had just eaten a familiar, safe food than to follow leaders that had just eaten a food that the potential followers had been trained to avoid. Hungry rats exhibited both a readiness to follow others to feeding sites and an ability to select others to follow on the basis of the desirability of the foods those others had been eating.

Furthermore Galef and Wigmore (1983) have shown that rats that were familiar with the locations at which particular foods were sometimes to be found, but did not know which of several foods was currently available, could use information garnered from a recently fed conspecific to decide where to look for food. After interacting with an "informer" rat that had just eaten cinnamon-flavored diet, a subject rat went to the location where it had previously learned that cinnamon-flavored diet was to be found. After interacting with an "informer" rat that had just eaten cheese-flavored diet, the same subject went to the location where it had previously learned that cheese-flavored diet was to be found. Rats familiar with the location of food patches within their home ranges can find out from others which foods were available and can use that information to orient their foraging trips in profitable directions (Galef, 1983).

V. CONCLUSION

The preceding review leads to two conclusions. First, that rats and, by extrapolation, other omnivores, are not as efficient either at selecting balanced diets or at avoiding repeated ingestion of toxins as is generally believed. Second, that information acquired from others can improve the performance of native rats faced with the need to select a nutritionally adequate diet while avoiding ingestion of poisons. Successful others can serve the naive animal as useful sources of information about where to eat, what to eat, and what to avoid eating.

In discussing the results of her previously mentioned, classic studies of diet selection by human infants, Clara Davis (1939, p. 261) concluded that "the results of the experiment . . . leave the selection of the foods to be made available to young children in the hands of their elders, where everyone has always known it belongs." A similar conclusion can be drawn from the present review of diet selection by rats. Naive, young rats are not generally capable of making appropriate food choices. The selection of foods on which to subsist is better made by their more experienced elders. Elders that either had the misfortune to eat substantial quantities of toxic substances or failed to compose a nutritionally adequate diet die and are not available to serve as behavioral models for juveniles. Other adults,

successful in diet selection, remain in a population and are available to shape the ingestive behavior of succeeding generations.

In effect, living adults increase the availability of the foods they are eating to the young with whom they interact. Living adults attract pups to feeding sites and expose the juveniles to olfactory cues that bias the diet preferences of the young. Adult rats, like adult humans, induce their naive young to eat safe, nutritious foods and reduce the probability of exposure of their young to potentially deleterious substances.

Although, in benign environments, naive individuals probably can compose adequate diets, in less congenial circumstances the naive are often not able to identify either toxic or nutritionally adequate diets fast enough to survive. By acting as though adult others are more likely to be eating nutritious, safe substances than useless substances or toxic ones, the naive can facilitate the development of their own adaptive feeding repertoires. Information acquired from successful others may make the difference between survival and failure for naive weanlings searching for adequate diets among the "great variety of beneficial, useless, and even harmful substances" to be found in natural circumstances.

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DISCUSSION

Rozin: I'm amazed at the power of this effect. It seems that a rat is more affected by one contact with a demonstrator than by one personal experience with a diet being, say, safe or unsafe; so familiarity would have less of an effect than one short exposure to a demonstrator. Now, I'm puzzled as to the adaptive evolutionary significance. It's obvious why it's useful to learn from conspecifics, but it's not obvious why your own experience should be of less value than a roughly equivalent exposure to another animal with all the errors that might occur in the filtration of that to you. My first question is, Why is this so powerful with respect to individual experience? Second, though I agree that you're certainly showing a greater role of social transmission in animals than any of us had thought, it is also true that your own work shows how narrowly defined social transmission is in rats; that is, the context in which social learning occurs is so tightly limited to an exposure in the presence of a particular chemical. In the case of humans, "instruction" is an elaborate social structure to convey things rather than accidental exposure over time. I'm sure you'll agree with that.

Galef: Let me answer the second point first because it's easier to deal with. That just seems to me to be anthropocentric. Rats have this very broad ability to use all kinds of chemical information, whereas we're limited to a single verbal channel in communicating to one another about what to eat. The first question is more difficult. My own view is that wild rats are, as you know, very reluctant to eat unfamiliar foods. What I'm looking at are the situations in which the animal has no information, and is much better off assuming that those who are alive have done the right thing in the past than it is in trying to figure out for itself what's going on. You see, I'm looking always at a situation of the animal being somehow induced to eat unfamiliar things. That's a very dangerous situation for rats; they're very reluctant to do it, as you know. I assume in those situations, indeed evolutionarily, they've been better off attending to live others, because the live others have obviously never made a really serious mistake.

Scott: But you're saying "find an almost dead other," that is, a deeply anesthetized rat.

Galef: It's hard to get into that right now. I believe that the importance of poison avoidance in the life of rats has been exaggerated and that the critical issue for animals is in finding needed nutrients, not in avoiding ingesting toxins.

Kissileff: Is the conditioning stimulus in these experiments always an odor? Will a taste ever work?

Galef: I believe a taste will work. We're going to try to do that next year. We have preliminary data that indicates if a rat is anosmic and interacts with the demonstrator, the observer can still determine what food the demonstrator ate. Possibly, by licking the mouth of the demonstrator.

Kissileff: Wouldn't it be simpler to use a taste as the conditioning stimulus instead of an odor? Then you would be sure that you had completely removed all the olfactory cues.

Galef: Yes, that procedure might work.

Stricker: If the demonstrator had had access to a food and then had been poisoned before giving the demonstrator to the observer and giving the observer that food, would the observer then avoid or eat the food that the demonstrator had consumed?

Galef: You bring up the one great counterintuitive outcome in these experiments. No matter how hard we work at it, and we've tried for three years, we find that a sick demonstrator induces just as much of a preference for a food in its

observer as does a well demonstrator. Returning to Dr. Scott's question, that's one of the reasons why I think this system is designed to tell animals what to eat, and not to tell them what not to eat. That suggests to me that this is a more important problem in the lives of the rats than avoiding toxins.

REFERENCES

Barnett, S. A. (1956). Behaviour components in the feeding of wild and laboratory rats. *Behaviour,* 9:24–42.

Barnett, S. A. (1958). Experiments on "neophobia" in wild and laboratory rats. *Br. J. Psychol.* 49:195–201.

Bean, N. J., Galef, B. G., Jr., and Mason, J. R. (1988). At biologically significant concentrations, carbon disulfide both attracts mice and increases their consumption of bait. *J. Wildl. Manage.* 52:502–507.

Beck, M., and Galef, B. G., Jr. (1988). Social control of diet selection: How do animals find nutritious food? Paper presented at the April meeting of the Eastern Psychological Association, Buffalo, NY.

Beck, M., Hitchock, C., and Galef, B. G., Jr. (1988). Diet sampling by wild Norway rats (*Rattus norvegicus*) offered several unfamiliar foods. *Anim. Learn. Behav.* 16:224–230.

Booth, D. A. (1985). Food-conditioned eating preferences and aversions with interoceptive elements: Conditioned appetites and satieties. *Ann. N.Y. Acad. Sci.* 443:22–41.

Boyd, R., and Richerson, P. J. (1985). *Culture and the Evolutionary Process.* University of Chicago Press, Chicago.

Chitty, D. (1954). The study of the brown rat and its control by poison. In *Control of Rats and Mice,* Vol. 1, D. Chitty (Ed.). Oxford University Press (Clarendon), London, pp. 160–299.

Davis, C. M. (1928). Self-selection of diet by newly weaned infants: An experimental study. *Am. J. Dis. Child.* 36:651–679.

Davis, C. M. (1939). Results of the self-selection of diets by young children. *Can. Med. Assoc. J.* 41:257–261.

Domjan, M. (1980). Ingestional aversion learning: Unique and general process. In *Advances in the Study of Behavior,* Vol. 11, J. S. Rosenblatt, R. A. Hinde, C. Beer, and M.-C. Busnel (Eds.). Academic Press, New York, pp.000–000.

Domjan, M., and Galef, B. G., Jr. (1983). Biological constraints on instrumental and classical conditioning: Retrospect and prospect. *Anim. Learn. Behav.* 11:151–161.

Dove, W. F. (1935). A study of individuality in the nutritive instincts and of the causes and effects of variations in the selection of food. *Am. Nat.* 69:469–544.

Epstein, A. N. (1967). Oropharyngeal factors in feeding and drinking. In *Handbook of Physiology,* Vol. 1, *Alimentary Canal,* C. F. Code (Ed.). American Physiological Society, Washington, DC, pp. 197–218.

Galef, B. G., Jr. (1977). Mechanisms for the social transmission of food preferences from adult to weanling rats. In *Learning Mechanisms in Food Selection,* L. M. Barker, M. Best, and M. Domjan (Eds.). Baylor University Press, Waco, TX, pp. 123–150.

Galef, B. G., Jr. (1981). The development of olfactory control of feeding site selection in rat pups. *J. Comp. Physiol. Psychol.* 95:615–622.

Galef, B. G., Jr. (1983). Utilization by Norway rats (*R. norvegicus*) of multiple messages concerning distant foods. *J. Comp. Physiol. Psychol.* 97:364–371.

✓Galef, B. G., Jr. (1985a). Studies of social learning in Norway rats: A brief review. *Devel. Psychobiol.* **15**:279–295.

Galef, B. G., Jr. (1985b). Socially induced diet preference can partially reverse a LiCl-induced diet aversion. *Anim. Learn. Behav.* **13**:415–418.

Galef, B. G., Jr. (1986a). Olfactory communication among rats of information concerning distant diets. In *Chemical Signals in Vertebrates*, Vol. IV, *Ecology, Evolution, and Comparative Biology*, D. Duvall, D. Muller-Schwarze, and R. M. Silverstein (Eds.). Plenum Press, New York, pp. 487–505.

Galef, B. G., Jr. (1986b). Social identification of toxic diets by Norway rats (*R. norvegicus*). *J. Comp. Psychol.* **100**:331–334.

Galef, B. G., Jr. (1986c). Social interaction substantially modifies learned aversions, sodium appetite, and both palatability and handling-time induced dietary preference in rats (*R. norvegicus*). *J. Comp. Physiol. Psychol.* **100**:432–439.

Galef, B. G., Jr. (1987). Social influences on the identification of toxic foods by Norway rats. *Anim. Learn. Behav.* **15**:327–332.

Galef, B. G., Jr. (1989a). An adaptationist perspective on social learning, social feeding, and social foraging in Norway rats. In *Contemporary Issues in Comparative Psychology*, D. A. Dewsbury (Ed.). Sinauer, Sunderland, MA, pp. 55–79.

✓Galef, B. G., Jr. (1989b). Innovation in the study of social learning in animals: Developmental and biological perspectives. In *Developmental Psychobiology: Current Methodological and Conceptual Issues*, H. N. Shair, G. A. Barr, and M. A. Hofer (Eds.). Oxford University Press, New York.

Galef, B. G., Jr., and Beck, M. (1985). Aversive and attractive marking of toxic and safe foods by Norway rats. *Behav. Neurol. Biol.* **43**:298–310.

Galef, B. G., Jr., and Beck, M. (1990). Diet selection and poison avoidance by mammals individually and in social groups. In *Handbook of Neurobiology*, Vol. 11, E. M. Stricker (Ed.). Plenum Press, New York, pp. 329–349.

Galef, B. G., Jr., and Clark, M. M. (1971a). Parent–offspring interactions determine time and place of first ingestion of solid food by wild rat pups. *Psychonomic Sci.* **25**:15–16.

Galef, B. G., Jr., and Clark, M. M. (1971b). Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. *J. Comp. Physiol. Psychol.* **75**:341–357.

Galef, B. G., Jr., and Heiber, L. (1976). The role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. *J. Comp. Physiol. Psychol.* **90**:727–739.

Galef, B. G., Jr., and Henderson, P. W. (1972). Mother's milk: A determinant of the feeding preferences of weaning rat pups. *J. Comp. Physiol. Psychol.* **78**:213–219.

Galef, B. G., Jr., Kennett, D. J., and Stein, M. (1985). Demonstrator influence on observer diet preference: Effects of simple exposure and the presence of a demonstrator. *Anim. Learn. Behav.* **13**:25–30.

Galef, B. G., Jr., Mason, J. R., Preti, G., and Bean, N. J. (1988). Carbon disulfide: A semiochemical mediating socially-induced diet choice in rats. *Physiol. Behav.* **42**:119–124.

Galef, B. G., Jr., Mischinger, A., and Malenfant, S. A. (1987). Further evidence of an information centre in Norway rats. *Anim. Behav.* **35**:1234–1239.

Galef, B. G., Jr., and Sherry, D. F. (1973). Mother's milk: A medium for the transmission of cues reflecting the flavor of mother's diet. *J. Comp. Physiol. Psychol.* **83**:374–378.

Galef, B. G., Jr., and Stein, M. (1985). Demonstrator influence on observer diet preference: Analysis of critical social interactions and olfactory signals. *Anim. Learn. Behav.* **13**:31–38.

Galef, B. G., Jr., and Wigmore, S. W. (1983). Transfer of information concerning distant food in rats: A laboratory investigation of the "information centre" hypothesis. *Anim. Behav.* **31**:748–758.

Garcia, J., Ervin, F. R., and Koelling, R. A. (1966). Learning with prolonged delay of reinforcement. *Psychonomic Sci.* **5**:121–122.

Garcia, J., and Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Sci.* **4**:123–124.

Harris, L., Clay, J., Hargreaves, F., and Ward, A. (1933). The ability of vitamin B deficient rats to discriminate between diets containing and lacking the vitamin. *Proc. R. Soc. B,* **113**:161–190.

James, L. F. (1978). Overview of poisonous plant problems in the United States. In *Effects of Poisonous Plants on Livestock*, R. F. Keeler, K. R. Van Kampen, and L. F. James (Eds.). Academic Press, New York, pp. 3–5.

Kon, S. K. (1931). LVIII. The self-selection of food constituents by the rat. *Biochem. J.* **25**:473–481.

Lát, J. (1967). Self-selection of dietary components. In *Handbook of Physiology*, Vol. 1, *Alimentary Canal,* C. F. Code (Ed.). American Physiological Society, Washington DC, pp. 367–386.

Le Magnen, J., and Tallon, S. (1968). Préférence alimentaire du jeune rat induite par l'allaitment maternel. *C.R.S. Soc. Biol.* **162**:387–390.

Logue, A. W. (1979). Taste aversion and the generality of the laws of learning. *Psychol. Bull.* **86**:276–296.

Martin, L. T., and Alberts, J. R. (1979). Taste aversions to mother's milk: The age-related role of nursing in acquisition and expression of a learned association. *J. Comp. Physiol. Psychol.* **93**:430–445.

Mason, J. R., Bean, N. J., and Galef, B. G. Jr. (1988). Attractiveness of carbon disulfide to wild Norway Rats. *Proceedings of the 13th Vertebrate Pest Conference,* **13**:47–95.

Meehan, A. P. (1984). *Rats and Mice: Their Biology and Control.* Brown, Knight and Truscott, Tonbridge, Kent.

Posadas-Andrews, A., and Roper, T. J. (1983). Social transmission of food preferences in adult rats. *Anim. Behav.* **31**:265–271.

Revusky, S. (1977). The concurrent interference approach to delay learning. In *Learning Mechanisms in Food Selection*, L. M. Barker, M. Best, and M. Domjan (Eds.). Baylor University Press, Waco, TX, pp. 319–370.

Richter, C. P. (1942–1943). Total self regulatory functions in animals and human beings. *Harvey Lect. Ser.* **38**:63–103.

✓ Richter, C. P. (1956). Salt appetite of mammals: Its dependence on instinct and metabolism. In *L'instinct dans le comportement des animaux et de l'homme.* Masson, Paris, pp. 577–629.

Richter, C. P., Holt, L., and Barelare, B. (1938). Nutritional requirements for normal growth and reproduction in rats studied by the self-selection method. *Am. J. Physiol.* **122**:734–744.

Rozin, P. (1969). Adaptive food sampling patterns in vitamin deficient rats. *J. Comp. Physiol. Psychol.* **69**:126–132.

Rozin, P. (1976). The selection of foods by rats, humans and other animals. In *Advances in the Study of Behavior*, Vol. 6, J. S. Rosenblatt, R. A. Hinde, E. Shaw, and C. Beer (Eds.). Academic Press, New York, pp. 21–76.

Rozin, P., and Kalat, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychol. Rev.* 78:459–486.

Scott, E. M. (1946). Self-selection of diet: I. Selection of purified components. *J. Nutr.* 31:397–406.

Scott, E. M., and Quint, E. (1946). Self-selection of diet: IV. Appetite for protein. *J. Nutr.* 32:293–301.

Scott, E. M., Smith, S., and Verney, E. (1948). Self-selection of diet: VII. The effect of age and pregnancy on selection. *J. Nutr.* 35:281–286.

Seligman, M. E. P. (1970). On the generality of the laws of learning. *Psychol. Rev.* 77:406–418.

Shettleworth, S. J. (1983). Function and mechanism in learning. In *Advances in Analysis of Behavior*, Vol. 3, M. Leila and L. Harzem (Eds.). Wiley, Chichester, pp. 1–37.

Steiniger, von F. (1950). Beitrage zur Soziologie und sonstigen Biologie der Wanderratte. *Z. Tierpsychol.* 7:356–379.

Story, M., and Brown, J. E. (1987). Do young children instinctively know what to eat? The studies of Clara Davis revisited. *N. Engl. J. Med.* 316:103–106.

Tribe, D. (1954). The self-selection of purified food constituents by the rat during growth, pregnancy and lactation. *J. Physiol.* 124:64.

Tribe, D. (1955). Choice of diets by rats: The choice of purified food constituents during growth, pregnancy, and lactation. *Br. J. Nutr.* 9:103–109.

Young, P. T. (1959). The role of affective processes in learning and motivation. *Psychol. Rev.* 66:104–125.

Young, P. T. (1968). Evaluation and preference in behavioral development. *Psychol. Rev.* 75:222–241.

Zahorik, D., and Maier, S. (1969). Appetitive conditioning with recovery from thiamine deficiency as the unconditioned stimulus. *Psychonomic Sci.* 17:309–310.

10

Primate Gastronomy: Cultural Food Preferences in Nonhuman Primates and Origins of Cuisine

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I. INTRODUCTION

This paper is concerned with the similarity between human food practices and those of higher primates. First I will show that human primates share their gustatory sense with their close relatives, chimpanzees. Second, I will show the evidence that human food culture has its counterpart in nonhuman primates by illustrating, in particular, the transmission of food preferences in nonhuman primates. I will limit most of my discussion to chimpanzees, macaques, and baboons, because, like humans, they are typical omnivores and they have also been studied in many different locations.

II. GUSTATORY SENSE

Three pieces of evidence demonstrate that the gustatory sense of chimpanzees is similar to that of human beings.

First, chimpanzees cause damage to crops. Chimpanzees of Mahalé, for example, feed on sugarcane, corn stalks, and fruits of the banana, mango, lemon, and guava trees (Nishida and Uehara, 1983).