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Edward M. Stricker

*University of Pittsburgh
Pittsburgh, Pennsylvania*

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Diet Selection and Poison Avoidance by Mammals Individually and in Social Groups

BENNETT G. GALEF, JR. AND MATTHEW BECK

INTRODUCTION

There is great diversity in the feeding behavior of mammals. Some are essentially monophagous, feeding on a single food or class of foods; others are eclectic in their ingestive behavior, composing exceptionally varied diets.

True ingestive specialists, such as vampire bats (*Desmodus rotundus*), sustained entirely by mammalian blood, acquire nutritionally balanced diets simply by identifying and then eating their staple food. Omnivores cannot compose an adequate diet so easily. Be they men, rats, gulls, or roaches, omnivores must ingest a suitable mix of different foods if they are to thrive outside the laboratory.

Lát (1967) has proposed that the need for omnivores to ingest selectively a number of different foods arises from the fact that, for an omnivore, there is no single natural food that contains adequate amounts of all the constituents required for optimal living. The same fact, that most free-living omnivores live in areas in which no single food provides an adequate diet, can be viewed quite differently. Development of an ability to compose an adequate diet by selectively eating a number of different foods allows omnivores to occupy areas in which no single satisfactory food is available and in which no monophage could sur-

BENNETT G. GALEF, JR. AND MATTHEW BECK Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1, Canada.

vive. Omnivory thus both broadens the range of environments in which mammals can live and requires greater sophistication in selective ingestion than does monophagy.

Because ingestive specialists can meet their nutritional requirements by identifying and ingesting a single class of foods, they have little need to contact or ingest potential toxins. Omnivores, sampling broadly among foods in an attempt to locate sources of needed nutrients, should be exposed to any toxic agents in an environment more frequently than are specialists. In consequence, life as an omnivore could be facilitated not only by the ability to choose a balanced diet but also by the ability to identify and reject toxic substances (Rozin, 1976b). Each omnivore must steer a narrow course between the Scylla of dietary insufficiency and the Charybdis of ingestion-induced toxicosis, neither selecting such a restricted range of foods that it fails to include all required nutrients nor sampling so widely that it ingests harmful quantities of toxins.

Selecting an adequate diet and avoiding ingestion of toxins, the two main behavioral challenges faced by omnivores as a consequence of their omnivory, usually have been treated as separate problems. Investigators working on diet selection and those studying poison avoidance have developed different research paradigms, contributed to relatively independent literatures, and employed different theoretical perspectives.

In a landmark series of papers, Rozin (1965, 1967a, 1967b, 1968, 1976a, 1976b; Rozin & Kalat, 1971) provided an integrative framework that, quite unlike Richter's (1943) earlier model, permitted discussion of diet selection and poison avoidance as a unitary problem. Richter (1943) had hypothesized that each of the dozens of nutrients required by omnivores is regulated by an innate mechanism that detects a specific deficiency state, detects a needed nutrient in foods, and motivates its ingestion. Rozin proposed that although intake of three critical dietary elements (e.g., water, sodium, and calories) was controlled in the manner Richter had suggested, intake of most nutrients was not so controlled. On Rozin's model, sensitivity to the novelty or familiarity of a food, together with a capacity to respond behaviorally to the physiological consequences of eating a food, underlies both selection of an adequate mix of unregulated nutrients and avoidance of repeated ingestion of toxins. For example, an omnivore maintained on an inadequate food develops an aversive deficiency state that is similar to toxicosis. This aversive deficiency state produces a learned aversion to the taste of the inadequate diet. Conversely, eating an isolated meal of an unfamiliar food that produces recovery from illness leads to a learned preference for the flavor of the unfamiliar food.

If diet choice is to be optimized, consequences of ingestion must be associated with food-related stimuli despite long delays between eating a food and experience of consequences. Normally, association of stimuli with their consequences does not occur when they are separated by more than a few seconds. Rozin argued from data provided by Garcia and his co-workers (Garcia & Koelling, 1966, 1967; Garcia, Kimeldorf, & Hunt, 1961) that the learning of dietary aversions and preferences rests on two adaptive specializations of a more general Pavlovian learning process: first, attribution of changes in internal state to the consequences of ingestion ("belongingness"), and, second, a capacity to tolerate long delays between ingestion and the onset of the consequences of ingestion ("long-delay learning"). On this view, belongingness (Revusky, 1971) and long-

delay learning have evolved expressly to facilitate solution of the problems of diet selection and poison avoidance faced by omnivores in natural habitat.

Rozin's model of food choice explains the results of many laboratory experiments in which rats succeeded in avoiding repeated ingestion of toxic foods or in selecting from among several diets the sole diet permitting redress of a deficiency state. Although we accept Rozin's general view of the causes of rats' successes both in selecting adequate diets and in avoiding poisons, we believe that it is incomplete in one important respect.

Rozin's model was designed to explain how omnivores select adequate diets and avoid eating poisons; it neither pays much attention to nor offers any explanation of their failures. We argue below that consideration of failures, both of diet selection in the laboratory and of poison avoidance in the field, may be of considerable importance in understanding the capacity of omnivores to select foods successfully in either setting.

It is important to keep in mind, especially when discussing Norway rats or other mammalian species capable of rapid rates of population growth (Pianka, 1970), that individuals often fail to respond adequately when challenged by the environment. Failure to find shelter, failure to avoid predators, failure to find safe and adequate food, failure to resist disease, failure of some sort results in the death of more than 90% of rats before they reproduce (Brooks, 1973). Such failures can be as instructive as less frequent successes in understanding the feeding-related behavioral capacities of omnivores. Focus on failure may also provide a useful cautionary message in this age of Panglossian explanations of apparently ubiquitous behavioral optimality. Animals fail when their behavioral capacities are insufficient to respond to environmental demands, and failure is common.

DIET SELECTION

CAN RATS SELF-SELECT ADEQUATE DIETS?

It has long been known that rats choosing from a cafeteria of purified nutrients can select a diet adequate for normal rates of growth. In a classic study, Richter, Holt, and Barelare (1938) found that rats offered 11 containers, each containing a different, relatively purified nutrient (casein, dextrose, olive oil, baker's yeast, water, salt mix, etc.) gained weight more rapidly and on fewer calories than did a control group of rats maintained on a standard laboratory chow. Young (1944) confirmed this result in groups of 12 rats, each group having access to the 11-food cafeteria used by Richter *et al.* (1938). Clearly, under some circumstances, rats can self-select an adequate diet from among a variety of potential foods.

Richter had expected his subjects to be successful in the cafeteria feeding situation. "The survival of animals and humans in the wild state in which the diet had to be selected from a variety of beneficial, useless and even harmful substances is *proof* [emphasis added] of this ability . . . to make dietary selections which are conducive to normal growth and development" (Richter *et al.*, 1938, p. 734). In Richter's view, the laboratory data illustrated a capacity for diet selection that could be deduced from the survival of omnivores in the natural world. Consequently, when omnivores failed to self-select an adequate diet in some

experimental situation, the failure was interpreted by Richter as the result of an artifact of one sort or another: the use of complex natural foods (Richter *et al.*, 1938), inherited defects of the sensory system in domesticated subjects, age-related exhaustion of regulatory functions, or, in humans, perverse cultural influences (Richter, 1943).

Yet, review of the literature on dietary self-selection by rats in cafeteria feeding situations reveals that failure, as indicated by markedly slowed growth, is at least as common as success (Kon, 1931; Scott, 1946; Pilgrim & Patton, 1947; see Epstein, 1967; Lát, 1967, for reviews). Such failures to self-select, together with the theoretical considerations discussed below, suggest that Richter's deduction from the fact of the persistence of omnivores in nature, of a capacity for dietary self-selection in cafeteria feeding situations, was overdrawn.

Members of any species, even those as cosmopolitan in distribution as Norway rats or "primitive" *H. sapiens*, are not found everywhere within their respective species' ranges. By definition, individuals can survive only in those portions of the environment that both provide all resources necessary for life and lack insurmountable threats. An area would be devoid of rats if it contained either lethal substances that rats were unable to learn to avoid or a necessary nutrient only in a form that rats couldn't learn to eat. Existence of an omnivorous species in nature tells us little about the range of environments in which species members have the ability to self-select nutritionally adequate, safe diets. Persistence of omnivores outside the laboratory shows only that there exist portions of the environment where the behavioral capacities of species members are sufficient to permit development of a dietary repertoire conducive to self-maintenance, growth, and reproduction. In particular, existence of an omnivorous species in nature does not suggest that in the laboratory omnivores should be able to select nutritionally adequate diets from among a cafeteria of purified dietary components.

CAUSES OF FAILURE IN SELF-SELECTION

In discussing selection of foods containing nutrients other than salt, neither Rozin (1976b) nor Richter paid much attention to the relative palatability of foods. The flavor of a food is not necessarily a reliable indicator of its nutritive content. Consequently, selection of foods on the basis of their flavors cannot explain successful diet selection. Palatability may, however, be an important determinant of failure of self-selection (Richter, 1943). As Epstein (1967, p. 201) concluded in his review of the literature on dietary self-selection by rats, "Rats tend to eat what they like, and what they like is determined largely by the palatabilities of the foods they are offered." In laboratory cafeteria feeding studies, growth rate has been determined largely by protein intake (Lát, 1967). As Scott (1946, p. 403) indicated, "[individual] rats either do or do not like casein; if they like it, they eat an average of 3 grams a day and grow well; if they do not, they eat less than 0.1 gram per day, lose weight, and die within a short period."

Such laboratory findings can be extrapolated, with caution, to extralaboratory environments. How successful animals are in selecting an adequate diet will depend on their intake of the relatively less palatable available foods that contain necessary nutrients. If an animal eats enough of a relatively unpalatable food to allow evaluation of the consequences of eating that food, then the problem of dietary self-selection can, at least potentially, be solved. If an animal cannot

overcome its initial aversion to the taste of some food so as to eat sufficient amounts of the food to permit its evaluation, then a capacity to learn about consequences of ingestion will be of no use.

The question "Can omnivores self-select adequate diets?" is unanswerable in that form. In benign ingestive environments, such as the one constructed by Richter *et al.* (1938), the relative palatabilities of the foods provided may lead directly to selection of an adequate diet by all individuals. In the Richter *et al.* (1938) study, the presence both of multiple sources of protein and of a relatively unpalatable carbohydrate (Epstein, 1967) probably rendered the problem immediately soluble (Scott & Quint, 1946). In less benign environments, spontaneous sampling, coupled with response to positive postingestional consequences, suffices to permit most subjects to overcome their initial avoidance of the least-palatable needed food or foods. In yet more challenging situations, no individual's spontaneous behavior may be sufficient to overcome the flavor-induced avoidance of one or more needed foods.

Failure to solve a diet-selection problem can result from the unpalatability of foods containing one or more necessary nutrients limiting ingestion of valuable foods to the point that discovery of their beneficial properties is unlikely. Results of several classic studies of diet selection in which rats were taught to solve cafeteria feeding problems they did not solve spontaneously suggest that rats often fail to solve problems that are, in principle, soluble. For example, when six of 12 rats selecting among four purified diet components (casein, sugar, salt mix, and fat) steadily lost weight because of low protein intake, McDonald, Stern, and Hahn (1963) fed them only casein for 4 weeks and then returned them to the choice situation. All subsequently ate casein and showed excellent weight gain. Similarly Harris, Clay, Hargreaves, and Ward (1933) found that vitamin-B-deficient rats, unable to select a single vitamin-B-rich food from among ten foods, could solve the problem after 2 or 3 days of access only to that food rich in vitamin B. The initial problem was not insoluble. Rather, the rats' behavioral proclivities were not sufficient to produce an ingestive pattern leading to a solution.

Contradictory outcomes both within and between studies of dietary self-selection are consistent with the view that both the particular foods offered to subjects and individual differences in dietary preference are significant determinants of success. One should not ask whether rats can select adequate diets but rather inquire as to the characteristics of foods that affect the probability of adaptive dietary selection by individuals with differing dietary preferences. In benign ingestive environments, like that of Richter *et al.* (1938), the palatability spectra of many animals may be sufficient to produce a relatively immediate solution. In less benign environments, spontaneous sampling and sensitivity to the consequences of ingestion can sometimes produce solutions. In harsh environments, animals are unable spontaneously to create situations leading to identification of needed nutrients.

The results of Davis' (1928) pioneering studies of diet selection by human infants, like the results of Richter's studies of dietary self-selection by rats in cafeteria feeding situations, have frequently been interpreted as providing evidence that naive omnivores can instinctively select a well-balanced diet from a cafeteria (Story & Brown, 1987). Davis herself, however, was well aware that human infants could self-select an adequate diet only when nutritious unsweetened foods were offered as choices. As Davis (1939, p. 261) stated, "Self-selection can have no, or but doubtful value, if the diet must be selected from

inferior foods." In humans, as in rats, the capacity to self-select adequate diets depends on the diets offered for choice. The provision of an assortment of nutritious, roughly equipalatable foods rather than a capacity to self-select needed foods probably underlay much of the success of Davis' subjects (Rozin, 1976b).

ARE CAFETERIA FEEDING STUDIES ADEQUATE ANALOGUES OF DIET SELECTION IN NATURAL HABITAT? A DEVELOPMENTAL PERSPECTIVE

For the first few weeks or months of life, young mammals are ingestive specialists, sustained by a single nutritionally adequate diet, mother's milk. At some point in development, each individual's caloric needs outstrip either the energy transduction capacities of its dam (Babicky, Ostradalova, Parizek, Kolar, & Bibr, 1970) or her willingness to invest further resources (Trivers, 1974). It is at this point in development, at weaning, that each young omnivore must undertake the transition to omnivory, the potentially arduous task of developing an adequate diet of solid foods. Although adults may be challenged occasionally by a failure of one or another resource on which they have come to depend, every weanling must deal with withdrawal of its major source of sustenance. Thus, one would expect weanlings to solve laboratory analogues of diet selection problems that occur in nature.

It is, therefore, surprising that weanling rats presented with a self-selection task in the laboratory, even one that adults solve easily, often fail dismally in maintaining their body weight. Tribe (1954, 1955) presented 15 100-g female rats with seven foods (corn starch, glucose, margarine, yeast, casein, salt mix, and cod liver oil). Thirteen solved the problem and grew, but only two of ten rat pups survived placement "at weaning" in the same situation. Scott, Smith, and Verney (1948) offered 12- to 15-week-old rats a choice of but four foods [casein, vegetable oil, sucrose, and salt mix (vitamins were fed by pill)]. Thirteen of 20 12- to 15-week-olds gained weight, and all survived, but only nine of 31 weanlings survived in the same situation. Kon (1931) offered 28-day-old rats three dietary elements (casein, sucrose, and salt mix) supplemented with vitamins by hand. Two of his four weanling subjects died, and one gained no weight for 7 weeks. Such failures of weanling rats to solve dietary selection problems far simpler than one might expect them to face in natural circumstances suggest that the laboratory analogue of dietary selection, the cafeteria feeding experiment, does not capture some important aspect of dietary self-selection as it occurs outside the laboratory.

SOCIAL SOLUTIONS TO SELF-SELECTION PROBLEMS

If the ability to self-select an adequate diet is typical of weaning omnivores, then the not infrequent failure of weanling rats to survive diet selection studies in the laboratory poses a problem. Either the genotypes of domestic strains of Norway rat are deficient, the environment in which rats are maintained in the laboratory is so deviant as to preclude the development of a species-typical behavioral capacity, or the cafeteria feeding situation is not an appropriate analogue of the problem faced by weanling rats in natural circumstances.

One unchanging feature of the environment in which all mammals that survive to weaning age develop, absent in all reported laboratory studies of

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dietary self-selection, is the presence of a dam who, by her very existence and reproductive success, has demonstrated the adequacy of her dietary selections. Data from our laboratory suggest that the presence of an adult that has solved the problem of diet selection can be a major factor in the success of juveniles in composing an adequate diet.

In a recent experiment (Beck & Galef, 1989), we presented individual weanling rats with a cafeteria of four distinctively flavored diets. Three of these diets contained inadequate levels of protein (5%), and one had ample protein (20%) for the support of normal growth. We found (see Figure 1), as had Kon (1931), Scott *et al.* (1948), and Tribe (1954, 1955), that our weanling subjects did very poorly in such a situation. None was able to develop a preference for the protein-adequate diet. Each pup appeared well on its way to a premature demise if we had not terminated the experiment. Weanling rats faced with the same diet selection problem while in the presence of adults previously trained to ingest the protein-rich alternative grew rapidly in the experimental situation. Clearly, information acquired from a knowledgeable adult permitted weanlings to select an adequate diet in what we assume is the normal, species-typical fashion of rats.

Our analysis of the behavioral processes involved in social enhancement of dietary self-selection by weanling rats in a cafeteria situation is still in its early stages (Beck & Galef, 1989). However, enough is known about mechanisms of social influence on diet choice in young rats more generally to propose two alternative pictures of how the results shown in Figure 1 might be produced. First, juvenile rats prefer to eat at locations where adults are feeding rather than at locations that adults are ignoring (Galef & Clark, 1971). The simple presence of an adult rat at a feeding site attracts young to that site and causes them to begin feeding there (Galef, 1971, 1981). Adult rats also deposit residual olfactory cues around and in feeding sites they use, and these residual cues attract weanlings and cause them to eat where adults have eaten (Galef, 1986a; Galef & Beck, 1985; Galef & Heiber, 1983). Such social influences on diet selection are in a sense indirect. The presence or activity of adults at a feeding site attracts young and increases the probability that juveniles will eat the food to be found at the socially enhanced site (Galef, 1977). There is, however, no direct specification of what food to eat.

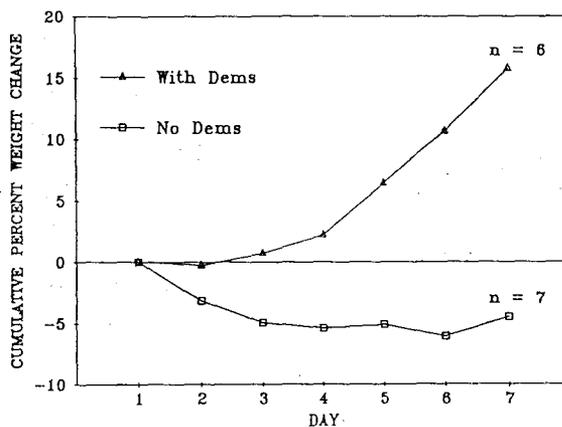


Figure 1. Mean cumulative percent weight change seen in juvenile rats choosing among four diets in the presence and absence of knowledgeable demonstrators.

There is, in addition, considerable evidence of social effects acting directly on diet selection by naive rats. If one rat (a "demonstrator") eats a diet and then interacts with a naive rat (an "observer"), the observer rat subsequently exhibits a markedly enhanced preference for the diet its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983).

In sum, a naive rat pup can exhibit socially enhanced intake of a diet for one of two reasons: either an adult induced the pup to begin feeding at a location where a particular food is found, or an adult directly induced an enhanced preference in the pup for a food that the adult was eating. Either direct or indirect induction of eating of the protein-rich diet could be responsible for the social facilitation of protein ingestion shown in Figure 1.

The fragility of weanling rats and their frequent failure to self-select adequate diets when alone in laboratory cafeteria feeding studies has imposed a research strategy on laboratory investigators of dietary self-selection by rats. Investigators extend the young rat's period of total dependence on others for diet selection by weaning pups from mother's milk to a nutritionally adequate chow compounded by nutritionists. Weaning from milk to chow maintains animals in a state of naiveté with respect to problems of nutrient selection. Adults maintained on chow from weaning and faced for the first time with a need to self-select nutrients have served as model systems for studying a process that normally occurs at the time of weaning from mother's milk.

Naive adult rats, like naive weanlings, often have difficulty in solving even relatively simple diet-selection problems. McDonald *et al.* (1963) offered 12 individually housed 90-day-old rats a four-choice cafeteria (sugar, salt mix, casein, and vegetable oil), and six lost weight. Similarly, Schutz and Pilgrim (1954) found that 21 of 43 young adult rats were losing weight 3 weeks after being offered a four-choice cafeteria similar to those used by Scott (1946) and Pilgrim and Patton (1947). Rozin (1968) offered ten thiamine-deficient rats a choice among three novel diets only one of which contained thiamine, and four of his ten subjects failed to select the thiamine-rich food.

Adult rats, like weanlings, will show facilitation of diet selection when in the presence of knowledgeable adult conspecifics. As can be seen in Figure 2, when individually housed adult rats were offered a choice of four novel diets, only one

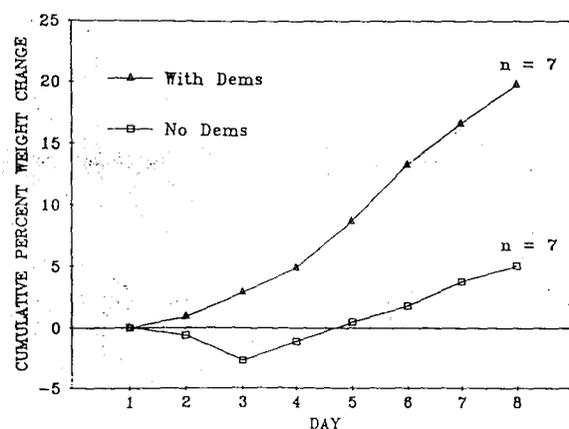


Figure 2. Mean cumulative percentage weight change seen in adult rats choosing among four diets in the presence and absence of knowledgeable demonstrators.

of which contained adequate protein, their weight gain was poor. Adult rats housed with a conspecific trained to eat the protein-rich diet gained weight rapidly.

From the point of view of a naive individual, an environment containing conspecifics that have already solved the problem of selecting an adequate diet is benign in comparison with the same environment lacking social sources of information. Rats that cannot select an adequate diet when alone in a cafeteria feeding situation do well in the presence of a successful other. The presence of knowledgeable conspecifics in demanding environments can expand the range of situations in which naive individuals are able to choose the foods they need to survive.

POISON AVOIDANCE

As noted in the introduction to the present chapter, a specialist feeder may limit its encounters with most poisonous substances simply by eating a restricted range of foods. For a koala, the simple rule "eat it if it tastes and smells like eucalyptus, don't eat it if it doesn't" would go a long way both toward solving the problem of diet selection and toward reducing the probability of eating most environmental toxins. Omnivores, on the other hand, sampling widely among foods to locate needed nutrients, greatly increase their probability of eating poisons.

The congenital tendency of many mammals to reject bitter-tasting foods has been discussed as an adaptive response to flavors characteristic of many naturally occurring toxins (Garcia & Hankins, 1975; Young, 1968). Although some toxins could be avoided simply by rejecting bitter-tasting foods, the importance of palatability in identification and rejection of poisonous foods by free-living animals has been, so far as we can determine, very poorly explored (see, for review, Fowler, 1983). It is easy to imagine circumstances in which simple palatability-based avoidance of toxins would be sufficient to protect individuals against feeding on deleterious substances. On the other hand, it seems likely that for an omnivorous species to colonize areas containing diverse toxins, an ability to learn to recognize and avoid ingestion of not-unpalatable dangerous foods would be advantageous. Rozin (1976a) and others have suggested that the tendency of rats and other omnivores to take small initial meals of unfamiliar foods (Barnett, 1958; Rzoska, 1953) is a potentially useful tactic in minimizing ingestion of possible poisons. Similarly, belongingness and long-delay learning are capacities of possible use both in identifying toxic foods and in avoiding repeated ingestion of them.

As in diet selection, environmental characteristics will determine the behavioral sophistication needed for successful poison avoidance. In benign environments, a simple tendency to eat what tastes good might suffice. In more complex or demanding situations, tentative sampling of unfamiliar foods and sensitivity to their postingestional consequences could be useful. The question "How do animals avoid ingesting lethal quantities of toxic substances?" like the question "Can omnivores select nutritionally adequate diets?" is unanswerable in that form. It depends on the animal, the toxins, and the environment in which the toxins and the animal are located.

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SHOULD RATS BE ABLE TO AVOID CRYPTIC POISON BAITS?

In study of taste-aversion learning, attention has focused on the ability of rats to learn to avoid repeated ingestion of good-tasting baits with long-delayed aversive postingestional consequences, what one of us has previously called "cryptic poison baits" (Domjan & Galef, 1983). Although such baits are used by exterminators to control rodent pests, there is some reason to question whether they are in any way typical of naturally evolved toxins (Domjan & Galef, 1983). Prey species that evolve means to manufacture or sequester toxins do so, at least in part, to deter their potential predators or consumers. Evolution of palatable toxins with delayed effects seems to us less likely than evolution of vile-tasting, fast-acting poisons. Immediately perceived unpalatability and rapid induction of illness or pain should be more reliable deterrents to potential predators than palatability coupled with long-delayed negative aftereffects. Rats would not have evolved an ability to cope with "cryptic" toxic foods unless the natural habitat provided exposure to cryptic toxic foods.

Review of the literature suggests that, because each rat has a variety of behavioral tactics to avoid ingesting lethal quantities of poison bait, killing free-living rats by poisoning them is a formidable task. It is somewhat surprising to find that, although total extermination of a population of rats by poisoning is difficult, killing 80% to 90% of a target population is not hard (Meehan, 1984). Even if one is quite crude in one's approach, the majority of rats usually succumb to an introduced poison. Chitty (1954), for example, found that poison baits, introduced without prebaiting into censused colonies of wild rats, typically eliminated 75% of colony members (median success in poisoning 37 colonies). Further, there was no evidence that survivors in Chitty's study (or in others) had learned to avoid eating the poison bait: perhaps some individuals found the bait unpalatable, were exceptionally neophobic, were unusually resistant to the poison, or failed to encounter the bait. The ability to learn to avoid a cryptic toxin may be even less well developed than Chitty's (1954) data suggest.

When exposed to cryptic toxins, both rats and mice (Tevis, 1956) die in large numbers. There is no need to explain how rodents survive human attempts to poison them. In general, they don't. By increasing the probability that rats will consume a lethal quantity of poison prior to the onset of symptoms of toxicosis (by using palatable baits, by prebaiting, by using highly toxic rodenticides with delayed onset of symptoms, etc.), one can create an environment in which individual rats have a very low probability of survival. Of course, if one's goal is total extermination of a rodent population, survival of even one pregnant female means failure.

ARE LABORATORY STUDIES OF TASTE-AVERSION LEARNING ADEQUATE
ANALOGUES OF POISON AVOIDANCE OUTSIDE THE LABORATORY?

During the 20 years since discovery of the exceptional properties of taste-toxicosis conditioning in rats (Garcia & Koelling, 1966; Garcia, Ervin, & Koelling, 1966), there has been extensive discussion of the relationship between the characteristics of taste-aversion learning revealed by laboratory studies and the requirements for successful poison avoidance in the natural habitat (e.g., Rozin & Kalat, 1971; Shettleworth, 1984; Zahorik & Houpt, 1981). Treatment of taste-toxicosis conditioning as an adaptively specialized learning process shaped by

selective pressures exerted on free-living rats by environmental toxins has been of heuristic value, both orienting research on taste-toxicosis conditioning in fruitful directions and promoting integration of field and laboratory studies of animal learning. As was the case in the development of models of diet selection, in discussions of poison avoidance attention has been focused on the success of omnivores. Once again, we shall focus on failure because such focus calls attention to often-ignored issues.

ADAPTIVE PATTERNS OF DIETARY SAMPLING. Laboratory-maintained rats, sustained throughout life on a single food and exposed to a single novel food prior to toxicosis induction, form an apparently adaptive aversion to the sole novel element in their diets. However, in the more complex feeding environments presumably found outside the laboratory, the decision as to what food to avoid after toxicosis is more difficult. If rats faced with a choice among novel foods ate discrete meals, each composed of a single food, and waited long enough between such meals to evaluate the postingestional consequences of each (e.g., Zahorik & Houpt, 1981), then one could with some confidence extrapolate from the simplified laboratory situation to the more complex outside world. If, to the contrary, rats tend to sample several unfamiliar foods in rapid succession, then the problem of toxin identification after onset of toxicosis is insoluble without further sampling of suspect foods.

It is commonly believed that rats faced with a number of new foods eat discrete meals of each unfamiliar, potentially dangerous food. Such discrete sampling would permit ready identification of a toxic food should illness occur after a meal of unfamiliar food. However, the few studies actually describing the behavior of rats the first time they encounter a number of novel foods do not support the assertion that rats sample discretely among them. Rozin's (1969) data, most frequently cited as demonstrating discrete sampling of novel foods by rats, in fact demonstrate the opposite. Five of the six subjects whose behavior Rozin described in detail ate either two or all three of the novel foods presented during the first 30 minutes of exposure to them.

Barnett (1956) reported that laboratory-born descendants of wild Norway rats, like Rozin's domesticated rats, tended to sample each of four novel foods available to them during their first feeding bout. It is difficult to see how a rat sampling several different novel foods upon first encounter with them could subsequently identify a toxic item if one were present (see also Beck, Hitchcock & Galef, 1988).

POISON-AVOIDANCE LEARNING OR DEVELOPMENT OF "FOOD PHOBIAS." Taste-toxicosis association learning over long delays has been extensively discussed as an adaptive specialization of a more general Pavlovian conditioning process. Implicit in this view is the assumption that, on average, it is beneficial for organisms outside the laboratory to learn an aversion to a novel food ingested several hours before an experience of nausea. However, learning of an aversion after a single pairing of novel taste and toxicosis carries potential costs as well as potential benefits. Chance ingestion of a food, particularly an unfamiliar one, in the hours prior to the onset of a bout of gastrointestinal distress induced by factors (bacterial, viral, or organic) unrelated to ingestion would result in learning of a maladaptive "food phobia" rather than learning of an adaptive aversion to a toxic agent. Indeed, if occurrence of gastrointestinal upset unrelated to inges-

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In the laboratory, rats are protected from many naturally occurring sources of malaise. Consequently, if a rat is fed an unfamiliar food and becomes ill, it appears obviously adaptive for the rat to learn an aversion to the unfamiliar food. In environments where occurrence of nausea is sometimes related to eating of a novel food and sometimes not, the utility of the acquisition of aversions to foods may be a less straightforward matter. Arguments to the effect that because rats can learn aversions over long delays the capacity to do so must be adaptive are only assertions without evidence that such learning actually enhances survival in natural environments.

We are ignorant of the frequency with which rats in natural habitat eat unfamiliar toxic foods and suffer toxicosis. We also do not know how often rats outside the laboratory eat unfamiliar safe foods and subsequently experience gastrointestinal upset. Hence, the usefulness, on average, of the capacity to learn aversions in a single trial over long delays between feeding and onset of illness remains speculative.

Outside the laboratory, the learning of "food phobias" as the result of fortuitous temporal associations of ingestion and illness is not a hypothetical event. Logue, Ophir, and Strauss (1981) asked 517 college undergraduates to describe their learned aversions. Respondents reported 23 aversions to eggs, 18 to shellfish, seven to organ meats, six each to Chinese food and mushrooms, three to hamburgers, etc., and none to true toxins. Similarly, M. L. Pelchat (personal communication, 1986), in recollecting her subjects' responses to questionnaires on learned flavor aversions (Pelchat & Rozin, 1982), could not recall a single instance of a learned aversion to a toxic substance other than alcohol. Even if the particular sample of egg or hot dog eaten by those who formed aversions to those foods was tainted and the cause of subsequent nausea, the learned aversion resulted in a long-lasting "food phobia" rather than adaptive avoidance of a true toxin. Although it is possible that some of these aversions to normally safe foods were, in fact, adaptive, perhaps the result of idiosyncratic allergic reactions to foods that most people can eat without ill effect, it seems reasonable to suggest that many were not adaptive. In humans there are costs of one-trial taste-toxicosis conditioning over long delays.

It might be proposed that the tendency to form aversions to relatively novel rather than to familiar foods, demonstrated many times in the laboratory (e.g., Kalat & Rozin, 1973; Revusky & Bedarf, 1967; Siegel, 1974), would provide protection against learning fortuitous, maladaptive aversions to safe foods. However, self-reports of behavior outside the laboratory are not consistent with such a view. Hot dogs, eggs, and hamburgers are unlikely to have been novel to those who formed aversions to them. Foods "known" to be safe are, at least occasionally, excluded from future ingestion by humans as the result of eating of a single tainted sample or happenstantial temporal pairing of ingestion with nausea unrelated to ingestion.

Although extrapolation from man to rat is as fraught with potential for error as is extrapolation in the opposite direction, the literature concerning taste-aversion learning in humans suggests that the learning of aversions after single pairing of taste and toxicosis is not necessarily adaptive. Rats living in areas containing few toxic potential ingesta and providing frequent exposure

nausea-inducing bacteria, viruses, or parasites could gain little if anything from the capacity to form aversions in a single trial over long delays. Those rats occupying niches containing many toxic foods and providing few other sources of malaise could gain a great deal from the same capacity.

The point of the preceding arguments is not that taste-aversion learning is maladaptive or that individuals are unable to learn selectively to avoid naturally occurring toxins outside the laboratory. Obviously, under many conditions, animals can learn to avoid toxins, and taste-toxicosis conditioning is responsible for development of adaptive patterns of poison avoidance. Rather, we would conclude that the abilities of individual organisms to learn to identify and avoid toxins are far from perfect. Consequently, it is possible that individuals might benefit from learning processes other than taste-toxicosis conditioning in developing aversions to toxic foods.

SOCIAL SOLUTIONS TO SOME PROBLEMS IN POISON AVOIDANCE. In the literature, models of poison avoidance rest on five laboratory or field observations: (1) hesitancy of rats (particularly wild rats) to ingest unfamiliar foods (Barnett, 1958; Rzoska, 1953), (2) a tendency of rats to sample among several unfamiliar foods in such a way as to permit independent evaluation of each (Rozin, 1969; Zahorik & Houpt, 1981), (3) a tendency to attribute aversions to unfamiliar rather than familiar foods (Kalat & Rozin, 1973; Revusky & Bedarf, 1967), (4) attribution of illness to foods rather than other aspects of the environment (Garcia & Koelling, 1966), and (5) a capacity to form flavor-illness associations in spite of long delays between experience of an unfamiliar flavor and onset of illness (Garcia *et al.*, 1966). Understanding of the processes of poison avoidance, like understanding of the process of diet selection, has been focused on the ability of individuals to identify appropriate substances for rejection. As we have already noted, outside the laboratory, rats live as members of social groups during part, if not all, of their lives. Many remain in their respective colonies from birth to death (Telle, 1966). Even those rats that disperse to become founders of new populations are obliged to spend their infancy and adolescence with their dams. Information acquired by any one colony member concerning the safety or toxicity of potential foods would be of use to all.

Review of the five capacities listed above, believed to be important in permitting individual rats to learn to avoid repeated ingestion of toxins, reveals that three of the five involve recognition of a potential food as novel. Weanling rats emerge from the nest into a totally unfamiliar environment without information permitting focus of concern on one or a few unfamiliar foods. Yet weanlings are in greatest need of strategies for developing safe, nutritionally adequate diets. The problem of identifying toxic foods appears more severe for naive weanlings than for knowledgeable adults that have developed inventories of known, safe foods to eat.

There is a simple strategy that would permit weanling rats to thrive in unfamiliar habitat. A new recruit to a population, whether a weanling or recent immigrant, could "assume" that living conspecifics had not eaten lethal doses of any poison food present in their shared environment. Naive individuals could also "assume" that, with high probability, senior colony members had already learned to avoid eating any noxious but nonlethal substances present in the environment. Thus, a naive individual could solve the problem of poison avoidance, as it could solve the problem of diet selection, by eating whichever foods

adults of its group were eating. The result would be an avoidance of poisons dependent on socially acquired rather than individually acquired information. The same processes that could facilitate selection of nutritionally adequate diets could simultaneously preclude ingestion of toxins. Indeed, in stable environments, where the same foods were available for generations, the simple rule, "eat what others are eating," would suffice for both nutrient selection and poison avoidance.

Information garnered from conspecifics could be used in a number of different ways to facilitate avoidance of poisons. First, as indicated above, an individual could avoid eating toxic foods simply by eating those foods others of its social group were eating. The results of a number of studies indicate that socially induced preference for one food results in avoidance by weanlings of potentially dangerous alternatives present in the environment. In wild rats, such socially induced preferences have resulted in total avoidance by weanlings of both feeding sites and foods that adults of their colony have learned to avoid (Galef & Clark, 1971).

Not only can socially acquired information play an indirect role in poison avoidance by directing ingestive behavior toward safe foods, socially transmitted information about foods can act to influence directly the course of poison avoidance learning. As mentioned above, results of experiments in several laboratories have shown that interaction of a naive rat (an observer) with a conspecific previously fed some food (a demonstrator) results in substantial enhancement of the observer's preference for its demonstrator's diet (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984). Such socially mediated exposure to foods that others have eaten can act, as does actual ingestion of a diet (Revusky & Bedarf, 1967; Rozin & Kalat, 1971; Siegel, 1974), to attenuate subsequent learning of an aversion to socially experienced diets.

Consider a situation in which some members of a rat colony are exploiting a palatable, safe, nutritious food that one member of the colony has not yet eaten. The naive individual encounters the novel food for the first time, ingests it, and an hour or two later becomes ill, perhaps because the particular sample of novel food it ate was spoiled, perhaps because of a viral, bacterial, or parasitic infection unrelated to ingestion of the novel food. On the individual learning model, the naive individual, eating an unfamiliar food and becoming ill, should develop a profound aversion to the unfamiliar food. The naive individual would develop "food phobia," foreclosing for some time exploitation of a potentially valuable source of nutrition. If, to the contrary, the naive individual could make use of socially acquired information, indicating that others are eating the unfamiliar food, the naive individual might ignore its own experience of toxicosis and continue to eat the food its fellows are eating.

In a recent experiment, Galef (1989) permitted naive, 23-hour food deprived rats (observers) to interact for 20 minutes with either one (1-dem group) or two (2-dem group) conspecific demonstrators that had recently eaten a highly palatable diet (Normal Protein Test Diet, Teklad, Madison, WI, referred to below as Diet NPT). The hungry observers then were fed Diet NPT for 15 minutes and, immediately thereafter, were injected with LiCl solution to induce an aversion to Diet NPT. After a 24-hour period of recovery from illness, each observer was given a 22-hour choice between Diet NPT (the averted diet) and an unfamiliar, relatively unpalatable diet. As can be seen in Figure 3, many observers

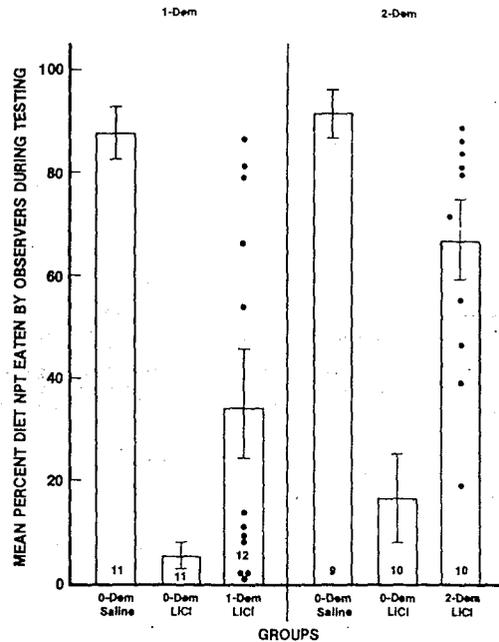


Figure 3. Mean amount of Diet NPT eaten by observers as a percentage of total amount consumed by observers during testing. Flags on histograms represent 1 S.E.M. Numbers within histograms are *n*s per group. See text for explanation of groups.

ers in both 1-dem and 2-dem groups failed to exhibit an aversion to Diet NPT. Prior interaction of an observer with a demonstrator or demonstrators that had eaten Diet NPT attenuated subsequent learning of an aversion to Diet NPT. Socially mediated dietary information had the capacity to prevent formation of a "food phobia."

Subjects in one control group (labeled group 0-dem, LiCl in Figure 3) were treated exactly as were observers in the experimental group described above but received no exposure to demonstrators fed Diet NPT. As one would expect, subjects in this control group exhibited profound aversions to Diet NPT. Subjects in a second control group (0-dem, Sal in Figure 3) were treated as were subjects in the first control group but were injected with isotonic saline solution rather than LiCl solution following ingestion of Diet NPT. These subjects exhibited a marked preference for Diet NPT.

Individual data points in Figure 3 reveal that behavior of observers in the experimental groups was highly variable. Some observers were unaffected by socially mediated exposure to Diet NPT and exhibited strong aversion to it. Aversion learning by other observers was completely blocked as a result of prior exposure to conspecifics that had eaten Diet NPT. Although the causes of such variability need to be determined, the data clearly indicate that socially mediated exposure to a diet can profoundly attenuate subsequent learning of an aversion to that diet. Rats may be substantially less likely to learn an aversion to a diet others of their social group have eaten than to totally unfamiliar foods.

This failure of rats to learn aversions to foods that conspecifics have eaten has been the subject of a number of recent studies in our laboratory. Two findings are of particular relevance to the present discussion.

First, approximately 50% of rats that ate a novel food (Diet NPT), were injected with LiCl, and therefore had learned an aversion to Diet NPT abandoned that aversion after a 15-minute period of interaction with each of two

avoidance of poisons required information. Socially adequate diets, in stable environments, the simple rule, eat selection and poison

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conspecific demonstrators that had eaten Diet NPT prior to interaction with averted subjects (Galef, 1985, 1986c).

Second, observer rats that interacted with a demonstrator recently fed one of two foods (either Diet N₁ or N₂), both unfamiliar to the observer, ate both Diets N₁ and N₂, and then suffered toxicosis, preferentially formed aversions to that novel food their respective demonstrators had not eaten. That is, those observers whose respective demonstrators had eaten Diet N₁ formed an aversion to Diet N₂; those observers whose demonstrators had eaten Diet N₂ formed an aversion to Diet N₁ (Galef, 1986b, 1987). Within this paradigm, substantial attenuation of learning of aversions by observers to the diets eaten by their respective demonstrators was seen even if interaction with a demonstrator fed Diet N₁ or N₂ occurred 8 days prior to observer sampling of Diets N₁ and N₂, toxicosis induction, and testing for aversion learning (Galef, 1987).

We know that the messages passing from demonstrators to observers, affecting the latter's aversion learning, can be olfactory (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983). Because simply eating a diet does not enhance a subject's subsequent preference for that diet, whereas exposure to the same diet on a demonstrator does enhance an observer's subsequent preference for that diet (Galef, Kennett, & Stein, 1985), we suspect that each olfactory message passing from demonstrator to observer consists of two parts: first, an olfactory signal identifying the diet eaten by a demonstrator, and, second, a pheromone emitted by demonstrators that acts in concert with the diet-identifying olfactory signal to alter an observer's subsequent choice of food (Galef *et al.*, 1985; Galef & Stein, 1985). The diet-identifying component of a message is simply the smell of a food a demonstrator has eaten diffusing both from food particles clinging to a demonstrator's pelage and from the demonstrator's digestive tract (Galef *et al.*, 1985).

The contextual component of a message appears to be composed of volatile sulfur compounds, particularly carbon disulfide (CS₂), a chemical we have found on the breath of rats (Bean, Galef, & Mason, 1988; Galef, Mason, Preti, & Bean, 1988). Behavioral data support the contention that CS₂ may be an important component of messages that enhance diet preference in rats. Rats prefer foods moistened with CS₂ solution to those moistened with water (B. G. Galef, Jr., unpublished data). Rats preexposed to a diet moistened with a few drops of a dilute aqueous CS₂ solution, but not rats preexposed to the same diet moistened with an equal quantity of water, subsequently exhibit attenuation of aversion learning to the preexposed diet (Galef *et al.*, 1988).

Socially mediated exposure to diets provides potential solutions, albeit imperfect ones, to both acquisition of "food phobias" and failure to discretely sample several unfamiliar foods. Interaction with conspecifics that have eaten an unfamiliar food can attenuate aversion learning to that unfamiliar food should chance illness strike during the hours after it was eaten. Encounters with conspecifics that have eaten a food have the potential to reverse a previously learned aversion to the food.

One can picture a naive rat as utilizing information extending far beyond its own experience of the consequences of ingestion of particular foods in deciding which foods to eat and which to avoid. A naive individual can exploit information acquired from its fellows both to select needed nutrients and to reduce the probability of excluding beneficial diets from its own feeding repertoire.

It is tempting to interpret the results of studies of social mediation of taste-aversion learning as suggesting that the ability of rats to avoid eating lethal doses of toxin is even more perfect than previously suspected. However, use of socially mediated information concerning foods, like individual taste-toxicosis association learning, can lead to error. Consider a rat that has eaten a lethal quantity of a toxic bait with effects delayed by several hours. During the interval between eating the lethal dose of toxin and death, the doomed individual could lead its fellows both to eat the toxic bait and to fail to form an aversion to the poison bait if they ate sublethal but illness-provoking first meals of it. There are rarely potential benefits without potential costs.

CONCLUSION

Because omnivores often live in environments where they must both select a mix of foods to formulate a balanced diet and learn to avoid repeated ingestion of any toxins they encounter, it has long been implicitly assumed that individual omnivores are adept at both diet selection and poison avoidance. Consequently, studies demonstrating the success of individual omnivores, either in selecting balanced diets or avoiding toxins, have received far more attention than studies demonstrating failure; the former studies appear to reflect real-world competence, whereas the latter appear to reflect laboratory artifacts.

The main argument of the present chapter is that failure of individual omnivores to self-select adequate diets or correctly identify toxins tells us as much about their behavioral capacities as does their success in diet selection or poison avoidance. The behavioral tactics available to individual omnivores for dealing with dietary insufficiencies or environmental poisons are adequate to cope with some environments but not with others. There is no simple answer to the question, "can omnivores avoid poisons or select balanced diets?" It depends on the omnivore, and it depends on the environment in which that omnivore is found. In benign environments, the sensory-affective systems of an animal may be sufficient to lead it to eat a balanced, safe mix of ingesta. In more demanding environments, the capacity of individuals to evaluate foods may be inadequate to the task of selecting a safe, balanced diet. Laboratory analogues both of benign and of demanding environments are informative.

The secondary argument of the present chapter is that, as social animals, omnivores can expand the range of environments in which they successfully avoid toxins and select balanced diets. An area inhabited by rats that have solved the nutritional problems posed by the foods found there may be far less challenging to naive newcomers than the same area would be in the absence of knowledgeable inhabitants. It is, for example, easy to imagine an area that contains so many palatable protein-deficient foods that only one in 100 naive rats introduced into that area would compose a protein-adequate diet before expiring. Yet one would not be at all surprised to find that all young born to a female that had located a reliable protein source in our imaginary area would thrive. The continued presence of groups of omnivores in an environment can not be used to infer that a naive individual would have the ability to survive there alone.

From the perspective of the present chapter, omnivores appear both better and worse at dietary selection and poison avoidance than they do from other

perspectives. The individual omnivore is seen as less sophisticated in its abilities to find needed nutrients and avoid poisons; the social omnivore is seen as able to maintain populations in areas where the survival of a naive individual would be unlikely.

Evolution by natural selection is a process that, over generations, stabilizes unlikely events in a species' gene pool. Social learning can play a similar role at the behavioral level on a far shorter time scale. If naive individuals incorporate into their own behavioral repertoires the unlikely acquired behaviors of successful colleagues, they can thrive in environments that otherwise would be closed to them. The data suggest that social learning can augment individual learning both about nutritious, safe foods and about toxins and can thus expand the range of environments in which populations of omnivores can succeed.

W. C. Allee, who studied ways sociality could enhance fitness and the presence of conspecifics could render environmental challenges less severe, suggested that "many animals change or 'condition' an unfavorable medium so that others following or associating with them can survive better and thrive when they could not do so in a raw, unconditioned medium" (Allee, 1958, p. 210). The present review leads to a similar conclusion. The behavior of successful individuals in an area provides information to naive individuals that can lead them to succeed in selecting adequate diets and avoiding toxins where they otherwise would fail.

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