

Social Learning in Rats

Historical Context and Experimental Findings

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Abstract

This chapter reviews studies undertaken to understand how young Norway rats (*Rattus norvegicus*) use information acquired from others of their species to learn where and what to eat. The robust laboratory paradigms developed for studying social learning about foods in rats have proven useful in asking a number of kinds of questions about the development, function, and causation of behavior. Consequently, the results of this work have provided useful information not only about the role of social learning in behavioral development, but also concerning the nature of traditions in animals, the adequacy of formal mathematical models to predict behavior, the adaptive specialization of learning, and the success of Norway rats as human commensals.

Keywords: Norway rats, food choice, social learning

Introduction

For more than 40 years, researchers in my laboratory have been conducting experiments designed to increase understanding of how young Norway rats (*Rattus norvegicus*) use information acquired from others of their species to learn where and what to eat. The willingness of members of the scientific community to support funding and publication of studies of social feeding in rats for so many years and of graduate students to devote a significant portion of their lives to such work suggest that information about social influences on rats' food choices continues to be relevant to the interests of the scientific community.

Maintaining interest in Norway rats' social learning about foods in the face of an ever-changing scientific zeitgeist has required considerable flexibility in presentation of our work. At one time or another, our findings have been presented as relevant to problems in animal learning, food choice, and behavioral development, as well as to the general concerns of ethologists, animal behaviorists, and behavioral ecologists (Galef, 1991b). Still, if the problem first

chosen for study had not been appropriate to the interests of the scientific community, the research program could not have acquired the momentum needed to sustain it for decades. Consequently, examining the context in which our research program on social influences on the food choices of Norway rats developed may provide some insight as to why, four decades later, the work continues to be of sufficient interest to lead to an invitation to contribute to this volume.

Studies of Social Influences on the Food Choices of Norway Rats

Why Food Choice?

In 1968, the year in which I completed my Ph.D. in physiological and comparative psychology at the University of Pennsylvania, progress in understanding the factors governing the food choice of animals had led to the study of food choice becoming one of the most exciting areas in experimental psychology. At the time, the processes of association learning were assumed to have general characteristics that could be discovered by studying learning in situations

selected for their experimental convenience rather than for their biological relevance. Experiments conducted in the mid-1960s were to challenge that assumption.

John Garcia discovered in 1966 that, when forming associations, rats showed a predilection to attend to tastes and to ignore auditory and visual cues that preceded aversive gastrointestinal events, and conversely, to attend to auditory and visual cues that preceded shocks (Garcia & Koelling, 1966). Further, contrary to findings in arbitrary situations, where an association between a stimulus and a subsequent event could be learned only if the stimulus preceded the event by a fraction of a second, rats could bridge gaps of many hours between tasting a novel food and becoming ill and still learn an aversion to the food (Garcia, Ervin, & Koelling, 1966). Garcia's discovery of both cue-to-consequence specificity and tolerance for long delays in the conditioning of associations between flavors and illness violated what were then assumed to be "general laws" of learning, and it is hard to convey either the disbelief with which these discoveries were initially greeted in some quarters or the controversy that they generated.

Preferentially learning to associate flavors with illness and to tolerate long delays between cue and consequence seemed to be ideal ways for rats living outside the laboratory to learn to avoid repeated ingestion of any toxic substances that they happened to ingest when sampling among unfamiliar, potential foods. Not surprisingly, it was not long before a number of investigators (e.g., Bolles, 1970; Rozin & Kalat, 1971; Seligman, 1970; Shettleworth, 1972) were interpreting the novel properties of taste-aversion learning as functional and suggesting that the study of learning in biologically arbitrary situations might not be relevant to understanding how learning occurred in at least some natural situations. These authors (and others) suggested that specialized mechanisms might have evolved to facilitate learning of biologically important associations. However, the dominant view at the time was that biology acted to "constrain" learning rather than to elaborate learning processes in adaptive directions. It was the latter interpretation that subsequently became the received view (e.g., Cosmides & Tooby, 1992). In any case, Garcia's work and interpretations of its significance introduced evolutionary or adaptive thinking into the study of animal learning, a perspective that had been lacking since Edward Thorndike initiated the field in 1898 (Galef, 1988).

A second revolution in understanding food selection lay in Paul Rozin's (1967) brilliant turning

on its head of Curt Richter's (1943) classic work on self-selection of nutritionally adequate diets. Richter had shown that, for example, Norway rats deprived of thiamine and then given a choice between thiamine-deficient and thiamin-rich foods preferred the latter. He interpreted such adaptive patterns of food choice as reflecting the action of unlearned specific appetites for each micronutrient that animals needed to prosper. Rozin explained the same adaptive pattern of food selection by nutritionally deficient animals as resulting from the acquisition of learned aversions to any foods eaten during the period when symptoms of dietary deficiency were emerging. Rozin thus treated deficiency states as illnesses that induced behavioral consequences homologous to those that Garcia had postulated in learned aversions to more conventional poisons.

This wave of unexpected findings concerning food selection in rats suggested that understanding how rats learned what to eat and what to avoid eating might be important in understanding behavior more generally, and interest in the study of food choice in rats was widespread among experimental psychologists.

Why Social Learning?

Clearly, the food choices of humans are profoundly influenced by social context, with foods considered inedible in some populations (e.g., insect pupae) treated as highly desirable in others. However despite Harlow's early experiments (Harlow, 1932) demonstrating social influences on food intake in Norway rats and von Frisch's (1967) extraordinary demonstrations of social effects on food selection in honey bees (*Apis mellifera*), those interested in feeding behavior (and in animal learning more broadly) had generally ignored the possibility that social learning was important in mammals' acquisition of adaptive behavioral repertoires. Consequently, studies of the social transmission of information concerning what to eat and what to avoid eating seemed to provide entrée into an aspect of behavioral development that had received far less attention from those interested in feeding behavior in particular, and behavioral development in general, than it might deserve. Indeed, armchair speculation suggested that social learning should be important in the development of many aspects of a young mammal's behavioral repertoire.

Many of the things that young mammals must learn, they must learn rapidly and, to the extent possible, without incurring whatever costs are an

inevitable consequence of the mistakes that are an important part of trial-and-error learning. In particular, weaning mammals leaving the relative safety of a burrow or nest where they have been provisioned by their parents have to find a nutritionally adequate diet both before they exhaust their limited internal reserves of food and without ingesting harmful amounts of toxins. Most important, any young mammal must learn to choose appropriate foods in an environment that it shares with a parent or other adults. To have survived, every adult must have learned to respond adaptively to each of the many challenges posed by its local environment. Consequently, a juvenile should be able to increase its relative fitness by parasitizing information from the locally adaptive behavior patterns of adults with which it interacts.

In the late 1960s, the suggestion that the food choices of rats might be influenced by "information" that they had extracted from others of their species was not likely to be well received by experimental psychologists. Indeed, talk of "information" in discussing animal behavior was pretty much taboo in North America so long as behaviorism provided the dominant perspective, as it surely did in the late 1960s. However, by the mid-1970s the grip of behaviorism on the study of behavior in North America had substantially weakened, and tolerance for more cognitive approaches to the study of animal behavior was increasing rapidly.

Why Norway Rats?

Because so little is known of the historical environment in which Norway rats evolved, the study of their behavior is, perhaps justifiably, highly suspect in some circles. Yet Norway rats seemed particularly appropriate animals for investigation of social influences on feeding behavior. Wild Norway rats are highly social animals that, in natural environments, live in colonies that vary in size from a mere handful to many hundreds of individuals (Telle, 1966).

Members of each colony share a burrow system, a place of refuge, from which colony members emerge to forage during the hours from dusk until dawn and to which they return between foraging bouts (Chitty, 1953). Such comings and goings of foragers from a shared burrow system would appear to provide ample opportunity for exchange of information among burrow residents about the foods and feeding sites that they are exploiting (e.g., Ward & Zahavi, 1973).

Norway rats are not only highly social, central-place foraging animals, they are also dietary generalists. They have to compose a nutritionally adequate diet from numerous constituents, and as a consequence of planet-wide dispersal by humans, rats often live in environments far removed from that in which the species evolved. Rats could not depend on evolved, hedonic responses to valuable foods found in their ancestral native environment (wherever it may have been) to guide their food selection in adaptive directions. Consequently, if members of any animal species learn about foods by extracting information from others of their species, Norway rats seemed likely candidates. Further, there was even a report in the literature (Steiniger, 1950) that provided observational evidence consistent with the view that Norway rats might learn from one another what to eat and what to avoid eating.

In the dark ages before the coming of Google, finding relevant literature was a challenge that demanded skills that have been rendered largely, but not completely, irrelevant by modern search engines (there is, after all, a considerable literature published before 1976, and much important work has been published in places other than refereed journals). Consequently, even today, numerous gems surely lie undiscovered in early journals, foreign languages, and edited books.

Among these invisible, but valuable, works was a paper with the unappealing title *Beitrage zur Soziologie und sonstigen Biologie der Wanderratte* written by an applied ecologist, von Fritz Steiniger (1950), who had spent a substantial portion of his career improving the efficiency of rodent-control measures in his native Germany. Steiniger had found that if he used the same poisoned bait in a rat-infested area for an extended period of time, despite great initial success, over time acceptance of the bait fell radically and remained extremely low.

Steiniger (1950) attributed this "traditional" poison avoidance, as he called it, to the behavior of older members of a clan, noting that their offspring refused even to sample a poisoned bait for themselves so long as a few animals remained in their colony that had learned directly to avoid it. If Steiniger's interpretation of his observations were correct, Norway rats learned socially what foods to avoid eating.

Most important for the initial success of studies of Norway rats' social learning about foods, in the late 1960s, most research on feeding behavior in animals was carried out using Norway rats as subjects. As a result, not only were a wide variety of

techniques available for studying the feeding behavior of rats, but findings on social aspects of rats' feeding behavior could be integrated easily into a large and growing body of knowledge.

Why Laboratory Studies?

Although observations of free-living animals such as Steiniger's (1950) were important in calling attention to a potentially very interesting behavioral phenomenon, observation in uncontrolled environments is rarely sufficient to determine the behavioral processes supporting an observed behavior. For example, and as mentioned above, Steiniger (1950) had observed that Norway rats born to a colony whose adults had learned to avoid ingesting a particular poison bait would not eat that bait. He hypothesized that adult rats deposited urine and feces on a food that they had learned to avoid and that these residual cues dissuaded younger, less experienced, colony members from ingesting marked foods.

While Steiniger's behavioral observations of behavior were surely accurate, his hypothesis concerning the cause of the behavior that he observed was probably not. Indeed, as discussed in a subsequent section, the presence of urine and feces at a potential feeding site increases, rather than decreases, the attractiveness of that site to young rats, though there is no way Steiniger could have known that from simply observing the feeding behavior of free-living colonies of rats.

Norway Rats' Social Learning About Foods

In late 1969, as a new assistant professor, I started laboratory work on the possibility that Norway rats making decisions as to which available substances to ingest and which to refrain from eating might rely, to greater or lesser extent, on information obtained from others of their species. Luckily, young wild rats' avoidance of a food that the adult members of their colony have learned to avoid described by Steiniger (1950) is a robust phenomenon, easily brought into the laboratory for analysis under controlled conditions.

My students and I spent many evenings trapping adult, wild Norway rats on garbage dumps in southern Ontario. We established the animals we had captured in mixed-sex groups of five or six in 2-m² enclosures, where for 3 hours each day we fed them two nutritionally balanced foods that differed from one another in color, taste, and smell.

To begin an experiment, we introduced a nauseating agent into one of the two foods that we provided each colony. Colony members rapidly learned

to avoid eating the noxious food and to eat only the safe alternative available to them. Most important, and as John Garcia would surely have predicted, for weeks after they learned to avoid a food, adult colony members would not eat the food that had been associated with illness, even when we provided them with uncontaminated samples of it. Then we waited for young to be born and to grow to weaning age.

When the pups began to leave their nest sites to eat solid food for the first time, we observed them throughout colony feeding periods on closed-circuit television and recorded the frequency with which the pups fed on each of the two, now uncontaminated, foods present in their colony enclosure. We found, as Steiniger (1950) had reported, that so long as pups remained with the adults of their colony, the pups ate only the food the adults were eating and totally avoided the alternative that we had trained the adults to avoid. Even after we removed pups from their colony's enclosure, put them in individual cages, and offered them uncontaminated samples of the same two diets we had provided for the colony that reared them, the pups continued for some days to avoid the food that the adults of their colony had learned to avoid (Fig. 40.1).

A series of experiments that I will not describe here in great detail (Galef & Clark, 1971a) revealed that, contrary to Steiniger's hypothesis, young rats

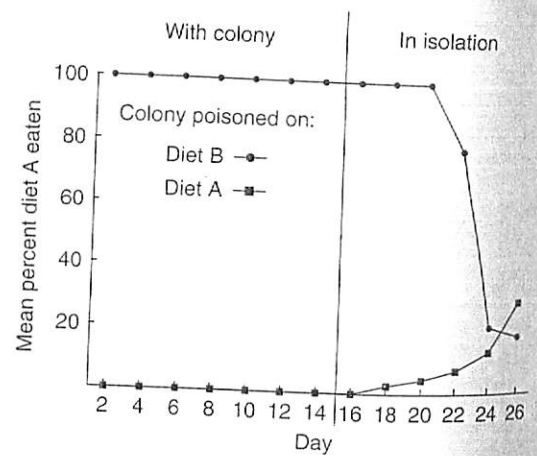
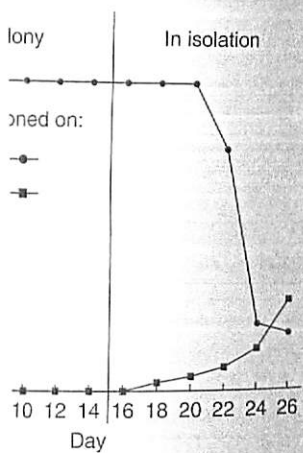


Fig. 40.1 Mean number of times that juvenile wild Norway rats ate diet A as a percentage of the total number of times juveniles ate both diets A and B during daily 3-hour feeding periods on the first 26 days that they fed on solid food. *Left panel:* Days when juveniles were caged with adults. *Right panel:* Days when juveniles were housed individually. Abscissa represents number of days since pups started to eat solid food (Galef, 2007; by permission of Chicago University Press).

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Number of times that juvenile wild Norway rats fed on solid food during daily 3-hour feeding periods. Left panel: rats were caged with adults. Right panel: rats were housed individually. Abscissa shows days since pups started to eat solid food (University of Chicago Press).

were not learning to avoid the food that the adults of their colony were avoiding. Wild Norway rats are extremely reluctant to eat any food that they have not previously eaten, and if offered only an unfamiliar food to eat, will often starve themselves for days before they begin to sample it (Barnett, 1958; Galef, 1970; Rzoska, 1953). Consequently, once rats have learned to eat one food, they are unwilling to ingest available alternatives (for review, see Galef, 1985), and as indicated in the next section, young rats learn what foods to eat by interacting with adults.

Mechanisms of Social Learning About Foods

Several decades of work both in my laboratory and elsewhere have revealed a half-dozen different ways in which rats are able to influence one another's food choices. Such transfer of information about foods begins before birth and extends throughout the lives of rats.

Prenatal Learning

After weaning, a rat pup that has been exposed while still in its mother's womb to a flavor injected into her amniotic fluid shows an enhanced preference for a food containing the flavor experienced *in utero* (Smotherman, 1982). Further, in the days following birth, young rats born to a dam who while pregnant ate a food with a strong odor (such as garlic) show an enhanced preference for the odor of the food that their dam ate (Hepper, 1988).

Taken together, Smotherman's (1982) and Hepper's (1988) findings are surely consistent with the view that flavors of foods a Norway rat ingests while pregnant will affect the post-weaning food preferences of her young, though these findings alone do not provide direct evidence that exposure to a flavor *in utero* affects food choices at weaning. Billko, Altbacker, and Hudson (1994) have provided direct evidence that the flavor of the food that a rabbit (*Oryctolagus cuniculus*) dam eats while pregnant affects the food preferences of her pups at weaning, and there is no reason to believe that Norway rats differ from rabbits in this respect.

Learning While Nursing

Researchers in several laboratories have found that the flavors of foods that a lactating female rat eats during the period she is suckling her young enter her milk, and when the young wean to solid food, they prefer foods that their dam ate while suckling them (Bronstein et al., 1975; Galef & Henderson, 1972; Galef & Sherry, 1973; Martin & Alberts,

1979). Consistent with such a view, when we expressed milk by hand from a lactating "donor" rat maintained on a distinctively flavored diet and fed that milk to rat pups whose own mother was eating a bland diet, the pups subsequently showed an increased preference for the diet that their donor mother had eaten (Galef & Sherry, 1973).

Learning While Weaning

When a young rat leaves the safety of its natal burrow to seek its very first meals of solid food, it looks for adults at a distance from the burrow entrance, approaches them, and begins to feed in their immediate vicinity. Pups often come up to an adult from behind, crawl along its belly to emerge directly under the adult's chin, and begin to feed there. Consequently, rat pups tend to take their very first meals of solid food from a food site that a feeding adult is exploiting (Galef & Clark, 1971b). Pups that have been rendered unable to see do not show similar movement towards adults feeding a few meters from a burrow entrance and, consequently, do not take their first meals where adults are eating (Galef & Clark, 1971b).

Even an anesthetized rat draped over a food bowl is attractive to young rats, and they will approach and eat far more frequently from whichever of two available food bowls has an anesthetized adult draped over it (Galef, 1981).

Adults need not be physically present at a feeding site to cause pups to prefer a site the adults have exploited to sites adults have not visited. While feeding, adult rats deposit residual cues both on food and in its vicinity, and young rats rely on such cues to guide their choice of a location in which to forage (Galef, 1981; Galef & Beck, 1985; Galef & Heiber, 1976; Laland & Plotkin, 1991). Further, when an adult rat leaves a feeding site to return to its burrow, it deposits a scent trail that serves as a guide for young rats seeking food, bringing them to a location from which adults have returned (Galef & Buckley, 1996). In general, and contrary to Steiniger's (1950) suggestion that adult rats dissuade young from eating poisoned baits by urinating and defecating on them, residual odors left by adult rats at sites that they have visited are attractive, rather than repulsive, to rat pups.

Learning Throughout Life

Perhaps most surprising, and consequently most thoroughly studied, interactions between rats taking place far from a feeding site can influence the subsequent food choices of rats of all ages (as well

as other mammals, from bats [Ratcliffe & ter Hofstede, 2005] to hyenas [Yoerg, 1991; see Galef, 1996, for review]).

After a naïve (observer) rat interacts with a conspecific (demonstrator) that has eaten a food, the observer rat shows a long-lasting enhancement of its preference for the food that its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984). For example, when we gave observer rats a choice between cinnamon- and cocoa-flavored foods a month after they had interacted for 30 minutes with demonstrator rats fed either cinnamon- or cocoa-flavored food, those observer rats whose demonstrators had eaten cinnamon-flavored food ate a significantly greater percentage of that food than did observer rats whose demonstrators had eaten a cocoa-flavored diet (Galef, 1989; Galef & Whiskin, 2003).

Such socially transmitted food preferences are not only durable, they are also surprisingly potent. We taught observer rats to avoid eating a palatable, unfamiliar diet by injecting them with a nauseating agent immediately after they ate it, and a day later allowed these observers to interact with demonstrator rats that had either eaten or not eaten the diet that the poisoned rats had been trained to avoid. We then gave both groups of observer rats a choice between the diet that we had trained them to avoid and an unfamiliar diet.

As expected, poisoned observer rats that had not interacted with demonstrators fed the diet that the observers had eaten before becoming ill ate almost none of it. However, observer rats that had interacted with demonstrator rats fed the diet that the observers had been trained to avoid ate as much of that diet as did naïve, unpoisoned rats simply offered a choice between the same two diets. Social information totally reversed a profound, learned, taste aversion (Galef, 1986).

Social information can also reverse preferences based on diet palatability. Rats normally dislike rat chow that has been adulterated with cayenne pepper. However, after interacting with demonstrator rats that had eaten cayenne-pepper-flavored rat chow, many observer rats actually preferred that diet to unadulterated rat chow (Galef, 1989).

What Causes the Change in Observer Rats' Food Preferences?

The question of how demonstrator rats effect changes in the food choices of their observers can be divided into two separate questions: (1) How do rats identify foods that other rats have eaten? and

(2) What causes the change in observer's food preferences for foods that they learn demonstrators have eaten?

A series of studies have revealed, first, that only those observer rats that sniff at the mouth of a demonstrator rat show enhancement of their preference for a food that a demonstrator ate, and second, that both food odors escaping from the digestive tract of a demonstrator rat and the scent of bits of food clinging to its fur and vibrissae allow an observer to determine what food its demonstrator has eaten (Galef & Stein, 1985).

However, simply smelling a food is not sufficient to cause an observer rat to increase its preference for that food. Only if an observer rat experiences the scent of a food and the breath of another rat simultaneously will the observer rat show enhanced preference for a food (Galef & Stein, 1985). For example, exposing an observer rat to a food on the rump of a live, anesthetized rat or on the head of a dead rat does not cause any increase in the observer's preference for that food, whereas exposing an observer to the same food on the head of an anesthetized, live rat does result in the observer having an enhanced preference for the food in question (Galef & Stein, 1985).

Gas chromatography has shown that rat breath contains large quantities of two sulfur compounds: carbon disulfide and carbonyl sulfide. Rats exposed to a food moistened with a dilute solution of carbon disulfide subsequently show an enhanced preference for that food, whereas rats exposed to the same food moistened with distilled water do not (Galef, Mason, Preti, & Bean, 1988).

Taken together, the results described in the preceding two paragraphs strongly suggest that there is something about the breath of rats that is important in changing the food preferences of their observers.

Perhaps surprisingly, it isn't just rat breath that will change an observer rat's food preferences. If a human "demonstrator" eats cinnamon- or cocoa-flavored food and then breathes on a rat observer before the observer rat is offered a choice between cinnamon- and cocoa-flavored foods, observer rats that interacted with a human demonstrator who ate cinnamon-flavored food show a greater preference for cinnamon-flavored food than observer rats that interacted with a human demonstrator who ate cocoa-flavored food (Galef, 2005; Lupfer-Johnson, personal communication). Given that carbon disulfide is a constituent of both rat and human breath, perhaps the ability of humans to act as demonstrators for rats isn't so surprising after all.

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Sophistication in Rats' Communications About Foods

In natural circumstances, before a rat leaves its burrow to forage, it may well interact not only with several rats, each of which has eaten a different food, but also with individual rats that have each eaten several different foods. Consequently, if free-living rats are to use all of the information that they might acquire from conspecifics, they would have to be able not only to remember information extracted from multiple demonstrators, but also to decode complex olfactory signals emitted by individual demonstrators. There is reason to believe rats have such abilities.

If an observer rat interacts with a series of demonstrator rats, each of which has eaten a different food, the observer subsequently shows enhancement of its preference for each of the foods eaten by its various demonstrators. So, for example, an observer rat offered a choice between cinnamon- and cocoa-flavored diets after it has interacted with four demonstrator rats, one fed cinnamon-, one fed vinegar-, one fed coffee-, and one fed marjoram-flavored diet will eat more cinnamon-flavored diet than an observer rat offered the same choice after interacting with four demonstrator rats, one fed cocoa-, one fed vinegar-, one fed coffee-, and one fed marjoram-flavored diet (Galef, 1983).

Similarly, if a demonstrator rat eats several different foods before it interacts with an observer rat, the observer develops a preference for each of the foods that its demonstrator ate. For example, in one experiment, before each member of one group of demonstrator rats (Group 1) interacted with an observer, we fed the demonstrator a three-flavored diet (for example, anise-, cocoa-, and marjoram-flavored rat chow). At the same time, we fed each member of a second group of demonstrator rats (Group 2) anise-, cinnamon-, and marjoram-flavored rat chow before it interacted with an observer. We then offered each observer rat a choice between cinnamon- and cocoa-flavored rat chow. We found that observers in the Group 1 preferred cocoa-flavored diet whereas observers in Group 2 preferred cinnamon-flavored diet (Galef, Attenborough, & Whiskin, 1990).

In the real world, two rats that have each eaten different foods are likely to interact with one another, so there should be opportunity for information exchange between rats rather than for a unidirectional extraction of information by an observer rat from a demonstrator conspecific. To mimic such a situation, we fed one rat subject (Condition 1)

either cinnamon- or cocoa-flavored diet and a second rat subject (Condition 2) either anise- or marjoram-flavored diet before allowing rats assigned to Conditions 1 and 2 to interact. We then offered subjects assigned to the Condition 1 a choice between anise- and marjoram-flavored diets and subjects assigned to Condition 2 a choice between cinnamon- and cocoa-flavored diets (Galef, 1983). As might be expected, given the results of our previous experiments, rats assigned to both Condition 1 and Condition 2 showed enhanced preferences for the foods that their respective partners had eaten.

Consequences of Rats' Social Learning About Foods

Invading Novel Environments

Availability of social information concerning the foods that others are eating can have important consequences for rats living in environments where simply eating whatever palatable foods are available does not lead to construction of a nutritionally adequate diet.

When we introduced individual young rats into enclosures where they had access to four different foods only the least palatable of which contained sufficient protein for normal growth and development, the young rats failed to eat sufficient amounts of the protein-rich food to prosper. They rapidly lost weight and surely would have died if left in the situation for more than a few days. In contrast, pups that shared their enclosures with adults that we had trained to eat the unpalatable, protein-rich diet grew at almost the same rate as pups maintained on a standard laboratory chow (Beck & Galef, 1989). Subsequent analysis showed that exposure to information carried on the breath of the demonstrator rat, rather than attraction to the feeding site it was exploiting, was critical in increasing subjects' intake of the protein-rich food (Galef et al., 1991).

The finding that young rats can learn socially to eat an unpalatable, but necessary, food suggests that portions of the environment that are closed to invasion by rats because some necessary nutrient is available only in an unpalatable potential food that rats are unlikely to select can be invaded by rats once a single individual learns to eat the unpalatable food. Terkel's (1996; Aisner & Terkel, 1992) demonstration that roof rats (*Rattus rattus*) learn socially to strip the scales from pinecones has a similar implication. Efficient exploitation of pinecones for food has permitted roof rats to invade pine forests in both Israel and Corsica that would otherwise be closed to them (Landova et al., 2006). Although, as yet, there

is no evidence from outside the laboratory that learning socially to eat unpalatable foods has permitted rats to invade otherwise inaccessible areas, the possibility of such a discovery remains an exciting possibility.

Traditional Exploitation of Foods

A little more than a half-century ago, Steiniger (1950, p. 368) suggested that Norway rats “appear especially able to develop local traditions, more so perhaps than other more-closely examined mammals, possibly including the anthropods.” Steiniger based this suggestion on comparisons of the feeding behaviors of allopatric populations of free-living Norway rats. For example, many members of some colonies of rats living along the banks of the Po River in northern Italy dive for mollusks that inhabit the river bottom, whereas no members of nearby colonies do so (Gandolfi & Parisi, 1992), and on the island of Norderoog in the North Sea, rats frequently stalked and killed sparrows and ducks (Steiniger, 1950), although they have not been reported to do so elsewhere; etc.

Steiniger’s method is an example of what has been called the “ethnographic,” “geographic,” or “group contrasts” method in more recent discussions of traditions in free-living primates (Fragaszy & Perry, 2003; van Schaik et al., 2003; Whiten et al., 1999). While the findings resulting from the method of group contrasts may suggest the existence of traditions based on social learning, it is difficult to exclude ecological causes of the differences in behavior seen in populations living in different environments. For example, Galef (1980) found that when alternative sources of nutriment are available on land, diving is inhibited in Norway rats that have previously dived for food. Possibly the reason why some colonies of rats along the Po River dive and other nearby colonies don’t reflects differences in the abundance of food in colony territories on land.

Although there is considerable evidence consistent with the view that free-living animals develop behavioral traditions, experimental evidence of patterns of behavior passed from generation to generation in rats or any other animal is rare. To determine whether social learning could support a tradition of food choice lasting for generations, one of my graduate students and I created two types of colonies and taught all four members of each of a dozen colonies of rats maintained in large floor enclosures to avoid eating either a base diet flavored with horseradish or the same base diet flavored with cayenne pepper (Galef & Allen, 1995).

Once the members of each colony were reliably eating the appropriate food, immediately after each colony’s daily feeding period ended, we removed one colony member and replaced it with a naïve rat. After 4 days, we had replaced all original colony members, and for 10 days thereafter, we replaced the most senior remaining member of each colony with a naïve rat. As can be seen in Figure 40.2, even after we had replaced the replacements of the replacements of the original colony members, we could still see clear effects of the food choices learned by original colony members on the food choices of their “descendants” (Galef & Allen, 1995).

In subsequent experiments (Galef & Whiskin, 1997) we found that: (1) the longer colonies had access to food each day, the less stable the tradition, (2) the shorter the time each rat spent as a colony member before being replaced, the more stable the tradition, and (3) the more palatable the food that a colony has been trained to avoid, the less stable the tradition. Taken together, these results suggest that a complex interplay of direct personal experience of the consequences of eating available foods and social acquired information as to which food to eat affects the stability of traditions in colonies of animals (for further discussion, see Galef, 2009).

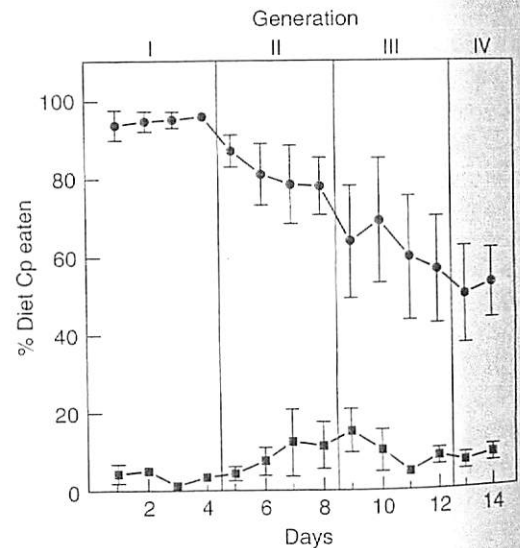


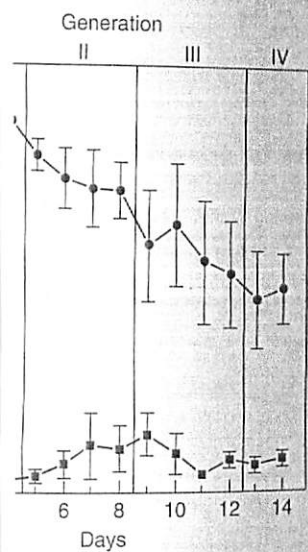
Fig. 40.2 Mean + SEM amount of cayenne-pepper-flavored diet (diet Cp) ingested as a percentage of total amount eaten by subjects offered both diets Cp and wasabi-flavored diet (diet W) in colonies where founding colony members ate only diet Cp (circles) or only diet W (squares). On day 1, enclosures contained only founding colony members; on days 2 to 4, both founding colony members and some replacement subjects; on days 5 to 14, successive generations of replacement subjects (Galef & Allen, 1995; by permission of the American Psychological Association).

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Summary

The picture that has emerged from 40 years of study of foraging traditions in Norway rats is that of a species able to exchange complex olfactory information concerning currently available foods. The evidence suggests that such information allows a colony burrow to serve as an information center (Galef, 1991) where successful foragers exchange information about the foods they are exploiting and unsuccessful foragers can learn what foods are available in the environment where they and their burrow mates are foraging. Such socially acquired information should permit rats to learn to exploit potentially valuable sources of nutrition that they might otherwise fail to recognize.

Things that Remain Difficult

for Me to Understand

Learning from Unhealthy Demonstrators

Perhaps the single most surprising finding regarding rats' sophisticated capacity for social learning about foods is the repeated observation that naïve observer rats acquire a preference for a food after interacting with a sick or unconscious demonstrator rat that has eaten that food (Galef, McQuoid, & Whiskin, 1990; Galef, Wigmore, & Kennett, 1983; Grover et al., 1988). Both sophisticated formal models of social learning and common sense suggest that rats should not copy the food choices of sick or unconscious animals, yet they very clearly do.

Although we have no definitive answer to the question of why rats appear to behave in such suboptimal fashion, there are some interesting speculations as to why rats should prefer, rather than avoid, foods eaten by those of their fellows that are obviously ill. For example, if rats that are living without exposure to human attempts to poison them (as rats surely have throughout most of their evolutionary history) rarely encounter toxic foods, so that they rarely become ill as a consequence of eating undesirable substances, then avoiding foods eaten by ill conspecifics might well be counterproductive. Rats, like other animals, become ill for a variety of reasons. They suffer from viral, bacterial, and parasitic infections. They experience noninfectious diseases of various kinds. If illness due to causes having nothing to do with ingestion is far more common in rat populations than is illness due to ingesting toxins, then failing to learn to prefer foods that ill conspecifics have eaten might result in lost opportunity costs that outweigh the rare advantage to be gained from avoiding foods eaten by demonstrator rats that are ill. And there is reason to believe

that rats that have become sick as a result of eating something toxic are rarely encountered in natural circumstances. Because wild rats (1) are extraordinarily hesitant to eat unfamiliar foods, (2) sample unfamiliar potential foods warily at first, and (3) associate gastrointestinal upset with any unfamiliar foods they have eaten, wild rats are unlikely repeatedly to ingest any toxic substance. Consequently, a naïve rat is quite unlikely to interact with rat that is ill because it ate something poisonous.

The probable rarity of encounters with rats ill because they ingested a toxin may have impeded evolution of behavioral mechanisms inhibiting a positive response to information regarding a food that ill rats have eaten (see Galef, 1991a, for further discussion). A similar hypothesis has been given elegant expression in a formal model demonstrating the feasibility of evolution of rats that do not learn to avoid eating foods eaten by ill conspecifics. The basic assumption of this model is that environmental toxins invariably kill those that ingested them, thus reducing the probability that poisoned rats would interact with conspecifics to zero (Tuci, Noble, & Todd, 1999). Of course, the unlikelihood of such extraordinarily lethal toxins poses a problem for the application of the model to events in the real world. However, as indicated above, factors other than the lethality of toxins could markedly reduce the probability that naïve individuals would interact with others that had recently eaten a toxic potential food, and could therefore similarly reduce the probability of evolution of a mechanism for learning to avoid foods eaten by sick conspecifics.

Specificity of Social Learning About Foods

It might be expected that experience of a food odor on the breath of a conspecific would increase the general attractiveness of that odor to those that had experienced it. However, rats do not develop a general affinity for an odor experienced while interacting with a conspecific demonstrator. To the contrary, it appears to be only appetite for foods that is affected by such experience. For example, as indicated numerous times above, when we offered an observer rat that had interacted with a demonstrator rat fed cinnamon-flavored food a choice between cinnamon- and cocoa-flavored food, it ate more cinnamon-flavored food than an observer rat that had interacted with a demonstrator rat that had eaten cocoa-flavored food. However, such observers did not prefer cinnamon-scented to cocoa-scented nesting material or cinnamon-scented to cocoa-scented nest boxes (Galef & Iliffe, 1994).

Such findings suggest that social induction of food preference is a learning process evolved specifically to facilitate foraging rather than the myriad other activities in which rats engage. Exactly how this works remains an unexplored mystery. Perhaps, as Hoppitt and Laland (2008) have recently proposed, social learning about foods, like long-delay learning, is an adaptive specialization of the feeding system, an hypothesis that is intriguing but difficult to test, at least at the behavioral level of analysis.

Using Rats' Social Learning About Foods as a Model System to Test Predictions from Formal Theories of Social Learning

One of the more interesting developments in the study of social learning during the past two decades is the introduction of formal mathematical models that consider: (1) the circumstances under which organisms choosing among alternative courses of action would be better advised to depend on socially acquired information than on their own prior experiences, and (2) which of the many conspecifics that a naïve individual might encounter it should use as a model for its own behavior.

All formal models start with the assumption that learning for oneself the consequences of alternative actions is costly. Not only is there some likelihood that errors will be made, but the time spent in exploring alternatives can involve exposure to predators, toxins, or other environmental threats. Such costs of individual learning suggest that it might be advantageous to invariably copy others. However, formal analyses have shown repeatedly that, although under some circumstances copying the behavior of others can reduce the cost of acquiring adaptive behaviors, copying others does not invariably enhance fitness. Copying others can lead to increased competition for resources, or the information provided by others may be out of date.

To take an extreme example, if everyone allowed the behavior of others to guide their own behavior and the environment changed, then, because no individual would be monitoring the environment, social learning would not result in population members acquiring adaptive behavior (Rogers, 1988). Or, more realistically, as argued among others by Boyd and Richerson (1985), in an environment that varies over either space or time (as essentially all

Table 40.1 Summary of the Relationship to Predictions from Formal Theory of Results of Experiments Examining "When" and "Who" Strategies of Norway Rats' Learning Socially About Foods

"When" Strategies	
Copy when established behavior is unproductive	Consistent
Copy when asocial learning is costly	Inconsistent
Copy when uncertain	Consistent
Copy when dissatisfied	Consistent
Copy when the environment is stable	Consistent
"Who" Strategies	
Copy older individuals	Inconsistent
Copy kin	Opposite to predicted outcome
Copy familiar individuals	Inconsistent
Copy successful individuals	Inconsistent
Copy if better	Inconsistent
Copy the majority	Possibly consistent
Copy good social learners	Inconsistent

(Adopted from Galef, 2009, with the permission of Elsevier)

environments do) a rat only adopt the behavior was adaptive in some time. As a result of... as to whether to... acquired information accuracy and cost... accurate and up-t... tion, while social... potentially outdat...

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environments do) a naïve individual might mistakenly adopt the behavior of a model whose behavior was adaptive in some other locale or at some prior time. As a result of such considerations, the decision as to whether to rely on individually or socially acquired information involves a trade-off between accuracy and cost. Individual learning provides accurate and up-to-date, though costly, information, while social learning provides cheap, but potentially outdated or misleading, information.

Further, adopting the behavior of some potential models (for example, the successful or experienced) should be more beneficial than adopting the behavior of other potential models (for example, the unsuccessful or inexperienced). Consequently, to optimize fitness, animals should have evolved strategies that both define the conditions when increased reliance on social learning would be adaptive (“when strategies”) and determine who social learners should choose as models (“who strategies”; e.g. Boyd & Richerson, 1985; Enquist et al., 2007; Giraldeau et al., 2002; Rogers, 1988). Some of the predictions from a range of formal models are summarized in Table 40.1, adopted from a review by Laland (2004) that provides a concise overview of the literature concerning both “when” and “who” strategies.

Norway rats’ social learning about foods provides a convenient model system for testing such predictions from formal theory. Table 40.1 also provides a summary of results of our explorations of a number of “who” and “when” strategies. It is a fairly simple matter to ask, for example, whether, as theory predicts, rats are more likely to prefer foods eaten by familiar or unfamiliar models, or whether rats eating a nutritionally deficient diet, and therefore relatively dissatisfied, are more likely than rats eating an adequate diet, and therefore relatively satisfied, to rely on social information when selecting foods. I have recently reviewed this work at length elsewhere (Galef, 2004, 2009), so here I provide only two examples of our work: first, an examination of the “who strategy” “copy familiar individuals,” and second, tests of the “when strategy” “copy when dissatisfied.”

Who Strategies

The procedures that we used to examine the tendency of rats to adopt the food choices of older individuals (Galef & Whiskin, 2004), familiar kin (Galef & Whiskin, 2008), and successful individuals (Galef et al., 1983, 1990) were similar. In each case, we allowed observers to interact with demonstrators fed either cinnamon- or cocoa-flavored diet

(counterbalanced across the two types of demonstrator) that were: (1) older or younger than their observers, (2) familiar kin or unfamiliar non-kin to their observers, or (3) relatively successful or unsuccessful. In each case, we determined which type of demonstrator had greater effect on its observers’ food choices.

COPY FAMILIAR KIN OR UNFAMILIAR NON-KIN

We fed demonstrators either cinnamon- or cocoa-flavored diet for 1 hour and then placed each demonstrator with an observer that was either: (1) both born and weaned in the same litter as the demonstrator and a cage mate of the demonstrator from weaning to testing at 35 days of age (familiar/kin), or (2) born into a litter and reared and maintained separate from its demonstrator (unfamiliar non-kin). At the end of the period of interaction of demonstrators and observers, we offered each observer a choice between cinnamon- and cocoa-flavored diet for 23 hours. Contrary to prediction, the food choices of observers that had interacted with familiar and unfamiliar demonstrators were similar (Galef & Whiskin, 2008; left panel of Fig. 40.3).

In a second study, we permitted each observer rat to interact simultaneously with two demonstrator rats—one fed cinnamon- and the other cocoa-flavored diet and one familiar kin and the other

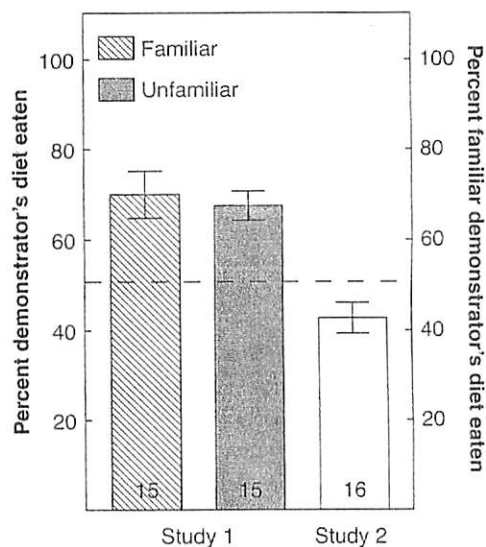


Fig. 40.3 Left two bars: Mean + SEM percentage of demonstrator’s diet eaten by observers that interacted with either a familiar or unfamiliar demonstrator. Right bar: Mean + SEM percentage of familiar demonstrator’s diet eaten by observers that interacted with familiar and unfamiliar demonstrators simultaneously (Galef & Whiskin, 2008; reprinted by permission of Elsevier).

unfamiliar non-kin—and once again then offered each observer a choice between cinnamon- and cocoa-flavored diets. As can be seen in the right panel of Figure 40.3, contrary to prediction from formal theory, the observers that had interacted with unfamiliar non-kin showed marginally greater ($p < 0.07$) social influence on their food choices than did observers that had interacted with familiar kin (Galef & Whiskin, 2008). When we repeated the experiment, we again found a marginally greater effect ($p < 0.07$) of unfamiliar than of familiar demonstrators on their observers' food choices (Galef & Whiskin, 2008). We conducted two additional experiments to try to better understand this failure of predictions from logically consistent formal theory to predict the behavior of our subjects.

Previous experience working with Norway rats suggested that when two rats meet for the first time they engage in unusually prolonged olfactory interaction. We hypothesized that the duration of exposure of an observer to olfactory cues emanating from a demonstrator influences the magnitude of the effect that demonstrator has on its observer's subsequent food choices. To determine whether rats spend longer interacting with unfamiliar than familiar individuals, we placed an observer rat in the central compartment of a choice apparatus separated from conspecific demonstrators held behind screen partitions. The demonstrators were restrained at opposite ends of the central compartment. One demonstrator was a familiar cage mate of the subject rat and the other was totally unfamiliar to it; one had eaten cinnamon-flavored and the other cocoa-flavored diet.

We observed the three rats for 30 minutes and determined how much time the focal subject rat spent near each of the restrained rats and found, as expected, that observer rats spent significantly more time interacting with their unfamiliar than with their familiar demonstrator (Fig. 40.4; Galef & Whiskin, 2008). When we subsequently offered the observers in isolation a choice between cinnamon- and cocoa-flavored diet, they again preferred whichever diet their unfamiliar demonstrator had eaten.

Of course, the finding that rats spend more time interacting with unfamiliar than familiar rats does not take us very far in understanding why unfamiliar demonstrators have greater effect than familiar demonstrator rats on their observers' subsequent food preferences. We also need to know whether the duration of interaction between a demonstrator and observer affects the magnitude of the effect that

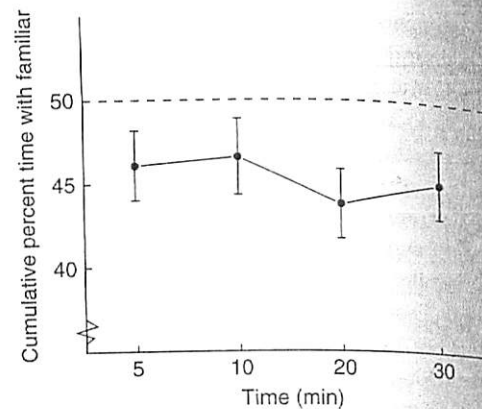


Fig. 40.4 Mean + SEM percent time during a 30-minute test that observer rats spent within 10 cm of familiar and unfamiliar demonstrators. Horizontal line indicates the mean expected percentage of time observers would spend with familiar observers if observer familiarity had no effect (Galef & Whiskin, 2008; reprinted by permission of Elsevier).

demonstrators have on their observers' subsequent food preferences.

It would be challenging to either control or measure the amount of olfactory information passing from a rat demonstrator to a rat observer. However, the finding discussed above that humans can serve as effective demonstrators for rats (Galef, 2005; Lupfer-Johnson, personal communication, 2008) allowed us to compare the magnitude of rat observers' food choices when exposed to 1, 2, 10, 20, or 40 breaths from a human demonstrator that had just eaten 10 g of either cinnamon- or cocoa-flavored food.

We found a significant positive linear relationship between the number of breaths to which observers had been exposed and their reliance on socially acquired information when subsequently choosing between cinnamon- and cocoa-flavored food (Fig. 40.5; Galef, 2009). The failure of the prediction from formal theory as to the effect of familiarity of demonstrators on their observers can thus be explained as a consequence of aspects of the social behavior of rats having nothing to do with social learning (see Galef, 2009, for further discussion).

When Strategies

We made rats "dissatisfied" (we hope) in several different ways: (1) by making them ill either by injecting them with a toxin or feeding them a deficient diet, (2) by maintaining them for days on a diet that was unpalatable either because it was adulterated with non-nutritive filler or cayenne pepper, or (3) by maintaining them in an excessively warm,

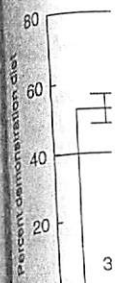
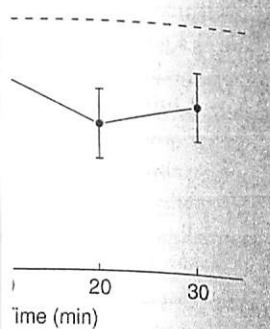


Fig. 40.5 Mean + SEM percent time during a 30-minute test that observer rats spent within 10 cm of familiar and unfamiliar demonstrators. Horizontal line indicates the mean expected percentage of time observers would spend with familiar observers if observer familiarity had no effect (Galef & Whiskin, 2008; reprinted by permission of Elsevier).

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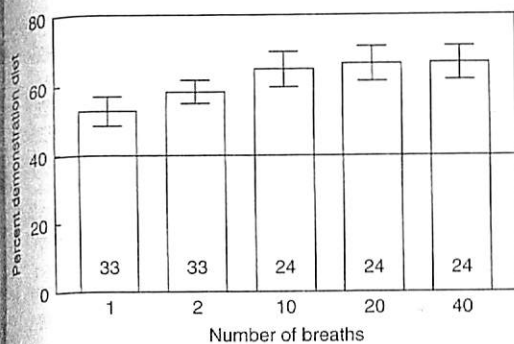


Fig. 40.5 Mean + SEM percentage of their human demonstrator's diet eaten during testing by observer rats offered a choice between cinnamon- and cocoa-flavored diets after interacting with a human demonstrator who had eaten one diet or the other and then breathed on the observer rat 1, 2, 10, 20, or 40 times. Horizontal line indicates the mean expected percentage of demonstrator's diet observers would eat if there were no influence of human demonstrators on rat observers. Number in histograms = N/group (Galef, 2009; reprinted by permission of Elsevier).

constantly illuminated room in cages with an uncomfortable substrate (Galef, Dudley, & Whiskin, 2008). In each case, we found that "dissatisfied" rats were more susceptible to social influence than presumably satisfied rats that we maintained under standard laboratory conditions (for review, see Galef, 2009).

As can be seen in Table 40.1, "copy when dissatisfied," like the majority of other "when strategies" examined in my laboratory, successfully predicted the behavior of our subjects. The sole exception is "copy when individual learning is costly" (which is usually taken in the literature to mean when under threat of predation). In two sets of experiments, we have failed to find evidence that either direct or indirect threats of predation increase reliance on social information in rats. Neither rats that were exposed to cats nor rats that had to forage at a distance from a safe harborage site showed greater reliance on socially acquired information as to which of two foods to eat than did rats that foraged close to a harborage site or with no predator present (Galef & Whiskin, 2006; Galef & Yarkovsky, 2009).

Conclusion

The robust laboratory paradigms that we developed for studying social learning about foods in rats has proven useful in asking a number of kinds of questions about the development, function, and causation of behavior. The multiple uses to which our experimental paradigm can be put have enabled my

students and me to run the same basic experiment several hundred times for more than 40 years and still maintain the interest of a reasonably broad audience.

The work has cast some light on questions not only about social learning generally and the role of social learning in behavioral development, but also about the nature of traditions in animals, the adequacy of formal models to predict behavior, the adaptive specialization of learning (Hoppitt & Laland, 2008), and the success of Norway rats as human commensals. Choosing a phenomenon for study that was, at least peripherally, related to a number of active controversies and using diverse intellectual frameworks to analyze the results of our experiments (Galef, 1991b) has been sufficient to sustain a lifetime of research. Consequently, I hope that, in addition to whatever its other virtues, the study of social learning about foods in Norway rats may provide some modest guidance to those new to the study of behavior when selecting a research problem to which to devote their own professional efforts.

Acknowledgments

Consistent financial support from the Natural Sciences and Engineering Research Council of Canada has been critical to the success of the research reported here, as has the enthusiastic participation of many students (both graduate and undergraduate) and technicians who actually conducted the hundreds of experiments carried out in my laboratory during the last 40 years. Preeminent among the latter is Elaine E. Whiskin, whose dedication to the work of the laboratory for 22 years, enthusiasm for research, and personal qualities so greatly facilitated our progress.

I thank Phillip Miller for assistance in putting pdfs of all of my laboratory's published work on social learning in Norway rats on my website. All of my published papers, listed chronologically, can be found at www.sociallearning.info under Curriculum Vitae.

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