Chapter 18 Social Learning by Rodents

Bennett G. Galef Jr.

MANY OF THE THINGS that animals, especially young animals, need to learn, they need to learn rapidly. A fledging bird or weanling mammal venturing from the site where it was born and reared by adult kin has to learn to avoid predators before being eaten by one. The individuial has to learn to select an adequate diet before its internal reserves of any critical nutrient are exhausted and without ingesting harmful amounts of toxins.

A naive young animal faced with such problems should take advantage of opportunities that interactions with adults provide. Adults have surely learned to avoid predators and to find both appropriate substances to ingest and appropriate locations in which to seek refuge. Most important, any adult with whom a juvenile interacts is feeding, avoiding predators, and navigating about the environment in which the juvenile is struggling to achieve independence. To the extent that a juvenile can use the behavior of adults to guide development of its own behavioral repertoires, it should be able to acquire adaptive responses to environmental demands without incurring all of the costs of individual trial-and-error learning.

Formal models (e.g., Laland et al. 1996) predict that dependence on social learning should evolve in environments that are neither too stable (where unlearned responses would be more valuable) nor too rapidly changing (where copying the behavior of others could lead to errors and individual learning would be most advantageous). And, in species that forage from a central location, as do most rodents, such models indicate that information exchange would be most valuable when foods are patchy in distribution and ephemeral, and naive individuals would be un-

likely to stumble upon rich feeding sites by chance (e.g., Waltz 1982). Unfortunately, theoretical approaches to the study of social learning have not yet had much impact on empirical work in the area (for review, see Galef and Giraldeau 2002), though increasing numbers of investigators are attempting to integrate theoretical and empirical approaches (e.g., Dewar 2004; Noble et al. 2001).

Behavioral processes supporting social learning range from relatively simple (e.g., local enhancement, where attention of one animal is focused on an aspect of the environment by the behavior of others [Thorpe 1956]) to cognitively complex (e.g., imitation, learning motor patterns by observing others' behavior [Galef 1988b; Whiten and Ham 1992]). Local enhancement of feeding site selection appears to be common in rodents, though apparently not of sufficient intrinsic interest to have provoked much study. Imitation has attracted considerable laboratory study but seems relatively rare in animals, and may well be nonexistent in rodents.

Observation of animals living free in undisturbed habitats has been important in calling attention to potential socially learned behaviors (i.e., behaviors the development of which is likely to have been influenced by interaction with conspecifics). However, although field observations have provided strong circumstantial evidence that some behaviors are learned socially, observation per se has not proven sufficient in most cases to conclude that social interaction is important in behavioral development. For example, chimpanzees (*Pan troglodytes*) living in East and West Africa dip for ants using both different tools and different methods of removing ants from tools (McGrew 1974; Boesch 1996).

However, whether such "traditions" reflect (1) differences in the genotypes of chimpanzees living on opposite sides of the continent (Morin et al. 1994), (2) differences in the environments with which individuals interact and about which they learn independently (Humle and Matsuzawa 2002), or (3) social influences on behavioral development (Whiten et al. 1999) is not known. Even after decades of observational study, it is not clear whether different patterns of ant dipping observed in different free-living chimpanzee populations involve social learning at all.

Identification of socially learned behaviors in populations of free-living rodents that are often small, nocturnal, shy, and subterranean is, if anything, even more difficult than in human-habituated chimpanzees, whose behavior and social interactions are relatively easily observed. Field studies are necessary to identify behaviors that rodents may learn socially. However, experiments carried out under controlled conditions are necessary to draw strong conclusions concerning the behavioral processes responsible for the development of suspect behaviors (Galef 1984, 1996c). Field experiments to determine whether any free-living animals actually learn any behavior socially are generally lacking, but needed (for review and further discussion, see Galef, 2004).

Field observations of some common rodent species reveal marked differences in the behavior of populations living in different areas that are at least superficially similar to the geographic variability in behavior observed in chimpanzees (Whiten et al. 1999) and orangutans (van Schaik et al. 2003). For example, Norway rats (*Rattus norvegicus*) living on the banks of ponds in a fish hatchery in West Virginia catch fingerlings and eat them (Cottam 1948). On the island of Norderoog in the North Sea, members of the same species frequently stalk and kill sparrows and ducks (Steiniger 1950), though they have not been reported to do so elsewhere. Colonies of black rats (*Rattus rattus*) thrive in the pine forests of Israel by removing scales from pinecones and eating the seeds that the scales conceal, a behavior not reported in other populations of black rats (Terkel 1996). Members of only some of the many colonies of Norway rats living along the banks of the Po River in Italy dive into the river and feed on mollusks inhabiting the river bottom (Gandolfi and Parisi 1972, 1973).

Almost all laboratory investigations of social learning in rodents have focused on feeding behaviors of one type or another in murids. Indeed, only six laboratories worldwide (those of Galef [Canada], Heyes [UK], Laland [UK], Terkel [Israel], Valsecchi [Italy] and Holmes and Mateo [USA]) have carried out sustained investigations of any aspect of social learning in any rodent. Four of these six laboratories have worked primarily with a single genus (*Rattus*) and five of the six within a single behavioral domain (foraging).

The other domain that has been extensively investigated is social learning of predator avoidance in a sciurid, the Belding's ground squirrel (see Mateo, chap. 17, and Holmes and Mateo, chap. 19 this volume).

The paucity of data on social learning in rodents makes my task here comparatively easy. In the space available, I can both describe, albeit briefly, five of the six major research programs mentioned previously (the sixth is discussed at length in the chapters by Mateo and Holmes and Mateo) and provide a fairly comprehensive set of references to studies in rodent social learning carried out in the last 20 years.

Pinecone Stripping by Roof Rats (*Rattus rattus*)

Roof rats living in the pine forests of Israel, but not those living elsewhere, strip the scales from pinecones and eat the seeds that the scales protect. This foraging behavior permits the rats to occupy a niche that is occupied in other parts of the world by tree squirrels; sciurids are not present in the Middle East (Aisner and Terkel 1992).

Laboratory investigation of pinecone stripping by wild-caught rats reveals that they must take advantage of the physical structure of pinecones to gain more energy from pine seeds than is expended in removing seeds from cones. To exploit pinecones efficiently, rats must first strip the scales from the base of a cone, then remove the remaining scales in succession as they spiral around the cone's shaft to its apex (Terkel 1996; fig. 18.1).

Studies of the development of the energetically efficient pattern of stripping scales from pinecones revealed that only 6 of 222 hungry laboratory-reared wild rats that were given access to a surplus of pinecones for several weeks independently learned the efficient method of feeding on them. The remaining 216 animals either ignored the cones or gnawed at them in ways that did not lead to a net energy gain (Zohar and Terkel 1995).

Figure 18.1 Pinecones in different stages of opening with the number of rows of stripped scales increasing from left to right (Terkel 1996, by permission of Elsevier).

Pups gestated by dams that stripped pinecones efficiently, but reared by foster mothers that did not know how to strip pinecones failed to develop the efficient technique (Aisner and Terkel 1992). However, more than 90% of pups learned to open cones properly if reared by a foster mother that stripped cones efficiently while her charges were present. Clearly, some aspect of postnatal interaction between a dam stripping scales from pinecones and the young that she rears permits transmission of the efficient means of feeding on pinecones from one generation to the next (Aisner and Terkel 1992; Zohar and Terkel 1992). Additional experiments showed that 70% of young rats with experience completing the stripping of cones that had been started appropriately by efficient adults (or by experimenters using pliers to imitate the pattern of scale removal used by proficient adult rats) themselves became efficient strippers of pinecones (Terkel 1996).

Terkel's (1996) observations of rats in the laboratory indicated that when a roof-rat mother opens pinecones by stripping scales and eating exposed seeds, her young gather around her and attempt to obtain seeds. As the young grow older, they snatch partially opened cones from their mother and continue the stripping process themselves. A mother rat's feeding activities thus appear to facilitate acquisition of pinecone stripping by her offspring in two ways: first, by focusing attention on pinecones as potential food sources (local enhancement), and later by providing young with partially opened pinecones that guide development of feeding on them (Terkel 1996). Simply watching an adult open pinecones without the opportunity to exploit pinecones started by an adult left young unable to open pinecones for themselves. Imitation seems an unlikely explanation of the behavioral process supporting transmission of the behavior from mother to young.

Poison Avoidance by Norway Rats (*Rattus norvegicus*) and Socially Learned Food Preferences in Rodents

Wild rats are social rodents that live in colonies that vary in size from a few to many hundreds of members. Each colony inhabits a burrow system from which colony members emerge to forage and to which they return between foraging bouts. The comings and goings of successful and unsuccessful foragers from a central location, where colony members can interact, provide opportunities for exchange of information about foods that would be of use to individuals both in finding food in natural environments and circumventing humans' attempts at rodent control.

When rodent control operatives attempt to use the economically efficient method of placing permanent poison bait stations in rat-infested areas they have great initial success with rats eating ample amounts of poison and dying in large numbers. However, later bait acceptance is poor and colonies soon return to their initial sizes (Steiniger 1950). Permanent baiting stations fail because young rats born to adult colony members that have survived their first ingestion of a poison bait and learned not to eat that bait never even taste the bait for themselves (Steiniger 1950).

Young wild rats' total avoidance of foods that adults of their colony have learned to avoid eating is a robust phenomenon that can easily be brought into the laboratory (Galef and Clark 1971b). We captured adult wild rats in southern Ontario and established them in small groups in 2 m² laboratory enclosures. For 3 hr each day, we provided each of our laboratory colonies with two easily distinguished, nutritionally adequate foods.

To begin a typical experiment we introduced sublethal concentrations of toxin into one of these two foods. Our rats soon learned to avoid the poisoned bait and for weeks thereafter would not eat the food that had been poisoned even when we gave them uncontaminated samples of it.

After we had trained our colonies we waited for young to be born and grow to weaning age. When these young began to eat solid food we observed them on closed-circuit television and recorded the frequency with which they ate each of the two foods that we placed daily in their enclosure: one that adult colony members were eating and the other that adults had learned to avoid.

We found that while pups remained with the adults of their colony, they ate only the food that those adults were eating, and completely avoided the alternative that the adults were avoiding. Even after we removed pups from their natal enclosures, housed them individually, and offered them the same foods that we had made available in their colony enclosure, the pups continued for several days to prefer the food that the adults of their colony had eaten (fig. 18.2).

To determine whether such social learning of a food preference could result in a tradition that lasted for generations, we created two types of colonies (Galef and Allen 1995). We used a poisoning technique to teach all four members of each colony of one type not to eat a horseradish-flavored food (wasabi) and all four members of each colony of the other type not to eat a cayenne-pepper-flavored food. Once colony members had learned what not to eat, we offered all members of both types of colony a choice between cayenne pepper-flavored food and horseradish-flavored food for 3 hr/day. Each day, immediately after we fed a colony, we removed one of its members and replaced that member with a naive rat.

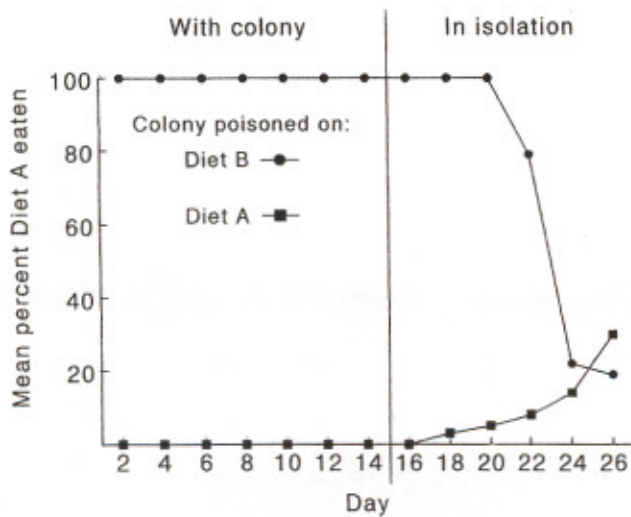After 4 days we had replaced all the original members of each colony. For 10 days thereafter, we replaced with a

Figure 18.2 Mean number of times that juvenile Norway rats ate Diet A as a percentage of the total number of times juveniles ate both Diet A and Diet B during daily 3-hr feeding periods. Left panel: days when juveniles were with adults, Right panel: days when juveniles were moved to individual cages. Abscissa: number of days since pups started feeding on solid food.

Figure 18.3 Mean ± SE amount of cayenne pepper-flavored diet (Diet Cp) ingested as a percentage of total amount eaten by subjects offered both Diet Cp and wasabi-flavored diet (Diet W) in enclosures where founding colony members ate only Diet Cp (●) or only Diet W (■). On day 1, enclosures contained only founding colony members, on days 2 to 4, both founding colony members and replacement subjects, and on days 5 to 14, successive generations of replacement subjects (Galef and Allen 1995; by permission of the American Psychological Association).

naive rat the individual in each colony that had been there longest, and we kept doing so day after day. As can be seen in figure 18.3, even after replacements of replacements of original colony members had been replaced, we still saw huge effects of the food preferences learned by original colony members (Galef and Allen 1995). The longevity of such traditions of food choice is affected by a number of factors, including colony size, rate of replacement of colony members, and number of hours each day that colony members have access to foods (Galef and Allen 1995; Galef and Whiskin 1997, 1998).

My students and I have studied how the feeding patterns of adult rats influence the food choices of young that interact with them (for reviews see Galef 1977, 1988a, 1996a, 1996b). Such social influences on food choice start before rats are born and extend throughout life. For example, a rat fetus exposed to a flavor while still in its mother's womb by injection of that flavor into its dam's amniotic fluid will, when grown, drink more of a solution containing the injected flavor than will control rats lacking such prenatal experience (Smotherman 1982). More realistically, feeding a food with a strong flavor (garlic) to a pregnant rat enhances the postnatal preference of her young for the odor of garlic (Hepper 1988).

Evidence from several laboratories indicates that flavors of foods that a lactating female rat eats affect the flavor of her milk. Exposure to food flavors in milk, a very simple sort of social learning, increases pups' preferences at weaning for foods that their mother ate (Galef and Henderson 1972; see also Galef and Sherry 1973: Bronstein et al. 1975; Martin and Alberts 1979).
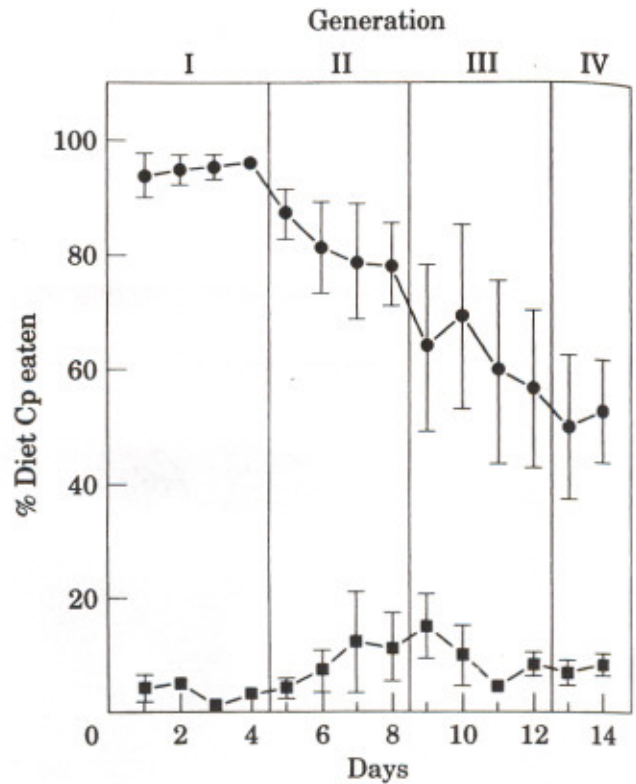
When weanlings leave the safety of their natal nest to feed on solid food for the first time, they use visual cues to locate an adult at a distance and then feed with that adult (Galef and Clark 1971a). Even an anesthetized adult rat placed near one of two otherwise identical feeding sites makes the occupied site far more attractive to pups than the unoccupied one, and young pups both visit and eat more frequently at the former than the latter (Galef 1981a).

Adult rats need not be physically present at a feeding site to cause young to prefer to eat there. When leaving a feeding site to return to their burrows, adult rats deposit scent trails (Calhoun 1962a; Telle 1966) that direct young rats seeking food to locations where the adults ate (Galef and Buckley 1996). Also, when feeding, adult rats deposit olfactory cues both in the vicinity of a food source (Galef and Heiber 1976; Galef 1981a; Laland and Plotkin 1991, 1992) and on foods they are eating (Galef and Beck 1985). These residual odors attract pups and, like the presence of an adult rat at a feeding site, cause young rats to prefer marked sites to unmarked ones.

Availability of social information as to what foods are best to eat can have profound consequences for rats in environments where ingesting the most palatable foods does not lead to a nutritionally adequate diet. We placed young rats in enclosures where they had access continuously for 7 days to four different foods (Beck and Galef 1989; Galef et al. 1991). Three of these (cinnamon-, cocoa- and thyme-flavored foods) were relatively palatable, but low in protein, while one (nutmeg-flavored food) was relatively unpalatable, but protein rich. The pups failed to solve even this apparently trivial foraging problem, lost weight, and would surely have died of protein deficiency had we not terminated the experiment after 1 week. By contrast, pups that shared their enclosures with adult rats that we had trained to eat the relatively unpalatable, protein-rich, nutmeg-flavored food grew at almost the same rate as control pups offered just the protein-rich diet.

Terkel's roof rats were able to invade pine forests because of their ability to learn socially how to efficiently exploit pinecones. Similarly, Norway rats could invade an environment where needed nutrients are present only in relatively unpalatable foods because they can learn socially how to select an adequate diet under such circumstances once one of their number has learned to do so (Galef 1991).

Norway rats can also influence the food choices of conspecifics by interacting with them at a distance from a feeding site. After a naive rat (an observer) interacts with a conspecific (a demonstrator) that has recently eaten a food unfamiliar to the observer, the observer exhibits substantial enhancement of its preference for whatever food its demonstrator ate (Galef and Wigmore 1983; Posadas-Andrews and Roper 1983; Strupp and Levitsky 1984). Such effects are relatively independent of the genetic or prior social relationship of demonstrator and observer (Galef et al. 1998) but depend to some extent on the rats' previous feeding history (Dewar, 2004). Laboratory studies using procedures similar to those used with Norway rats have provided evidence of increased preference of observers for the food preferences of their respective demonstrators in a number of other rodent species (table 18.1).

In rats, both food-related odors escaping from the digestive tract of a demonstrator and the scent of bits of food clinging to its fur and vibrissae allow naive conspecifics to identify what foods others have recently eaten (Galef et al. 1985; Galef et al. 1990; Galef and Whiskin 1992). Enhancement of food preference of observers depends on their experiencing food odors together with other olfactory stimuli that are normally emitted by live conspecifics (Galef et al. 1985; Galef and Stein 1985; Galef et al. 1988; Heyes and Durlach 1990; Stetter et al. 1995). For example, rats exposed to pieces of cotton batting that are dusted with a food and moistened with distilled water do not develop a

Table 18.1 Rodent species in which increased preference of observers for foods eaten by conspecific demonstrators has been found in laboratory experiments

Species	Reference
House mouse (*Mus domesticus*)	Choleris et al., 1997; Valsecchi and Galef, 1989; Valsecchi et al. 1989
Mice (*Mus musculus*)	Valsecchi et al. 1993
Mongolian gerbil (*Meriones unguiculatus*)	Valsecchi et al. 1996; Galef et al. 1998
Roof rats (*Rattus rattus*)	Chou et al. 2000
Spiny mice (*Acomys cahirinus*)	McFayden-Ketchum and Porter 1989
Pine voles (*Microtus pinetorum*)	Solomon et al. 2002
Belding's ground squirrel (*Spermophilus beldingi*)	Peacock and Jenkins 1988; Sherman, personal communication
Golden hamster (*Mesocricetus auratus*)	Lupfer et al. 2003
Dwarf hamster (*Phodopus campbelli*)	Lupfer et al. 2003

preference for the food dusted on the cotton batting. However, rats subsequently prefer that food if exposed to it on either the head of an anesthetized conspecific or a piece of cotton batting moistened with carbon disulfide, which is a constituent of normal rat breath (Galef and Stein 1985; Galef et al. 1988).

Effects of exposure to a recently fed rat on conspecifics' food choices are powerful (Galef et al. 1984; Richard et al. 1987). Observer rats that are first taught to avoid a food by following its ingestion with an injection of toxin, then placed with a conspecific that has eaten the food to which the observer rats learned an aversion, abandon their aversion to the food they ate before being injected with toxin. Most rats that interact with conspecifics who were fed a food adulterated with cayenne pepper, a spice that is inherently unpalatable to rats, subsequently prefer peppered diet to unadulterated diet (Galef 1986; Galef 1989). Such effects of social interaction on food choice are also enduring and, under some circumstances, can be seen more than a month after social learning took place (Galef and Whiskin 2003).

Although social exposure to an odor has profound effects on rats' subsequent preferences for foods, identical experiences have no effect on rats' odor preferences in other contexts. For example, rats that have interacted with a conspecific that has eaten cinnamon-flavored diet prefer cinnamon-flavored food, but show no enhancement of their preference for cinnamon-scented nest materials or cinnamon-scented nest sites (Galef and Iliffe 1994).

Surprisingly, rats that will readily acquire preferences for foods socially do not learn aversions to foods from their fellows. Indeed, rats generally show increased preferences for foods after interacting with sick or unconscious rats that have eaten them (Galef et al. 1983; Galef et al. 1990). We

surmise that, because rats encountering toxic foods are likely to eat them only once (Garcia et al. 1974), the probability that naive rats will be induced to eat toxic foods by conspecifics is low. Consequently, failure to discriminate between conspecifics that have eaten toxic and safe foods has little cost. Results of an evolutionary simulation of the effects on survival of discrimination between sick and healthy conspecifics when learning socially about foods (Noble et al. 2001) are consistent with such an explanation.

Norway Rats Diving for Mollusks

Gandolfi and Parisi (1972) reported that most members of some colonies of Norway rats living along the banks of the Po River in Italy dive to feed on mollusks that inhabit the river bottom, whereas no members of nearby colonies with equal access to mollusks do so. Nieder et al. (1982) observed such mollusk predation by small groups of rats that they confined in a large (22 × 10 m) outdoor enclosure built over a narrow branch of the Po River. Although observations in both the enclosure and the wild suggested that social learning of some sort might have been involved in diffusion of mollusk predation through rat populations, the data were not conclusive.

In a laboratory experiment undertaken to examine the role of social learning in the development of diving behavior in Norway rats, we placed second and third generation laboratory-bred female wild rats captured in Ontario together with their offspring in enclosures with separate nesting and diving areas connected by meter-long tunnels (Galef 1980). In the diving area, subjects could retrieve pieces of chocolate from beneath 15 cm of water in an aquarium.

We found that adults that had not been trained to dive for food never dove, even if housed with rats that we had trained to dive for food by placing chocolate squares in empty aquaria and, over a period of weeks, gradually increasing water levels to 15 cm. However, approximately 20% of juvenile wild rats reared in the enclosures in which adults never dove spontaneously dove for food. And juveniles were as likely to learn to dive whether their dam regularly dove and retrieved chocolates from under water or never did so. Such results suggest that observation of diving conspecifics does not, in itself, induce rats to dive.

In a subsequent study, we raised young wild rats in an enclosure where they had to swim 60 cm to reach food. When introduced into enclosures connected to a diving area, where food was available under 15 cm of water, more than 90% of rats trained only to swim spontaneously dove for food. The finding that swimming rats are effectively diving rats limits the potential role of social learning in diffu-

sion of diving behavior through a population. If rats learn to swim independently, and if swimming rats dive, then social learning could serve only to direct rats to dive in one area rather than another. However, development of swimming might itself be socially influenced. If so, then social learning might indirectly facilitate the spread of diving behavior by facilitating the spread of swimming behavior. However, wild rat pups that were reared by dams that either swam or did not swim 1.7 m down an alley to reach food did not differ in the age at which they started to swim, and all swam to food before they were 40 days old (Galef 1980).

The findings of high frequencies of willingness to swim to obtain food and to dive in wild rat pups suggests that (unless there is a relevant genotypic difference between Norway rats in Canada and Italy), all rats living along the Po River may know how to dive for mollusks, but that they do not dive unless they have to. In the laboratory, rats that reliably dove for food when food was available ashore for only 3 hr/day stopped diving when given ad libitum access to the same food on land, even if the food available ashore was considerably less palatable than that available under water (Galef 1980).

Taken together, the laboratory results offer little support for the hypothesis that variation in the frequency of diving observed among colonies of rats living along the Po River results from a socially learned tradition present in some colonies but not others. To the contrary, the laboratory data suggest that all rats may know how to dive for food, but will do so only when adequate food is not available on land.

In retrospect, some observations made in the field are consistent with the hypothesis that availability of food on land may be the major determinant of whether members of rat colonies living along the banks of the Po River feed on submerged mollusks. For example, Gandolfi and Parisi (1973, p. 69) report that in those locations where mollusk predation is observed, mollusks "represent one of the main sources, if not the main source of food for rats." Parisi and Gandolfi (1974, p. 102) suggest further that "the time dedicated by rats to mollusk capture depends greatly on the availability of other foods."

Naked Mole-Rats Recruitment of Colony Mates to Food Sources

Naked mole-rats (*Heterocephalus glaber*) are eusocial, subterranean rodents that, in nature, travel underground through an extensive labyrinth of tunnels to feed on patchily distributed bulbs and tubers. Observation of naked mole-rats kept in artificial burrow systems that mimic, albeit on a vastly reduced scale, their natural burrows, revealed that

while returning to the nest after finding a new source of food individuals give a special vocalization. Upon arrival at the nest, returning successful foragers on a new food source sometimes wave the food around (Judd and Sherman 1996).

In laboratory experiments, colony mates preferred the site where the initial forager had found food, and would bypass alternative sites containing the same type of food. Such recruits preferred to use the same tunnel that the successful forager had used, even when the burrow system had been rearranged so that recruits had to turn in the opposite direction from the original scout to reach the same location.

Recruits also preferred tunnels that the initial forager had recently traversed to tunnels traversed by other colony members that were carrying the same type of food that the initial forager had carried. Such preference disappeared if tunnel segments that the initial forager had traversed were cleaned. Taken together, the results offer strong support for the hypothesis that naked mole-rats follow each other's odor trails to food, thus facilitating location of the widely dispersed foods exploited by colonies of naked mole-rats (Faulkes 1999).

Norway Rats Digging for Food

Laland and Plotkin (1990, 1992) examined social effects on the frequency with which rats dig for buried pieces of food. They discovered that the probability of observer rats digging for buried food increased if they saw demonstrator rats digging for food, and that observer rats, after learning socially to dig for food, could serve as demonstrators for other observers, that could, in turn, become demonstrators. Such chaining of socially learned behavior was first demonstrated by Curio et al. (1978) in investigations of the development of predator recognition by European blackbirds (*Turdus merula*). Curio et al.'s technique captures some features of diffusion of socially learned behaviors through free-living populations of animals. However, it does not provide opportunity for individual learning of alternative rewarding behaviors by animals in the test situation, and presence of such alternatives can be important determinants of whether socially learned behaviors will be maintained long enough in individuals to be transmitted to others. For example, the longevity of socially induced food preferences in rat colonies of the type studied by Galef depended critically on the number of hours a day that foods were present in a colony enclosure. When foods were available for 2 hr/day, preferences lasted far longer than when food was available 24 hr/day, and rats could more easily learn for themselves the relative value of available diets (Galef and Allen 1995; Galef and Whiskin 1997, 1998).

Norway Rats' Social Learning of Arbitrary Behaviors

There is a large literature concerning social effects on the bar-pressing and maze-running behavior of Norway rats and house mice (reviewed in Zentall 1988; Denny et al. 1988). I shall discuss here only the one major research program concerned with the learning of arbitrary behaviors developed since these reviews were published.

Much early work on social learning in rodents was conducted by those trained in experimental animal psychology, and was concerned with the question of whether animals could learn by imitation, with imitation defined narrowly as "learning to do an act by seeing it done" (Thorndike 1898, p. 50). Thus defined, imitation differs from other sorts of social learning in that it involves learning to produce a behavior by observing the behavior of others rather than learning about the environment by observing the behavior of others (Heyes 1993). For example, if I watch someone open a screw-top jar and eat from it, I might learn to grasp the jar with one hand and apply rotational pressure with the other. This would be imitation. Alternatively, I might learn by watching that the jar can be opened and then use trial-and-error processes to acquire the appropriate motor patterns to open the jar. This would be a nonimitative form of social learning. Discussions of such distinctions are extensive in the literature and have been reviewed by Galef (1988b) and Whiten and Ham (1992). Heyes's (1993) empirical work, described here, is the most compelling examination of imitation in rodents to date.

Heyes used the "two-action method" or "bidirectional control" procedure, in which demonstrators direct one of two patterns of behavior toward a single target to control for many alternative explanations of apparent imitative behavior that had plagued earlier attempts to demonstrate imitation learning in animals (see Zentall 1988). Observer rats were given their first opportunity to push a joystick left or right immediately after observing a conspecific demonstrator push the same joystick either left or right. Heyes found that observers given access to their demonstrators' joystick tended to push it in the same direction relative to their own body axes as had their demonstrators (Heyes et al.1992: Heyes and Dawson 1990), even if the observers were given food rewards for pushing the joystick in either direction. A variety of control procedures provided data consistent with the view that observers were copying the motor behavior of their respective demonstrators, using the orientation of their own bodies as a referent (for review, see Heyes 1996).

However, subsequent studies by Mitchell et al. (1999) and Campbell and Heyes (2002) showed that if, after the demonstrator used the joystick and before the observer did so, the joystick was rotated 180 degrees about its main axis,

the direction in which the observer pushed the joystick was reversed. Apparently, demonstrators were depositing attractive odor cues on the side of the joystick against which they pushed, and these residual cues biased observers to push on the same side of the joystick as had their respective demonstrators. Heyes's experiments thus join a long line of failed attempts to find evidence of learning by imitation in rodents. Indeed, there is currently no convincing evidence of imitation learning in any rodent (or any nonhuman mammal other than dolphins and apes). This absence of laboratory evidence of imitation is somewhat surprising given the numerous examples of such learning in birds (reviewed in Zentall 2004). The reasons for the peculiar phylogenetic distribution of the ability to imitate remain obscure, though Moore (1996) has proposed that a capacity to imitate has evolved in vertebrates three times, sometimes based on vocal imitation and sometimes not.

Miscellany

In addition to the sustained research programs focused on social learning in rodents discussed earlier, there have been numerous isolated papers describing instances of social learning in rodents. Those of which I am aware are listed in table 18.2. The phenomena described in these papers are worthy of further exploration, so that their repeatability can be established and the behavioral processes supporting those that are reliable can be examined. Unfortunately, constraint on the space available here makes detailed description of each of these phenomena impossible. The interested reader is referred to the original reports.

Summary

The last 20 years have seen tremendous progress in understanding a handful of instances of apparent social learning in rodents. Obviously, it is too early to attempt generalizations as to which rodents learn socially and which learned behaviors of rodents are modified by social interactions. Less than one-half of 1% of rodent species has been examined even once in a social-learning paradigm and, even in those two species (Norway rats and house mice) that have been studied most frequently, focus has been almost entirely on social influences on foraging behavior (but see Mateo, chap. 17, and Holmes and Mateo, chap. 19, this volume). Essentially nothing is known of the role of social learning by rodents in mating, predator avoidance, predatory behavior, parental care, and so on.

We know from field observations that even congeneric rodent species can differ profoundly in the role that social cues play in various aspects of their behavior. For example, Telle (1966) observed that although both *R. rattus* and *R. norvegicus* tend to move about their territories on scent-marked runs, *R. norvegicus* attacks only those unfamiliar individuals encountered on a run, while *R. rattus* attacks unfamiliar individuals in areas between runs. Even within a species, differences in genotype (Kogan et al. 1997), hormonal state (Fleming et al. 1994), nutritional level (Galef et al. 1991), or rearing conditions (Levy et al. 2003) can affect the magnitude of social influences on learning. Such reports suggest that generalizations across species will be hard won.

Indeed, it is difficult to predict just how useful comparative approaches to the study of social learning in rodents

Table 18.2 Further instances of social learning in rodents

Species	Behavior	Reference
Mongolian gerbil	intake of novel food	Forkman, 1991; Tachiban, 1974
Golden hamster (*Mesocricetus auratus*)	chain pulling	Previde and Poli, 1996
Mouse[a]	swinging door opening	Collins, 1988
Grasshopper mouse (*Onychomys leucogastor*)[a]	cricket killing	Kemble, 1984
Red squirrels (*Tamiascurus hudsonicus*)	nut opening	Weigl and Hanson, 1980
Norway rat[a]	mouse killing	Flandera and Novakova, 1974
	avoiding flame	Lore, Blanc, and Suedfeld, 1971
	avoiding shock prod	White and Galef, 1998
	alcohol ingestion	Hunt, Lant, and Carroll, 2000; Hunt, Holloway, and Scordalakes, 2001; Honey and Galef, 2004
Prairie dog (*Cynomys gunnisoni*)[b]	alarm-call dialects	Perla and Slobodchikoff, 2002

[a]Findings my laboratory have tried to repeat without success.
[b]Authors do not discuss as an instance of social learning.

will prove to be. In all rodent species, whether solitary or social, altricial or precocial, young spend considerable time interacting with their mothers. Consequently, all juvenile rodents have an opportunity to learn about foods, harborage sites, predators, and other environmental factors from at least one other member of their species. Even European rabbits (*Oryctolagus cuniculus;* lagomorphs, not rodents) that interact with their dams for only a few minutes each day learn from her what foods to eat (Altbacker et al. 1995). Given that all rodents have opportunities to learn socially about at least some aspects of their environment, comparisons among species from different ecological situations or with different degrees of sociality may prove less informative than might be hoped.

Naive rodents generally seem to be able to learn where, when, and how to engage in a variety of behaviors from interactions with either knowledgeable conspecifics or changes that they have made in a shared environment. However, the behavioral processes underlying such social learning appear to be simple ones (e.g., local enhancment, environmental shaping), and to date, little or no reliable evidence of imitation or of teaching has been found in rodents. Of course, the observation that diffusion of behaviors through rodent populations rests on relatively simple behavioral mechanisms should not lessen our appreciation of the potentially important role that social learning can play in the development of adaptive behavioral repertoires of rodents.