

# Studies of Social Learning in Norway Rats: A Brief Review

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I review below some of the research on social learning in Norway rats carried out in my laboratory from 1969 to 1980. Two independent lines of research are discussed; both involve analysis in the laboratory of possible instances of social learning first described by observers of free-living, wild rats. The 1st research program analyzes social interactions important in the transmission of learned food preferences from adult rats to their young. The 2nd examines the possibility that the habit of diving in shallow water for food is socially transmitted from 1 rat to another.

In the decades before either comparative psychology or the study of animal behavior became experimental disciplines, it was widely believed by naturalists, pet owners, and others familiar with animals that mammals could learn to perform complex behaviors by observing and then imitating other organisms exhibiting such behaviors (see, for example, Lloyd-Morgan, 1896; p. 184).

George Romanes, the late 19th-century biologist, protégé of Charles Darwin, Fellow of the Royal Society, and leading figure in the scientific establishment of his day, was probably the foremost proponent of the view that observational learning is central to behavior acquisition in animals. In 1881, Romanes published a lengthy monograph, *Animal Intelligence*, in which he provided anecdotal descriptions and interpretations of instances in which animals exhibited what we today would consider rather remarkable intellectual powers in solving problems encountered in natural environments. Many of the examples of animal learning in nature reported by Romanes were, at best, exaggerated; for example, mice in Iceland were said to have been observed storing berries in dried mushrooms, loading these rations onto dried cowdroppings, and then guiding such improvised, provisioned vessels across flooded rivers, using their tails as rudders. Sighted rats were said to have been seen leading their blind fellows from place to place by means of a stick held in the mouth of both guide and dependent (Romanes, 1881). However, not all the instances of remarkable abilities in animals described by Romanes and his correspondents were quite so unlikely, and some proved of considerable historical importance in the development of experimental animal psychology.

Perhaps the most influential of the many cases Romanes discussed in *Animal Intelligence* concerned a cat which belonged to Romanes' own coachman. This animal had learned, without formal tuition of any kind, to open a latched door in Romanes' yard by leaping up and grabbing the door handle with 1 forepaw, depressing the thumb piece with the other, and simultaneously pushing at the doorpost with her hind legs. Romanes argued that the cat, in the absence of any other source of information, must have

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observed that humans opened the door by grasping the handle and moving the latch. Then, said Romanes (1881; p. 422), the cat must have reasoned, "If a hand can do it, why not a paw?" Finally, strongly motivated by this insight, the cat attempted to and succeeded in opening the door in question.

The problem with Romanes' interpretation, of course, is that simple observation of an animal behaving provides little information concerning the processes responsible for the development of the behavior exhibited. Unfortunately, you just can't tell from simply watching an animal perform an act in an uncontrolled environment what the necessary antecedent conditions of that performance are.

Experimental animal psychology in North America may well have arisen from Edward Thorndike's irritation with the excesses in Romanes' *Animal Intelligence*: its anecdotal method, its speculative conclusions, even its title. Thorndike pointed out that while accurate observation in nature may tell us what an animal does, observation alone can not tell us how the animal comes to do it. Discovery of the processes underlying behavior acquisition, Thorndike proposed, can come only from examining behavior acquisition under controlled conditions. Thus, in the late 1890's, Thorndike brought the door-opening behavior of cats into the laboratory and studied, in controlled and replicable situations, learning of the solution to problems analogous to that faced by Romanes' coachman's cat.

Figure 1 is an artist's conception of one of Thorndike's famous puzzle boxes. In this case a food-deprived cat was placed inside the apparatus and required to depress a treadle in order to escape confinement and achieve access to food. As is well known, on the basis of the results of his numerous studies in this and similar situations, Thorndike proposed that animals learn to solve *all* such problems as the result of their individual interactions with the environment, in accord with the laws of instinct, effect, and exercise. Less generally appreciated is Thorndike's explicit rejection, on both theoretical and empirical grounds, of the possibility of learning by imitation. Thorndike had found that animals in general, and cats in particular, did not learn to escape from puzzle boxes either by observing other cats do so or by observing humans demonstrate solutions. In fact, in some of the situations Thorndike studied, observation of a trained demonstrator by a naive individual interfered with acquisition of problem solution. Thus

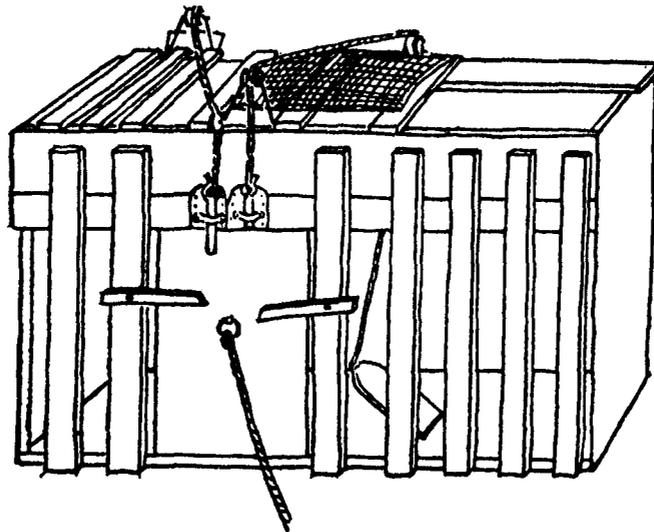


Fig. 1. Artist's conception of 1 of Thorndike's puzzle boxes.

when Thorndike published his classic "Experimental Study of Associative Processes in Animals" in the *Psychological Review* in 1898, experimental psychology began to turn away from the study of social learning in animals as a central concern and, instead, rather wisely I think, focussed on the processes underlying individual acquisition of behavior.

Of course, it cannot be inferred from the finding that observation of the performance of trained individuals does not facilitate behavior acquisition by their naive fellows that other sorts of social interaction might not be important to animals in learning to solve problems that they face in their natural environments. Thorndike himself (1911; pp. 76-77) was careful to point out that what he called "semi-imitative" phenomena or "indirect results of instinctive acts" of various kinds (these will be discussed further below) could accelerate learning. This was an important observation which was largely ignored for the better part of a century.

Indeed, there do exist behavioral phenomena in nature which appear to require explanation in terms of social learning of some kind. If you compare the behavior of members of a single mammalian or avian species living in nature in different social groups, you will find, not infrequently, that many of the members of 1 social group exhibit some pattern of behavior totally absent in other groups (Galef, 1976). Field biologists, observing such intergroup variations in behavior, have long assumed that such animal "traditions," as they often call them, are transmitted from individual to individual within a group by observational learning or imitation. However, laboratory data strongly suggest that observational learning and imitation are not very important processes in behavior acquisition in nonprimates. So there remain important questions as to the processes supporting the development and maintenance of the "traditional" patterns of behavior to be observed in many species.

During the past decade, my students and I have been studying the role of social process in the development of traditional patterns of feeding in wild Norway rats. Below, I describe 2 research programs in which my coworkers and I have attempted to determine the causes of idiosyncratic feeding patterns exhibited by groups of wild Norway rats. Our methods have been similar in the 2 cases I'll be discussing. In both, we began with field observations of a traditional pattern of behavior, brought the phenomenon into the laboratory, and then attempted to analyze its causes.

### Case 1

Some years ago, an ecologist, Fritz Steiniger, was working for the German government as a rodent control officer. He noticed a most peculiar thing. Steiniger found that if a poison bait was employed in an area for an extended period of time, despite initial success, with the rats eating lots of poison and dying in large numbers, later acceptance of the bait was very poor. Steiniger noted, in particular, that young born to those animals which had survived poisoning rejected the poison bait without ever sampling it themselves and fed exclusively on safe diets available in their colony territory (Steiniger, 1950).

This is a robust phenomenon and relatively easy to capture in the laboratory. In our basic experiment (Galef & Clark, 1971a) we established colonies consisting of 2 male and 4 female wild rats in enclosures like that illustrated in the Figure 2 (top). These were 1 X 2-m enclosures, each containing 4 wooden nest boxes. Water was continuously available and food was presented to the colony for 3 hr/day in 2 food bowls located about 1 m apart. Each bowl contained 1 of 2 nutritionally adequate diets, each

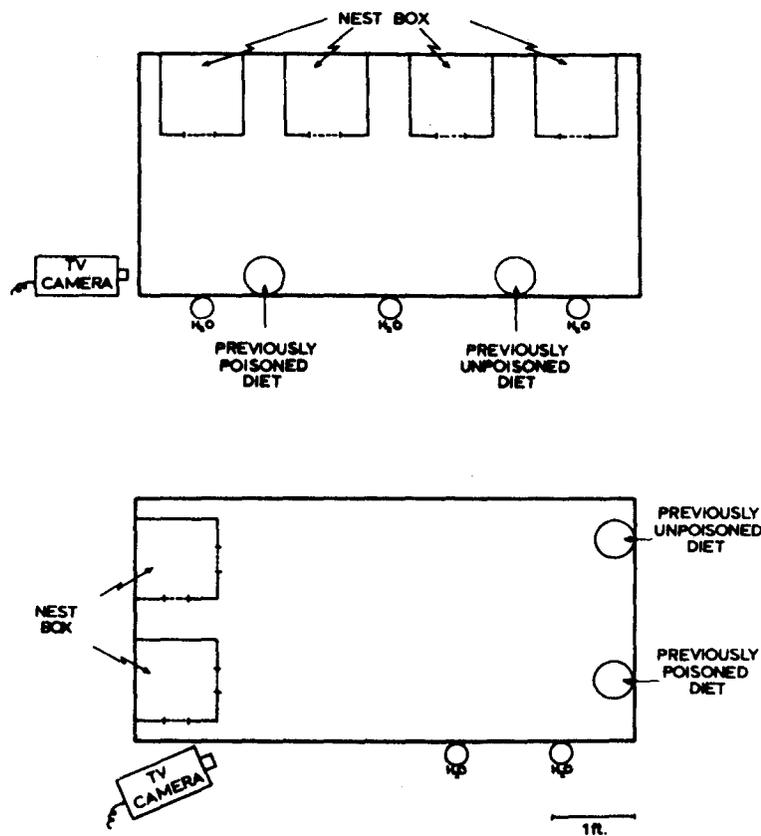


Fig. 2. One x two-meter enclosures (top) housing adult colonies and their young and (bottom) to which litters of weanlings were transferred. Reprinted from the *Journal of Comparative and Physiological Psychology*, 75:341-357. Copyright 1971 by the American Psychological Association. Reprinted by permission of the publisher.

discriminable from the other in color, texture, taste, and smell, which will be referred to as Diets A and B in all that follows. Diet A was powdered Purina Laboratory Chow and Diet B consisted mainly of sucrose and casein. The important thing to keep in mind is that naive rats strongly prefer Diet B to Diet A.

The adult members of our colonies were trained to eat 1 of the 2 diets presented each day and to avoid the other by introducing sublethal doses of poison into the samples of 1 of the diets offered to the colony during daily 3-hr colony feeding periods. Under these conditions, our wild rats rapidly learned to avoid ingesting the poisoned diet and, most important, continued to avoid ingesting the previously poisoned diet for some additional weeks when offered uncontaminated samples of it. Thus we have various colonies of wild rats eating either Diet A or Diet B and avoiding the other diet as a consequence of its previous association with poison.

Experiments proper began when a litter of pups born to colony members left their nest site to feed on solid food for the very 1st time. We observed the adults and pups throughout daily 3-hr feeding periods on closed-circuit television and recorded the number of times pups approached to within 10 cm of each food bowl and the number of times they ate from each of the 2 food bowls, now containing uncontaminated samples of Diets A and B.

After the pups had been feeding on solid food for a number of days, we transferred them to a new enclosure, illustrated in Figure 2 (bottom), where, without the adults of their colony, litters of pups were again offered a choice between uncontaminated samples of Diets A and B. The amount of each diet eaten by each litter of pups in this new situation was determined by weighing food bowls before and after each feeding session.

Typical results of such experiments are presented in Figures 3 and 4. Figure 3 (top) presents data describing the feeding behavior of a litter of wild rat pups born to a colony which had been trained to avoid ingesting the normally preferred Diet B. The abscissa indicates both the age in days of the pups and the number of days they had been feeding on solid food. The ordinate indicates the number of times the pups approached and fed from each of the 2 food bowls. As is clear from examination of Figure 3 (top), pups born to a colony trained to avoid ingesting the normally preferred Diet B ate only Diet A, which their parents had been trained to eat. We've run 36 litters of wild rat pups in this condition over the years and all but 1 has behaved similarly. They ate only Diet A and totally avoided Diet B.

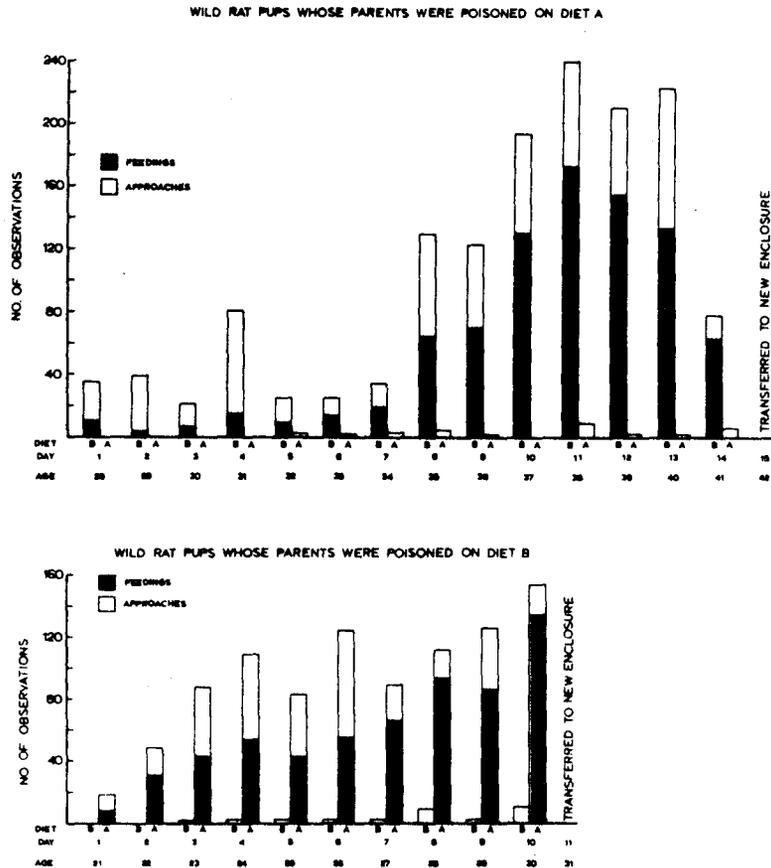


Fig. 3. Number of observed approaches to and feedings from bowls containing Diets A and B by wild rat pups the adults of whose colony had (top) been poisoned on Diet A, and (bottom) been poisoned on Diet B. Reprinted from the *Journal of Comparative and Physiological Psychology*, 75: 341-357. Copyright 1971 by the American Psychological Association. Reprinted by permission of the publisher.

Figure 3 (bottom) presents comparable data describing the feeding behavior of a litter of wild rat pups whose parents had been trained to avoid ingesting Diet A. Again the pups ate only the diet which the adults of their colony had been trained to eat (Diet B) and totally avoided the alternative. We've run 8 litters in this condition and all behaved identically. In the presence of adults of their colony, wild rat pups ingest only that diet which the adults of their colony are eating.

Furthermore, as shown in Figure 4, the learned dietary preference of the adults continues to affect the feeding preferences of their young for 8-10 days following transfer of pups to an enclosure separate from the adult colony. Pups removed from colonies eating Diet A continue to eat Diet A, and those removed from colonies eating Diet B continue to prefer that diet, even in the absence of adults.

Taken together these observations demonstrate, as Steiniger (1950) suggested, that adult rats can, in some fashion, lead their offspring to feed solely on a safe diet in an environment containing food known by the adults to have been poisoned. The data also show that food preferences learned in the presence of adults continue to affect the diet preference of pups for some time after the pups' removal from direct adult influence.

One interesting empirical question arising from these data is, what process or processes are responsible for pups weaning to diets eaten by the adults of their colony?<sup>1</sup>

During the last few years my students and I have found 3 ways in which adult wild rats can induce their young to wean to a given food. First, Clark and I (Galef & Clark, 1971b) have found that the physical presence of adults at a feeding site attracts pups to that feeding site and markedly increases the probability of young rats weaning to the food located there. If, for example, one establishes a colony of adult wild rats in a large enclosure like that illustrated in Figure 5, makes Diet A continuously available in 2 food bowls located behind a partition, and continuously monitors the area above the dotted line in the figure, one can determine the conditions under which each individual pup in a litter eats its very 1st meal of solid food. We have observed 9 individually marked pups from 3 litters take their very 1st meal of solid food, and all 9 ate their 1st meal under exactly the same circumstances. Each ate its 1st meal while an adult was eating

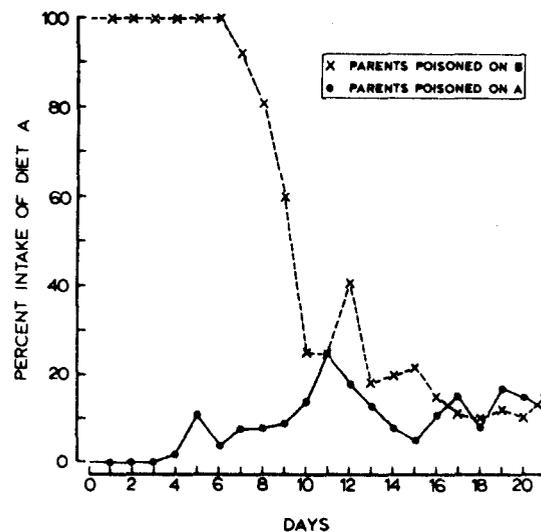


Fig. 4. Mean amount of Diet A eaten, as a percentage of total intake, by pups on the days following their removal from the adult colony. Reprinted from the *Journal of Comparative and Physiological Psychology*, 75:341-357. Copyright 1971 by the American Psychological Association. Reprinted by permission of the publisher.

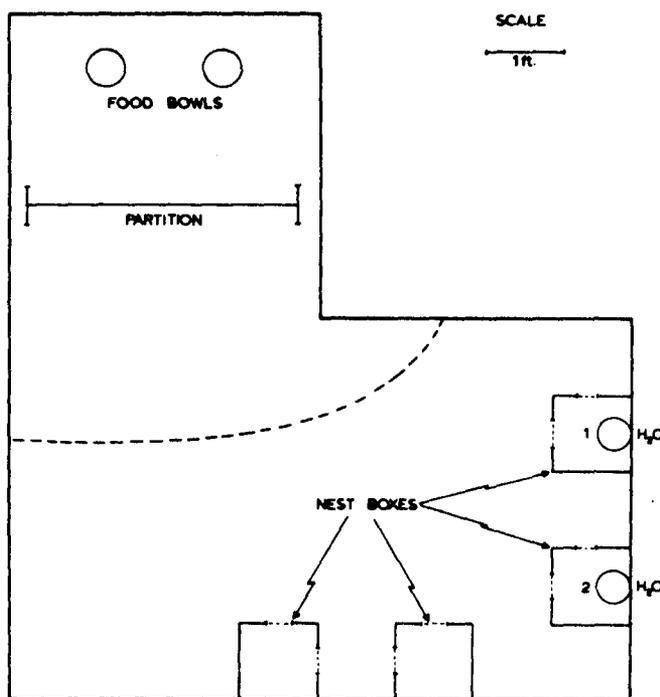


Fig. 5. Large enclosure for continuous observation of a wild rat colony. Reprinted from *Psychonomic Science*, 25:15-16. Copyright 1971 by the Psychonomic Society. Reprinted by permission of the publisher.

and each ate at the same food bowl as the feeding adult, not at the other bowl .5 m away. Given the observed temporal and spatial distributions of adult meals, the probability of these conditions occurring 9 out of 9 times by chance was very small indeed, less than 4 in a 1000. We, therefore, concluded that the presence of an adult at a feeding site serves to attract pups to that site and to cause pups to initiate feeding there. It is probably relevant to note that blinded pups showed no tendency to eat their 1st meal of solid food in the presence of a feeding adult under these conditions, so visual cues seem to guide approach in this situation (Galef & Clark, 1971b).

Second, Linda Heiber and I have found that adult rats deposit olfactory cues in areas which they visit and that these cues bias weaning pups' choice of areas both for

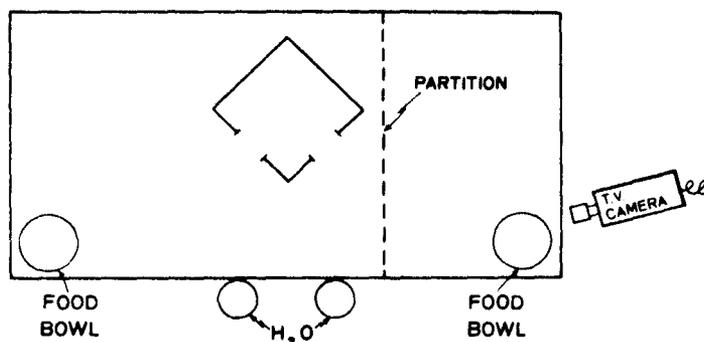


Fig. 6. Enclosure in which the effects of residual olfactory cues on pup behavior were measured. Reprinted from the *Journal of Comparative and Physiological Psychology*, 90:727-739. Copyright 1976 by the American Psychological Association. Reprinted by permission of the publisher.

exploration and for initiation of feeding. Heiber and I (Galef & Heiber, 1976) confined a dam and litter for several days in the larger portion of the enclosure, shown in Figure 6. Then we removed that dam, her litter, and the partition from the enclosure and observed individual food-deprived pups from another litter feed for 3 hr/day in the open enclosure with Diet A available in both food bowls. As can be seen in Figure 7, pups prefer to explore and eat at the end of the enclosure soiled by conspecifics rather than at the clean end.

In addition to being able to influence a pup's choice of feeding site, and thus indirectly its food preference, the mother of a litter of pups can also directly influence her own pups' dietary preference. Clark and I (Galef & Clark, 1972) conducted an experiment much like the 1st one described above, but with 1 importance difference. Colonies of adult rats were again housed in 1 X 2-m enclosures; however, in this experiment, adults were removed to a separate cage, where they were fed either Diet A or Diet B for 3 hr/day, depending on the experimental condition to which their colony was assigned. While the adults were out of the colony enclosure, the pups were presented with 2 standard food bowls, 1 containing Diet A and the other Diet B. Figure 8 presents data describing the percent of Diet A eaten by pups, the adults of whose colonies were eating either Diet A or Diet B. As can be clearly seen in Figure 8, the diet eaten by the adults profoundly affected the food choice of the pups even though, under the conditions of the present experiment, the adults and young had no opportunity to interact directly in the feeding situation.

Sherry (Galef & Sherry, 1973), Henderson (Galef & Henderson, 1972), and I have provided evidence that the milk of a lactating female rat contains cues directly reflecting the flavor of her diet. We believe that as a result of exposure to these gustatory cues present in mothers' milk, weaning pups will exhibit a preference for a diet that their dam has been eating during lactation. In 1 of our experiments (Galef & Sherry, 1973), Sherry and I took rat pups nursing from a lactating female eating Diet A, force-fed them  $\frac{1}{2}$  cc of milk manually expressed from another lactating female eating Diet B, and then poisoned the pups with lithium chloride. At weaning, we tested these experimental pups

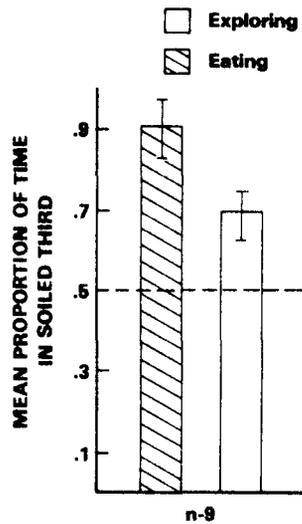


Fig. 7. Mean proportion of time spent by individual pups exploring and feeding in the end of an enclosure previously occupied by a lactating rat and her litter. Reprinted from the *Journal of Comparative and Physiological Psychology*, 90:727-739. Copyright 1976 by the American Psychological Association. Adapted by permission of the publisher.

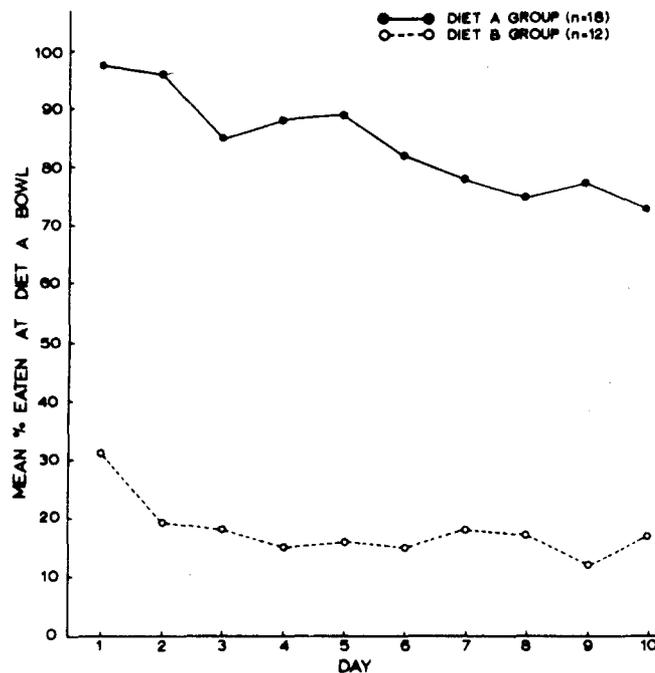


Fig. 8. Mean amount of Diet A eaten by pups, as a percentage of total intake, when adults and pups have no opportunity to interact in a feeding situation and adults are eating either Diet A or Diet B. Reprinted from the *Journal of Comparative and Physiological Psychology*, 28:213-219. Copyright 1972 by the American Psychological Association. Reprinted by permission of the publisher.

for their preference between Diets A and B. As can be seen in Figure 9, in comparison with a variety of controls, the experimental pups (those which had received milk from a female eating Diet B prior to poisoning) exhibited an aversion to Diet B.

Thus the results of our research to date indicate the existence of at least 3 mechanisms by which adult rats may bias choice of diet by conspecific young at weaning. Both the physical presence of adults at a feeding site and residual olfactory cues deposited by adults in the vicinity of a food source can influence pups' choice of a place at which to wean and consequently pups' choice of diet at weaning. Further, flavor cues in maternal milk have the potential to directly influence pup diet choice at weaning.

Fritz Steiniger was basically correct. The learned feeding preferences of adult wild rats can be socially transmitted to their young, reducing the probability that the young will ingest toxic food. Edward Thorndike was also correct. The indirect results of what might be conceived of as instinctive acts, in this case the tendency of rat pups to approach adults or their scents and to suckle from their dam, can result in introduction of the young to the diet of adults of their colony and consequent apparent imitation of learned adult food preferences by the young. Of course, the finding that 1 pattern of behavior idiosyncratic to a particular social group of wild rats develops as the result of social interaction cannot be taken to infer that all such "traditions" in wild rats are, in fact, the result of social process. Which brings us to Case 2.

## Case 2

Wild rat colonies exhibit traditional variation not only in their diet preferences but also in the motor patterns they employ in food acquisition. Members of some colonies of

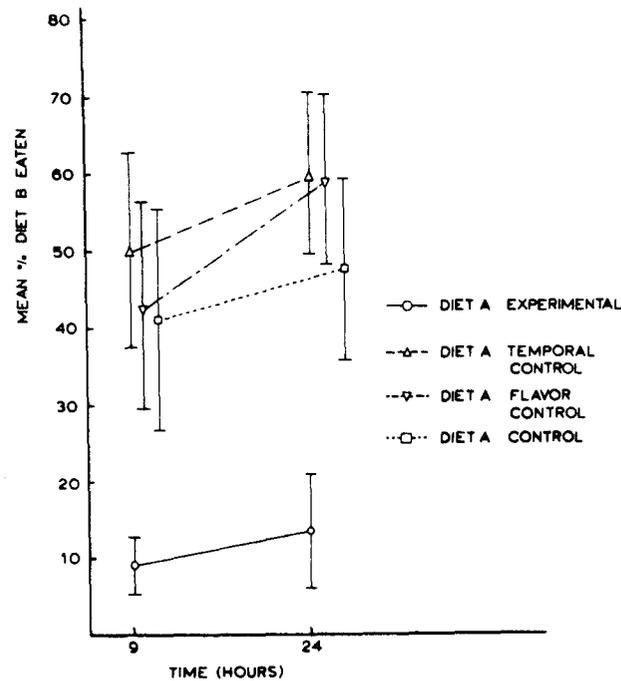


Fig. 9. Mean amount of Diet B eaten at weaning, as a percentage of total intake, by pups poisoned after receiving milk from a mother eating Diet B and by controls. Reprinted from the *Journal of Comparative and Physiological Psychology*, 93:374-378. Copyright 1973 by the American Psychological Association. Reprinted by permission of the publisher.

wild rats have been reliably reported to pursue and capture fingerling trout (Cottam, 1948); members of other colonies to stalk and kill sparrows and ducks (Steiniger, 1950); and members of yet other colonies to raid birds' nests for eggs and young (Austin, 1948; Norman, 1975).

More immediately relevant to the present discussion is the finding by two Italian field workers, Drs. Gandolfi and Parisi of the University of Parma, that many members of some colonies of wild rats living along the banks of the Po River in Northern Italy dive for and feed on mollusks inhabiting the river bottom, while no members of nearby colonies that have equal access to mullusks within their home ranges feed on them (Gandolfi & Parisi, 1972, 1973; Parisi & Gandolfi, 1974).

Gandolfi and Parisi interpreted these observations as indicating that predation on submerged prey spreads through a wild rat colony as the result of observational learning. If discovery of mollusks on the river bed by colony members is a rare event and if naive colony members readily learn to dive as a result of interacting with diving individuals, then one would expect the observed bimodality in the frequency of individuals diving in various colonies. Although the hypothesis that the habit of diving for food spreads by social learning is a very attractive one, once again evidence adequate to support it would be extremely difficult to collect in the uncontrolled natural situation. Described below are some experiments undertaken in my laboratory to explore the possibility that naive rats will come to dive for food in shallow water simply as a result of freely interacting with conspecifics exhibiting diving behavior (Galef, 1980).

Subjects were pairs of laboratory-bred, adult wild rats, pairs of adult domesticated Long-Evans rats, and wild rat dams and their litters.

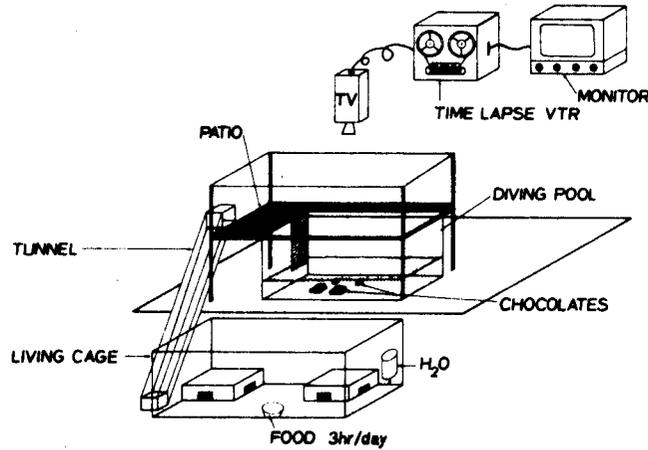


Fig. 10. The living cage, patio and diving pool, and tunnel of the diving enclosure. Reprinted from the *Journal of Comparative and Physiological Psychology*, 94:416-425. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher.

All subjects were housed and tested in diving enclosures like that illustrated in Figure 10. Each diving enclosure was constructed of 3 modules: a *living cage* providing harborage sites, ad lib water, and food (Diet A) for 3 hr/day; a diving area consisting of a caged patio and glass-walled diving pool; and a *tunnel* providing access between the living cage and diving area. All behavior on the patio and in the diving pool was recorded on a time-lapse videotape recorder and reviewed daily.

To begin, an individual adult rat was introduced into a diving enclosure and trained to dive for pieces of chocolate by starting with a dry diving tank with 5 pieces of chocolate on its floor and then gradually raising the water level to 15 cm over a period of days. The water level was maintained at 15 cm until completion of the experiment, and any chocolates eaten were replaced daily. Once the trained rat was regularly diving, a naive sibling of the trained individual was shaved along its back for identification and introduced into the diving enclosure for 36 days. Table 1 shows the treatment of trained and naive subjects throughout the experiment.

Dams of 3 litters of wild rat pups were trained to dive for food in the same way as other trained adults, and their pups were observed from 21 to 57 days of age to see if they exhibited diving behavior. The main results are presented in Table 2 which indicates the number of wild and domesticated naive rats recovering 1 or more chocolates from the diving-pool floor during the 36 days each was present in the diving enclosure. As is evident from examination of Table 2, naive adults did not learn to dive as the result of interacting with a diving conspecific. As can also be seen in Table 2, although some

TABLE 1. Treatment of Subjects.

		Days			
		1-21	22-24	25-32	33-36
Trained S	training	present	removed	returned	removed
Naive S	absent	present	present	present	present
Food in living cage <sup>a</sup>	3 hr/day	3 hr/day	none	3 hr/day	none

<sup>a</sup>An additional 5 chocolates/day were available on the bottom of the diving pool.

*TABLE 2. Number of Rats Not Trained to Dive Diving During the 36 Days of the Experiment.*

Naive Rats	Diving	Not Diving
Adult wild	0	10
Adult domesticated	0	10
Juvenile wild	4	14
Juvenile wild (control)	3	15

juvenile rats in the experimental condition, that is juveniles living with a diving mother, did learn to dive for food, an approximately equal proportion of those in a control condition, whose mothers did not dive, learned to dive.

The failure of naive rats to learn to dive cannot be attributed to a failure on the part of their trained cagemates to demonstrate diving behavior. Trained rats retrieved an average of 4.6 chocolates/day from the diving-pool floor on each of the 28 days they cooccupied the diving apparatus with their naive partners. Similarly, the failure of naive subjects to learn to dive cannot be attributed to their failure to observe their trained cagemates diving. Naive subjects rapidly learned to await their diving cagemates on the patio and frequently attempted to snatch retrieved chocolates from the diver, but very rarely entered the water themselves. In 720 rat-days of observation, adult naive rats entered the water on only 2 occasions. The results suggest that interaction with a diving conspecific is not in itself sufficient to induce an adult or juvenile rat to dive for food.

Observation both of naive subjects and of trained individuals early in the training process suggested that a major impediment to acquisition of diving behavior was a reluctance to enter water. Thus, it seemed possible that rats which had learned to swim but not to dive might be socially induced to dive for food. I therefore initiated an experiment in which adult wild rats that had been trained to swim, but not to dive, were allowed to interact in the diving enclosure with a sibling who had been trained to dive. Unexpectedly, 2 of the 6 naive subjects (those trained to swim, but not to dive) began to dive in 15 cm of water and retrieve chocolates from the diving pool floor before their trained cagemates demonstrated diving behavior.

Thus the next experiment was undertaken to determine whether rats trained to swim would spontaneously dive and retrieve objects from beneath the water. Litters of pups were maintained in a swimming enclosure, a part of which is illustrated in Figure 11. The swimming enclosure required subjects to cross a small body of water to acquire food. Although the subjects were free to dive in the swimming pool, they received no extrinsic reinforcement for doing so.

Each subject litter of pups was taken from its dam and introduced as a group into the swimming enclosure at 30 days of age. The swimming pool was left empty until the litter had begun to feed at the food bin and the pool was then gradually filled with water over a 1-week period to a depth of 20 cm.

Each litter was left undisturbed in the swimming enclosure for a month. Then each member of a litter was individually introduced into a diving enclosure, with the diving pool already flooded to a depth of 15 cm and 3 chocolates available on the diving-pool floor. A bowl containing powdered Purina Laboratory Chow was placed in each living cage for 3 hr/day on each of the 7 days each subject remain in its diving enclosure. Control subjects were treated identically to experimental subjects except that no water was introduced into their swimming pools prior to their transfer to the diving enclosure for individual testing.

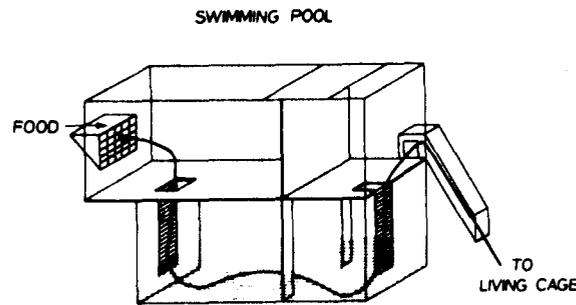


Fig. 11. The swimming pool of the swimming enclosure. Reprinted from the *Journal of Comparative and Physiological Psychology*, 94:416-425. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher.

The results are presented in Figure 12. As can be seen in the figure, swimming experience markedly facilitated diving behavior in both wild and domesticated rats. The finding that swimming rats are effectively diving rats severely limits the role which social factors could play in the spread of diving behavior through a population. If rats learn to swim independently, and if swimming rats dive, then social interaction could serve only to direct rats already prepared to dive to 1 locale rather than another. It is, however, also possible that social factors might indirectly result in the spread of diving behavior by facilitating the spread of swimming behavior.

The apparatus used to examine the role of social interaction in the development of swimming behavior is illustrated in Figure 13. It consisted of a living cage attached to a 2-m-long *swimming alley* with food available ad lib in a container mounted on a stand at the opposite end of the swimming alley from the living cage. A mother and litter were introduced into the living cage on Day 2 postpartum and the dam was trained to swim for food. Water was available in the living cage ad lib, and food (Diet A) was present there for 3 hr/day. Control litters were treated identically to experimental litters except that a

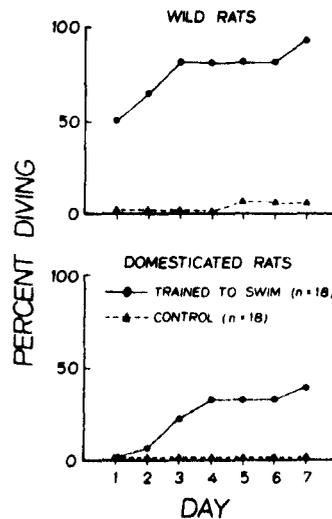


Fig. 12. Percentage of wild and domesticated rats diving for chocolates on each of 7 days in the diving enclosure, after either receiving or not receiving swimming experience in the swimming enclosure. Reprinted from the *Journal of Comparative and Physiological Psychology*, 94:416-425. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher.

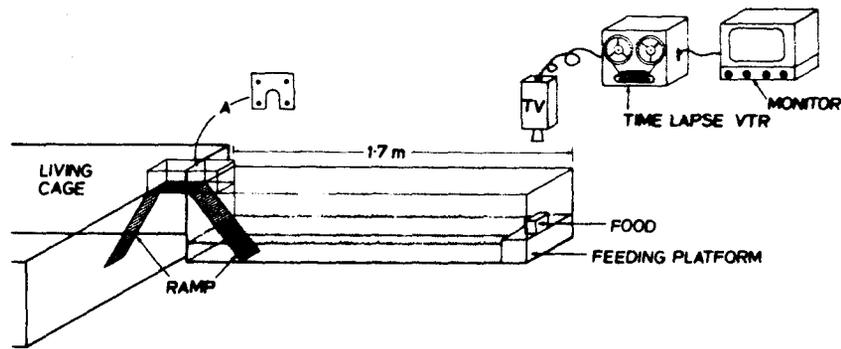


Fig. 13. The swimming alley. Reprinted from the *Journal of Comparative and Physiological Psychology*, 94:416-425. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher.

partition, which allowed pups but not dams access to the swimming alley, was placed in the tunnel between the living cage and swimming alley.

Figure 14 indicates the mean age of litters on the day 1 that their members 1st reached the food at the far end of the swimming alley from the living cage. As can be seen in the figure, wild rat pups will start to swim at an early age regardless of whether or not they are in the presence of a swimming adult rat, while Long-Evans rats will swim considerably earlier in the presence than in the absence of a swimming adult.

These results are not consistent with the hypothesis that social interaction is necessary for the spread of swimming behavior. All litters of rats, regardless of whether they were exposed to swimming conspecifics, came to exhibit swimming behavior prior to reaching maturity.

The results of the experiments I've described thus far suggest that members of all groups of rats living near water will spontaneously learn to swim and therefore, with high probability, to dive. Taken together with Gandolfi and Parisi's field observations, indicating that in natural settings no members of many colonies exhibit diving behavior, our laboratory data suggest that in the field, members of most colonies may acquire the diving response but that its subsequent performance is inhibited in some way in non-diving colonies.

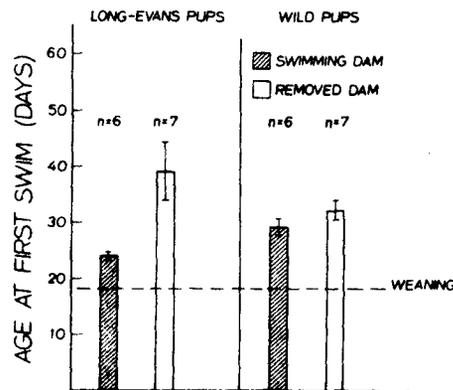


Fig. 14. Mean age at 1st incidence of swimming to the feeding platform in the swimming alley by rat pups reared either by a swimming or nonswimming mother. Reprinted from the *Journal of Comparative and Physiological Psychology*, 94:416-425. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher.

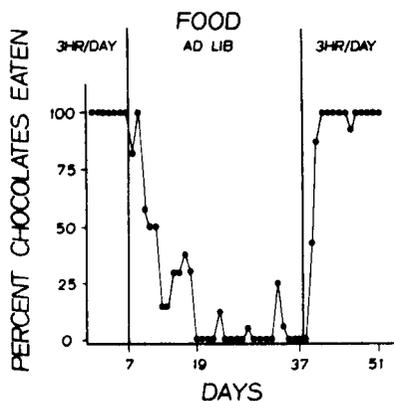


Fig. 15. Percentage of available chocolates retrieved from the diving-pool floor by wild rats on a 3 hr/day feeding schedule and while on ad lib food. Reprinted from the *Journal of Comparative and Physiological Psychology*, 94:416-425. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher.

Clearly, the habit of diving for food is only 1 element in the feeding repertoires of those rats which exhibit it, and it is conceivable that rats would prefer not to dive in water for food if alternative sources of nutrition were available to them. In the next experiment, the frequency of diving behavior in rats was examined as a function of the availability of alternative means of acquiring food.

Each wild rat subject was placed in a diving enclosure and trained to dive for 3 chocolates/day in 15 cm of water, while maintained on a 3-hr/day feeding schedule with Diet A offered in the living cage. After each individual had learned to dive for chocolates, Diet A was made available ad lib in that subject's living cage for 30 days. At the end of the period of ad lib feeding, each subject was returned to a 3-hr/day feeding schedule.

Figure 15 shows the mean percent of available chocolates eaten by subjects on each day of the experiment. As the figure demonstrates, even rats which have acquired the habit of diving for food will not do so if an adequate supply of food is available on land. This result is especially striking given that wild rats exhibit a strong preference for chocolate over Diet A in a simple choice situation. The results suggest that most rats living near water may have acquired the habit of diving for food, but that they only exhibit diving behavior if they lack adequate alternative rations within their home ranges.

Although the data I have presented cannot be interpreted as showing that social learning of the behavior of diving in shallow water for food is unimportant in natural settings, the data do suggest that the effects of environmental variables on diving behavior need to be examined in the wild before the social learning hypothesis is accepted. In particular, it would be valuable to know whether adult individuals trapped from nondiving colonies on the Po River would spontaneously exhibit diving behavior in the laboratory when placed on a restricted feeding schedule. It would also be useful to know whether introduction of an alternative food source into the home ranges of diving colonies along the Po would inhibit further diving.

### Conclusion

The message I would leave with you is that, although the existence of "traditional" patterns of behavior in social groups of free-living animals would seem to provide *prima*

*facie* evidence of an important role of social learning in the acquisition of behavior, it is as true today as it was in Romanes' time that simple observation of behavior in nature is not adequate to determine its origins or causes. Some of the intriguing differences in behavior to be found in different populations of a species are the result of social processes; others are not. The only way to determine which is which is, as Thorndike proposed in 1898, to examine phenomena of interest in controlled settings.

Experimental animal psychology in North America started with an analysis of the processes underlying the acquisition of a pattern of behavior observed in a free-living animal. In the past 80 years, the techniques and theory of the discipline have matured immensely, yet we know little more today of the processes underlying acquisition of naturally occurring behaviors of interest than we did at the turn of the century. Study of the processes underlying development of behaviors of importance in the survival of organisms in their natural environments has been too long ignored by experimental animal psychologists. It is time to return to our historical roots.

### Notes

<sup>1</sup>See Galef (1977) for a discussion of the mechanisms responsible for continued pup avoidance of adult-avoided diets following removal of pups from direct adult influence.

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