6 Social Learning in Wild Norway Rats

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In the decades before either comparative psychology or the study of animal behavior emerged as experimental disciplines, it was widely believed that learning by imitation was a central process in the acquisition of adaptive behavior by members of most vertebrate species. According to Morgan (1896):

> The young bird or mammal, especially in the case of gregarious species, is born into a community where certain behavior is constantly exhibited before its eyes. Through imitation it falls in with the traditional habits, and itself serves as one of the models for those that come after. There can be no question that this tradition is of great importance in animal life. (p. 184)

Instinct and imitation rather than instinct and learning were commonly considered the major alternative means of development of behaviors observed in natural circumstances. "Often we are unable to say in the present condition of our knowledge whether the performance of certain activities is due to heredity or tradition; whether they are instinctive or due to imitation" (Morgan, 1869, p. 184). Individual learning was treated as a modulator of instinct or antecedent to tradition rather than as a primary mode of behavior acquisition (Morgan, 1896, pp. 144–165; Romanes, 1884, pp. 220–229).

George Romanes, protégé of Charles Darwin, Fellow of the Royal Society, and a major influence in biology at the close of the Victorian era, was the foremost proponent of the view that learning by imitation is central to the development of behavior in animals. The importance of learning by imitation in Romanes' theory of behavior is clearly illustrated in his discussion of the causes of the perfection of instincts in allowing organisms to meet the challenges provided by their respective habitats.

Instincts were believed by Romanes (1884) to evolve in either of two ways: by Darwinian natural selection or "by the effects of habit on successive generations" (p. 177). Arguing by analogy, Romanes (1884) proposed that:

> Just as in the lifetime of the individual adjustive actions which were originally intelligent may by frequent repetition become automatic, so in the life-time of the species, actions originally intelligent may, by frequent repetition and heredity, so write their effects on the nervous system that the latter is prepared . . . to perform adjustive actions mechanically which in previous generations were performed intelligently. (p. 178)

In sum, intelligent behavior could modify instinct to increase its perfection and such learned modifications of behavior (now instinctive) could be inherited by future generations. One might expect Romanes to have argued, as had Darwin (1884) who held a similar view, that those learned behaviors that became instinctive were individually acquired. However, quite to the contrary, Romanes (1884) proposed "with animals, as with men, original ideas are not always forthcoming at the time they are wanted, and therefore it is often easier to imitate than to invent" (p. 219). For Romanes, the central process modifying instinct to ever greater perfection was imitation, particularly imitation of the behavior of members of one species by members of another.

Although such a model of the evolution of adaptive behavior may seem unnecessarily elaborate to the modern reader, we are fortunate in not having to attempt to explain the origins of species-typical behaviors as complex as those with which Romanes had to deal. The paucity of systematic observations of animal behavior available during the nineteenth century required Romanes to rely heavily on anecdotal accounts provided by correspondents for descriptions of relevant phenomena. Unfortunately, many of the reports of animal behavior provided by Romanes' contemporaries suggested that mammals were capable of achieving truly remarkable solutions to problems they encountered in their natural habitats. For example, mice in Iceland were said to store supplies of berries in dried mushrooms, to load these rations onto dried cow-paddies, and to launch and then steer such improvised, provisioned vessels across flooded rivers and streams using their tails as rudders in the rush of water. If one takes such an anecdote seriously, as Romanes did in consequence of his receiving two independent reports of the behavior (Romanes, 1881, p. 364), it suggests that the ability of animals to respond to environmental challenges is very sophisticated indeed. It is surely more parsimonious to hypothesize that mice first acquired such tricks by observing humans provision and steer boats and that the learned behavior became instinctive, than to assume that countless individual mice independently learned to provision, launch, and steer rafts; if such complex patterns of behavior can be learned by observation, it is surely reasonable to assume that simpler patterns of behavior can be acquired in the same way.

Perhaps the most historically important of the many instances of imitative learning in animals that Romanes discussed in his two major comparative texts, *Animal Intelligence* (1881) and *Mental Evolution in Animals* (1884), concerned a cat that belonged to Romanes' own coachman. This animal had learned, without formal tuition of any kind, to open a latched door in Romanes' yard by holding onto the latch guard with one forepaw, depressing the thumb-piece with the other, and simultaneously pushing at the doorpost with her hind feet. Romanes argued that the cat, in the absence of any other source of information, must have observed that humans opened the door by grasping the latch guard and moving the thumb-piece. Then, said Romanes (1881), the cat must have reasoned, "If a hand can do it, why not a paw?" (p. 422). Finally, the cat, strongly motivated by this insight, attempted to open the door in question, and succeeded.

Stephen Jay Gould (1977) has suggested (with tongue just barely in cheek) that Darwin's theory of evolution was conceived in response to the irritation provided by five years of forced conversation with the conservative, fundamentalist Robert Fitzroy, captain of *H.M.S. Beagle* and Darwin's constant dinner companion throughout their joint voyage of exploration. One might argue similarly that experimental animal psychology in North America arose from Edward Thorndike's irritation with excesses in Romanes' *Animal Intelligence:* its anecdotal method, its speculative conclusions, even its title (Thorndike, 1911, pp. 22–26, pp. 68–70). Thorndike pointed out that although accurate observation in nature may tell us what an animal does, observation alone cannot tell us how the observed behavior was acquired by its performer. The discovery of the processes underlying behavior acquisition, asserted Thorndike, can only come from examination in controlled and replicable situations of the behavior of subjects of known previous history. So in the late 1890s Thorndike brought the latch-opening behavior of cats, discussed by Romanes, into the laboratory and, under controlled conditions, observed the acquisition of the solution of problems similar to those posed by a latched garden gate. As is well known, Thorndike found that animals in general, and cats in particular, did not learn to operate mechanical devices by observing either other cats or humans do so. In fact, in some cases, observation of a trained demonstrator actually interfered with the gradual process of trial-and-error learning Thorndike believed necessary for naive individuals to acquire all rewarded responses. In 1898, when Thorndike published his now classic "Experimental study of associative processes in animals" in the *Psychological Review*, experimental psychologists began to turn away from the study of social learning in animals as a central concern and focused instead on the processes underlying individual acquisition of behavior.

Of course, as Thorndike (1911) emphasized, it cannot be inferred from the finding that observation of the performance of a trained individual does not facilitate response acquisition by naive individuals, that other types of social interaction might not prove important in the acquisition of adaptive behavior. Thorndike (1911, p. 76) discussed in some detail a number of ways in which behavior could be transmitted between individuals by processes he labeled "semi-" or "pseudoimitative." For example, he states (Thorndike, 1911):

> The young animal stays with or follows its mother from a specific instinct to keep near that particular object . . . It may thus learn to stay near trains, or scramble up trees, or feed at certain places and on certain plants. Actions due to following pure and simply may thus simulate imitation . . . more investigation and experimentation may finally reduce all the phenomena of so-called imitation of parents by young to the level of indirect results of instinctive acts. (pp. 77–78)

The possible role of such "indirect results of instinctive acts" in producing "semi-imitative" behaviors (a special case of incidental learning (Church, 1957) was largely ignored within psychology for the better part of a century. Psychologists turned from analysis of the mechanisms underlying behavior acquisition of animals in nature to study of acquisition processes in animals presumed analogous to those observed in humans. Learning by observation or imitation, assumed to underlie much of human learning (Bandura, 1962), was a phenomenon of interest to psychologists. Consequently, myriad experiments were undertaken (in large part unsuccessfully) to demonstrate learning by observation in mammals and birds. Learning incident upon close association with conspecifics was largely ignored, possibly because it was perceived to be irrelevant to processes underlying human learning.

There is, however, good reason to believe that social learning may be an important factor in the acquisition of adaptive behavior by free-living animals. Field biologists engaged in the systematic observation of mammals and birds in their natural habitats have described a variety of behavioral phenomena that seem to require explanation in terms of social learning of some kind. Comparison of the behavior of members of a single species living in nature in different social groups has frequently revealed that many of the members of one social group exhibit some pattern of behavior totally absent in other groups (see Galef, 1976, for a review). Those observng idiosyncratic behaviors typical of a social group have long assumed that such animal "traditions," as they are frequently called, are socially transmitted from individual to individual within a group as the result of imitation of one animal by another.

Although the fact that groups of conspecific animals may differ from one another in their behavior is well established, the role of either imitation learning or other social processes in the establishment and maintenance of such differences is not. As Thorndike stated, simple observation of an animal behaving in nature provides little useful information concerning the processes responsible for the development of the behavior observed. Field observers' reports of animal "traditions," thus, leave unanswered important questions concerning the necessary antecedent conditions for the development of idiosyncratic behaviors in groups of animals, questions that can only be answered under controlled conditions.

For 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 (*Rattus norvegicus*). In the remainder of the present chapter I briefly review two series of experiments in which my coworkers and I have attempted to determine the causes of colony-specific feeding patterns exhibited by groups of wild rats. Our methods have been similar in the two cases described. In each, we began with field reports of a traditional pattern of behavior in rats, then brought the phenomenon into the laboratory, and finally attempted to analyze its causes. In both cases, our analyses of potential social learning phenomena has been in terms of the observable behavior of the individuals comprising social groups. Consequently, our studies have been largely dependent on techniques developed within experimental animal psychology.

SOCIAL TRANSMISSION OF DIET PREFERENCE

Some years ago, Fritz Steiniger, an ecologist working in Germany, was studying the causes of difficulties experienced in controlling rat populations by means of poisoned baiting stations permanently placed in rat-infested areas. Steiniger (1950) had found that if a single poison bait were employed in a rat-infested area for an extended period of time, despite initial success, later acceptance of the bait was very poor. He noted, in particular, that young rats, born to those animals that had survived poisoning, rejected the poison bait without even sampling it themselves. These young fed exclusively on safe diets available in their colony territory. Steiniger attributed such avoidance of contact with potentially toxic baits by naive young animals to the behavior of experienced individuals which he believed disuaded inexperienced juveniles from ingesting poisoned food.

The tendency of juvenile wild rats to avoid ingesting diets that the adults of their colony have learned to avoid is a robust phenomenon that proved relatively easy to bring into the laboratory. In our basic experiment (Galef & Clark, 1971a), we established colonies of adult wild rats in 1 by 2 m enclosures like that illustrated in Fig. 6.1a. Water was continuously available in each enclosure and food was presented to each colony for 3 hours each day in two food bowls located about .8 m apart. Each food bowl contained one of two nutritionally adequate diets, each discriminable from the other in color, texture, taste, and smell. I refer to these two diets 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. Naive rats strongly prefer Diet B to Diet A).

The adult members of our colonies were trained to eat one of the two diets presented each day and to avoid the other by introducing sublethal doses of poison (lithium chloride) into the samples of one of the diets offered to the colony during daily 3-hour feeding periods. Under these conditions our wild rats rapidly

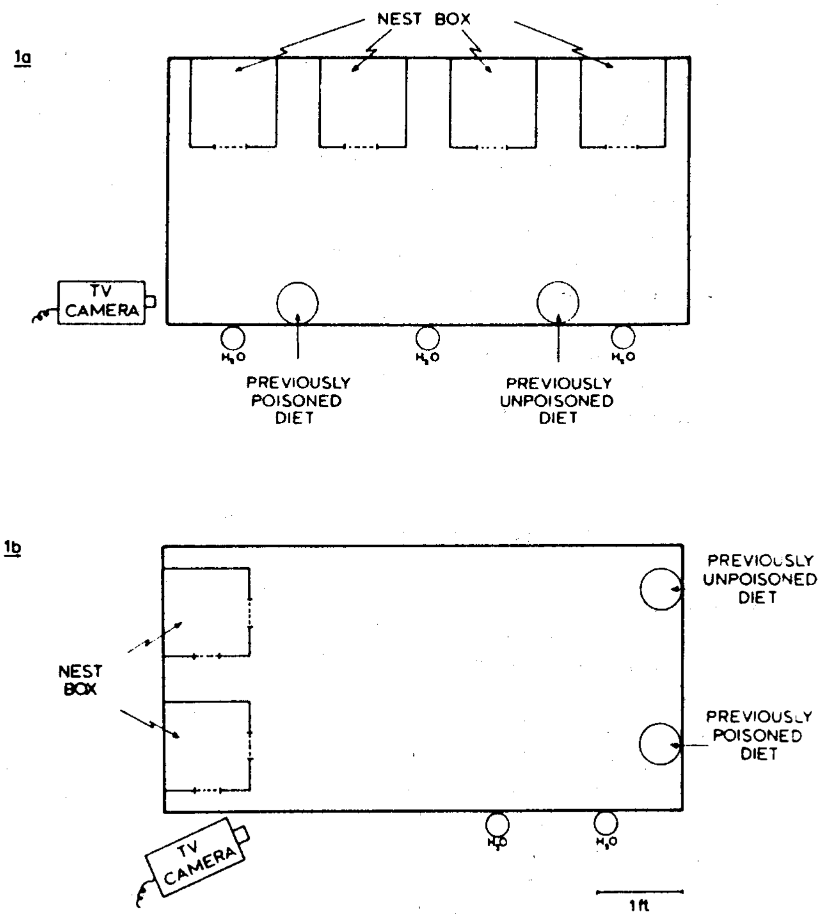

FIG. 6.1. One by two meter enclosures: (1a) housing adult colonies and their young and (1b) to which litters of weanlings were transferred. (Galef & Clark, 1971a. Copyright 1971 by the American Psychological Association. Reprinted by permission of the publisher and author.)

learned to avoid ingesting the poisoned diet, and, most importantly, they continued to avoid ingesting the previously poisoned diet for some additional weeks when offered uncontaminated samples of it.

The experiment proper began when litters of pups born to trained colony members left their nest-sites to feed on solid food for the very first time. We observed both adults and pups throughout daily 3-hour feeding periods on closed circuit television and recorded the number of times pups approached to within .1 m of each food bowl and the number of times pups ate from each food bowl, now containing uncontaminated samples of diet.

After a litter of pups had been feeding on solid food for a number of days, we transferred them to a new enclosure (illustrated in Fig. 6.1b), where, without the adults of their colony, they were again offered a choice between uncontaminated samples of Diets A and B. The amount of each diet eaten by the pups in this situation was determined by weighing food bowls before and after each feeding session.

Typical results of such experiments are presented in Figs 6.2 and 6.3. Figure 6.2a presents data describing the feeding behavior of a litter of wild rat pups born to a colony whose members had been trained to avoid ingesting the normally

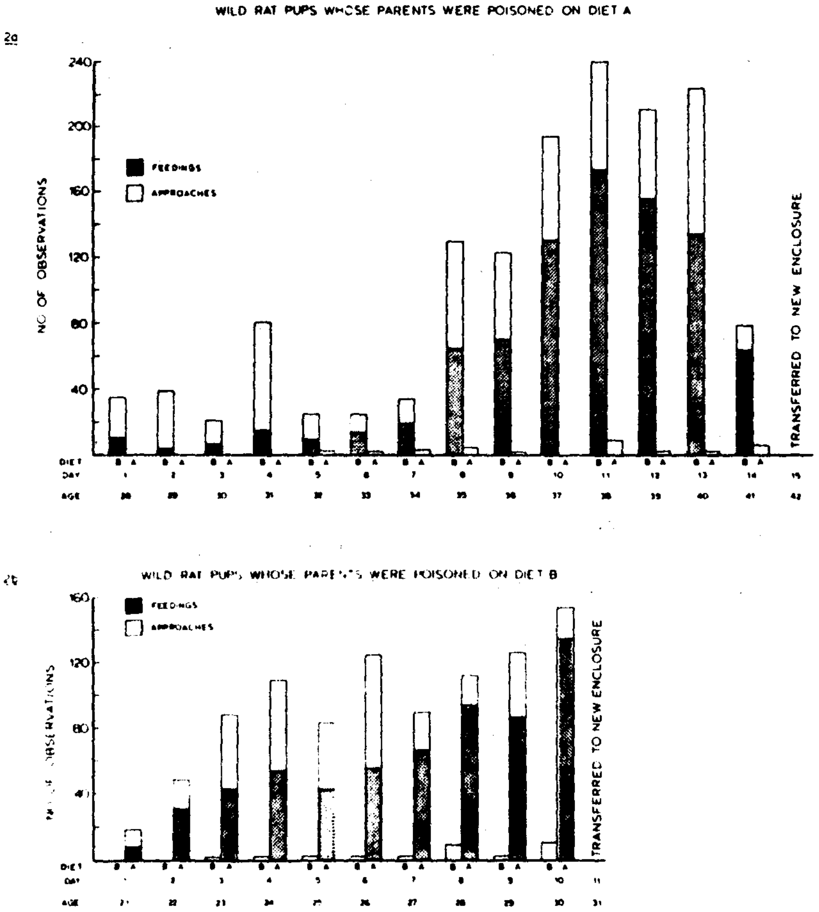

FIG. 6.2. Number of observed approaches to and feedings from bowls containing Diets A and B by wild rat pups, the adults of whose colony had been poisoned A (2A) or Diet B (2B). (Galef & Clark, 1971a. Copyright 1971 by the American Psychological Association. Reprinted by permission of the publisher and author.)

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 two food bowls. As is evidence from examination of Fig. 6.2a, pups born to a colony trained to avoid ingesting the normally preferred Diet B ate only Diet A, the diet that the adults of their colony had been trained to eat. Over the years, we have observed 36 litters in this condition and all but one has behaved similarly. Pups born to colonies trained to eat Diet A ate only Diet A and totally avoided eating Diet B.

Fig. 6.2b presents comparable data describing the feeding behavior of a litter of wild rat pups whose parents had been trained to avoid ingesting Diet A. As can be seen in Fig. 6.2b, again the pups ate only the diet that the adults of their colony have been trained to eat (Diet B) and totally avoided the alternative (Diet A) that their parents had learned to avoid. We have observed eight wild rat litters in this condition and all behaved identically. The data lead to the conclusion that, in the presence of adults of their colony, wild rat pups ingest only that diet that the adults of their colony are eating and avoid available alternatives that the adults are avoiding.

Furthermore, as shown in Fig. 6.3, the learned dietary preference of the adults of a colony continues to affect the feeding preference of their young for 8 to 10 days following transfer of the pups to an enclosure separate from those adults. Pups removed from colonies eating Diet A continued to eat Diet A, and those removed from colonies eating Diet B continued to prefer that diet, even in the absence of adults.

Taken together, our observations demonstrate, as Steiniger indicated, that adult rats can bias 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 the 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 obvious question arising from these observations concerns the process or processes responsible for pups weaning to that diet eaten by adults of their colony.[1] How do young rats come to know and prefer the foods their adult fellows are exploiting? The results of experiments conducted in my laboratory during the past several years have provided evidence of three ways in which adult wild rats can induce young conspecifics to wean to a specific food.

First, Mertice Clark and I (Galef & Clark, 1971b, 1972) have found that the physical presence of adult rats at a feeding site attracts pups to that site and markedly increases the probability of young rats weaning to the food located

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[1] See Galef (1977) for discussion of the mechanisms responsible for continued pup avoidance of adult-avoided diets following removal of pups from direct adult influence.

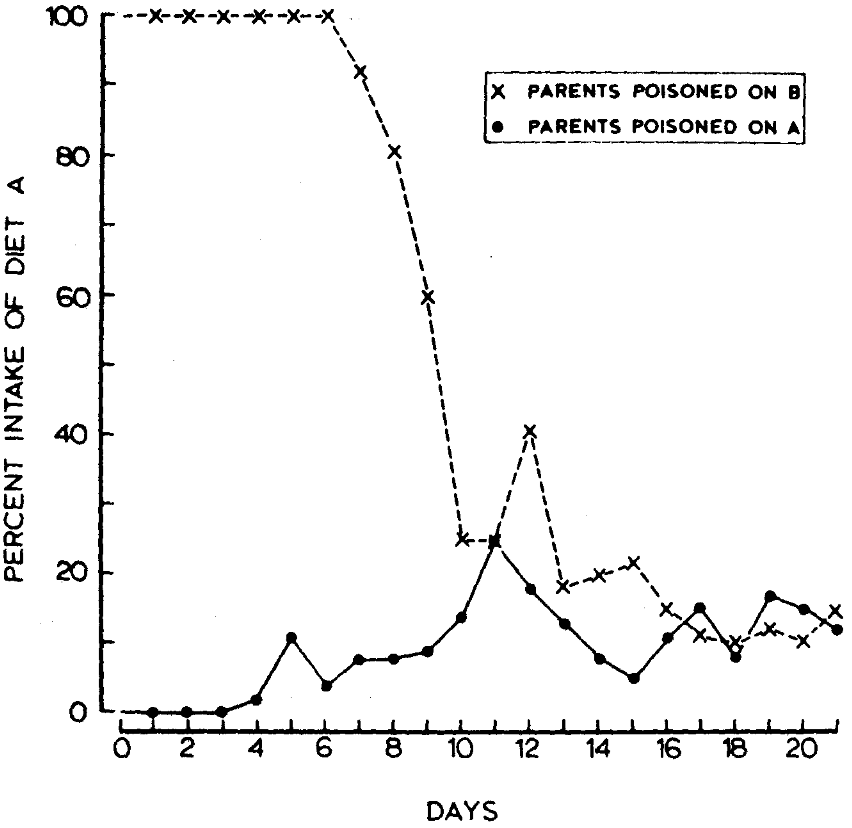

FIG. 6.3. Mean amount of Diet A eaten, as a percentage of total intake, by pups on the days following their removal from the adult colony. (Galef & Clark, 1971a. Copyright 1971 by the American Psychological Association. Reprinted by permission of the publisher and author.)

there. If, for example, one establishes a colony of adult wild rats in a large enclosure like that illustrated in Fig. 6.4, makes Diet A available in two food bowls located behind the partition, and continuously monitors the area above the dotted line, one can determine the conditions under which each individual pup in a litter eats its very first meal of solid food. We have observed nine individually marked pups from three litters take their first meal of solid food, and each of the nine subjects ate its first meal under exactly the same circumstances. Each ate for the first time while an adult was eating and each ate at the same food-bowl as the feeding adult, not at the other food-bowl .5 m away. Given the observed temporal and spatial distributions of adult meals, the probability of pups eating their first meal under these conditions occurring nine of nine times by chance was less than four in a thousand. We concluded that the

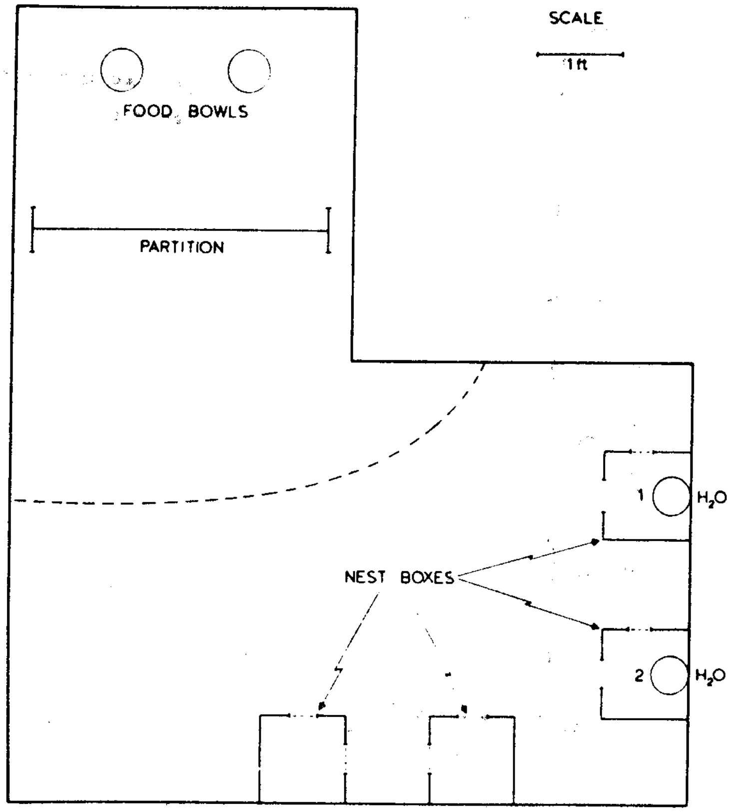

FIG. 6.4. Large enclosure for continuous observation of a wild rat colony. (Galef & Clark, 1971b. Copyright 1971 by the Psychonomic Society. Reprinted by permission of the publisher and author.)

presence of an adult at a feeding site serves to attract pups to that site and to cause pups to initiate feeding there.

Second, Linda Heiber and I (Galef & Heiber, 1976) have found that adult rats deposit olfactory cues in areas that they visit and that these cues bias weaning pups' choice of areas for both exploration and initiation of feeding. Heiber and I confined a dam and litter for several days in the larger portion of the enclosure shown in Fig. 6.5. Then we removed this dam, her litter, and the partition from the enclosure and observed individual food-deprived pups from another litter feed for 3 hours each day in the open enclosure with Diet A available in both food-bowls. We found that pups ate 90% of their meals and spent 70% of their exloration time in the soiled end-third rather than clean end-third of the enclosure.

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

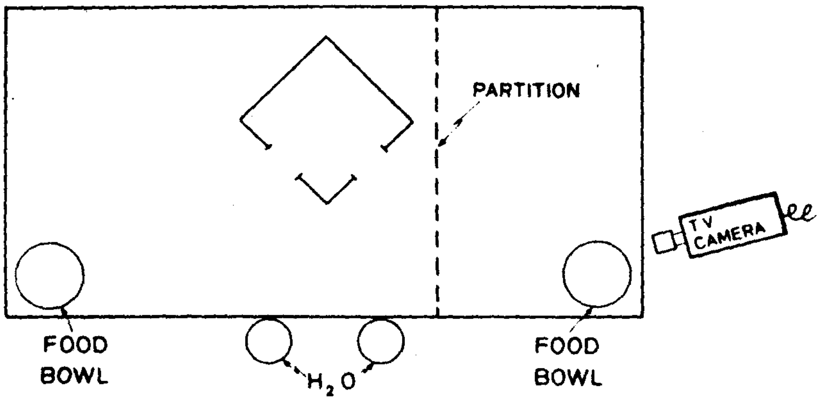

FIG. 6.5. Enclosure in which the effects of residual olfactory cues on pup behavior were measured. (Galef & Heiber, 1976. Copyright 1976 by the American Psychological Association. Reprinted by permission of the publisher and author.)

influence her pups' dietary preference. Mertice Clark and I (Galef & Clark, 1972) conducted an experiment much like the very first experiment described previously (see Fig. 6.1a), but with one important difference. Colonies of adult rats were again housed in 1 by 2 m enclosures. However, in the present experiment, adults were removed to a separate cage where all were fed for 3 hours each day either Diet A or Diet B 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 two standard food-bowls, one containing an uncontaminated sample of Diet A and one an uncontaminated sample of Diet B. Fig. 6.6 presents data describing the amount of Diet A eaten by pups, the adults of whose colonies were fed either Diet A or Diet B. As is evident from examination of the figure, the diet eaten by adult colony members profoundly affected the food choice of pups, even though under the conditions of the present experiment adults and young had no opportunity to interact directly in a feeding situation.

David Sherry, Pat Henderson, and I (Galef & Henderson, 1972; Galef & Sherry, 1973) have provided evidence that the milk of a lactating female rat contains cues directly reflecting the flavor of her diet. Our data suggest that as the result of exposure during nursing to flavor cues present in mother's milk, weaning pups exhibit a preference for a diet of the same flavor as that which their mother eats during lactation. In one of our experiments, Sherry and I (Galef & Sherry, 1973) took rat pups nursing from a lactating female eating Diet A, force-fed them ½ cc of milk manually expressed from another lactating female eating Diet B, and then poisoned the pups by intraperitoneal injection of .12 molar Lithium chloride solution. At weaning we tested these experimental pups for their preference between Diets A and B. As is evident in Fig. 6.7, in

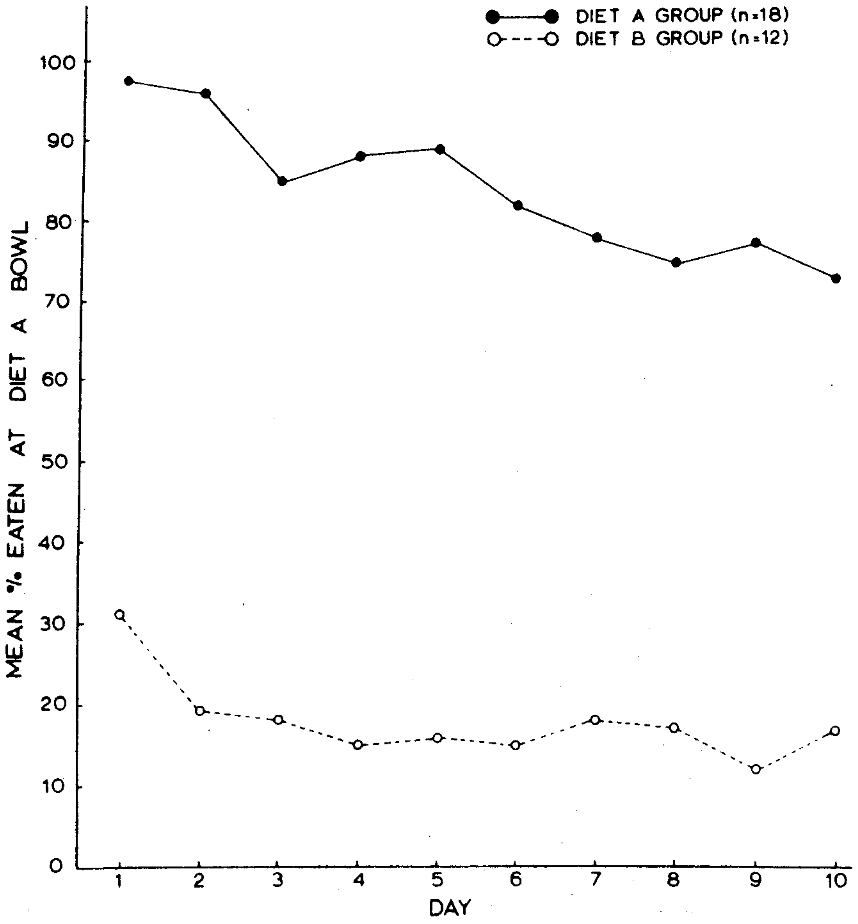

FIG. 6.6. Mean amount of Diet A eaten by pups, as a percentage of total intake, when adults and pups have no opportunity to interact in a feeding situation and adults are eating either Diet A or Diet B. (Galef & Clark, 1972. Copyright 1972 by the American Psychological Association. Reprinted by permission of the publisher and author.)

comparison with a variety of controls, experimental pups (those that had received milk from a female eating Diet B prior to poisoning) exhibited an aversion to Diet B.

So the results of our research to date indicate the existence of three ways in which adults may bias the 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 influence pups' choice of a place at which to wean and, thus, indirectly their choice of diet at weaning.

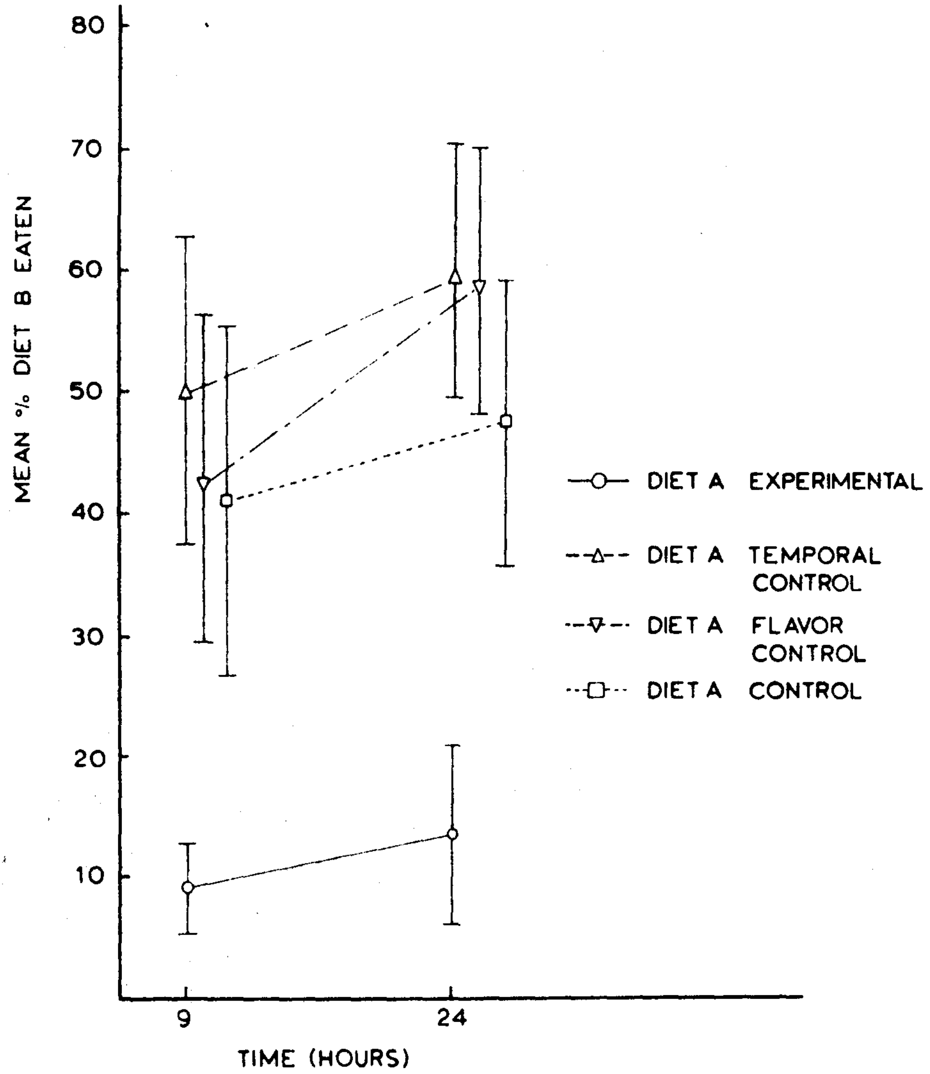

FIG. 6.7. Mean amount of Diet B eaten at weaning, as a percentage of total intake, by pups poisoned after receiving milk from a mother eating Diet B and by controls. (Galef & Sherry, 1973. Copyright 1973 by the American Psychological Association. Reprinted by permission of the publisher and author.)

Cues contained in maternal milk have the potential to directly influence diet choice by pups at weaning.

Fritz Steiniger was right. 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 right. The indirect results of what might be conceived of as instinctive acts, in this case the tendency of rat pups to suckle from their dam and to approach adults or their scents, can result in introduction of the young to diets eaten by adults of their colony and consequent simulated imitation of learned adult food preferences by young.

Of course, the finding that one pattern of behavior idiosyncratic to a particular social group of wild rats develops as the result of social interaction cannot be used to infer that all such "traditions" in wild rats are, in fact, the result of social processes, which brings us to the second series of experiments.

SOCIAL TRANSMISSION OF THE HABIT OF DIVING FOR FOOD

Wild rat colonies exhibit traditional variation not only in their food preferences but also in the motor patterns they employ in food acquisition. The range of feeding behaviors exhibited by different colonies of free-living Norway rats is very much greater than one might expect from observation of their fellows maintained in laboratory cages and eating pellets of rat chow. Members of some colonies of 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).

Recently, two Italian field workers, Drs. Gandolfi and Parisi of the University of Parma, have reported that many members of some colonies of wild rats (*Rattus norvegicus*) living along the banks of the Po River in Northern Italy dive for and feed on molluscs inhabiting the river bottom, whereas no members of nearby colonies, having equal access to molluscs within their home-ranges, feed on them (Gandolfi & Parisi, 1972, 1973; Parisi & Gandolfi, 1974).

Gandolfi and Parisi interpreted their observations as indicating that exploitation of submerged prey spreads through a wild rat colony as the result of observational learning. If discovery of molluscs 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, one would expect the observed bimodality in frequency of individuals diving in various colonies. Although the hypothesis that the habit of diving for food spreads by social learning is an attractive one, evidence adequate to support it would once again be extremely difficult to collect in the uncontrolled natural situation.

The series of experiments described in the following paragraphs (Galef, 1980) was, therefore, undertaken to assess the potential contribution of social processes to the development in rats of the habit of diving for food in shallow water. Although the present experiments involve laboratory analogues of the natural situation and cannot be extrapolated uncritically to the more complex natural situation, they do provide evidence relevant to the question of the necessity of invoking social learning as a mechanism to explain the observed distribution of the habit of diving for food among free-living rat colonies.

My subjects were sibling pairs of adult wild Norway rats (second and third generation laboratory-bred descendants of free-living animals captured on a garbage dump in southern Ontario), wild rat dams and their litters of young and sibling pairs of domesticated Long–Evans rats.

All subjects were housed and tested in *diving enclosures* like that illustrated in Fig. 6.8. Each diving enclosure was composed of three modules: first, a *living cage* providing harborage sites, ad lib water, and access to food for 3 hours each day; second, a *diving area*, consisting of a *caged patio* and glass-walled *diving pool;* and third, a *tunnel* providing access between the living cage and diving area. All behavior occurring on the patio or in the diving pool was recorded on a time-lapse video tape 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 five pieces of chocolate on its floor and then, over a period of days, gradually raising the water level to 15 cm. The water level was maintained at 15 cm until

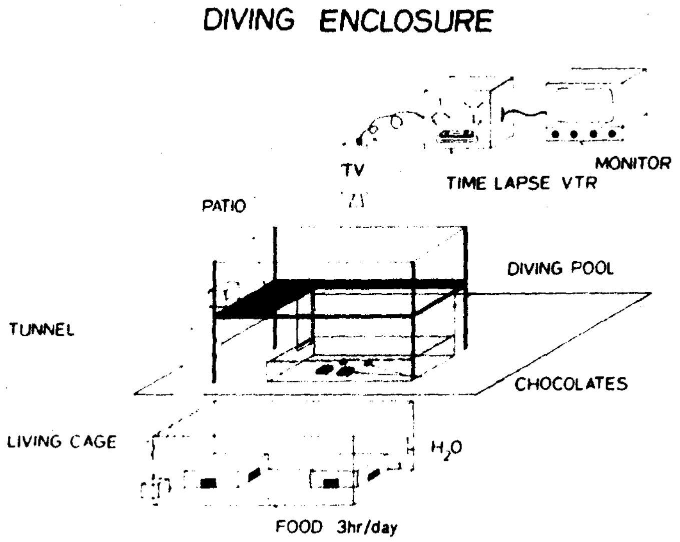

FIG. 6.8. The living cage, patio and diving-pool, and tunnel of the diving enclosure. (Galef, 1980. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher and author.)

completion of the experiment, and any chocolates eaten were replaced twice 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. The dams of three litters of wild rat pups were also trained to dive for food in the same way as were 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 6.1, which indicates the number of wild and domesticated naive rats recovering one 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 the table, naive adults did not learn to dive as the result of interaction with a diving conspecific.

Although some juvenile rats in the experimental condition, (juveniles living with a diving mother) did learn to dive for food, an approximately equal proportion of those in the control condition (those whose mothers had not been trained to dive) also learned to dive.

The failure of naive rats to learn to dive could not be attributed to a failure on the part of their trained cage-mates to demonstrate diving behavior. Trained rats retrieved an average of 4.6 chocolates/day from the diving-pool floor on each of the days they co-occupied the diving apparatus with their naive partners. Similarly, the failure of naive subjects to learn to dive could not be attributed to their failure to observe their trained cage-mates diving. Naive subjects rapidly learned to await their diving cage-mate on the patio and frequently attempted to snatch retrieved chocolates from the diver, but naive subjects very rarely entered the water themselves. The results suggest that interaction with a diving conspecific is not in itself sufficient to induce either 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 that 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

TABLE 6.1
Number of Naive Rats Diving or not Diving for Food

Subjects	*Diving*	*Not Diving*
Adult wild rats	0	10
Adult domesticated rats	0	10
Juvenile wild rats (Expt'l)	4	14
Juvenile wild rats (Control)	3	15

to swim but not to dive were allowed to interact in the diving enclosure with a sibling who had been trained to dive. Unexpectedly, two of the six subjects 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 diving-trained cage-mates had demonstrated diving behavior.

So 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 Fig. 6.9. The swimming enclosure required subjects to cross a small body of water to acquire food. Although 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. A 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 chocolates available on the diving pool floor. A bowl containing powdered Purina Laboratory Chow was placed in each living-cage for 3 hours on each of the 7 days each subject remained in its diving enclosure. Control subjects were treated identically to experimental subjects except that no water was ever introduced into their swimming pools prior to their transfer to diving enclosures. The results are presented in Fig. 6.10.

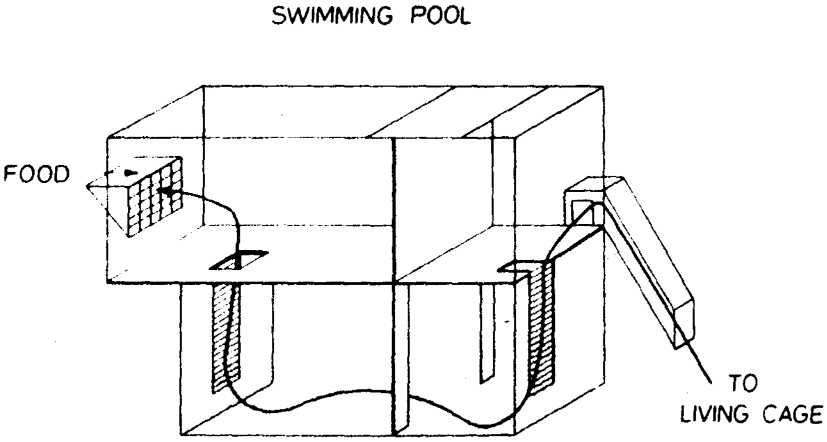

FIG. 6.9. The swimming pool of the swimming enclosure. (Galef, 1980). Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher and author.)

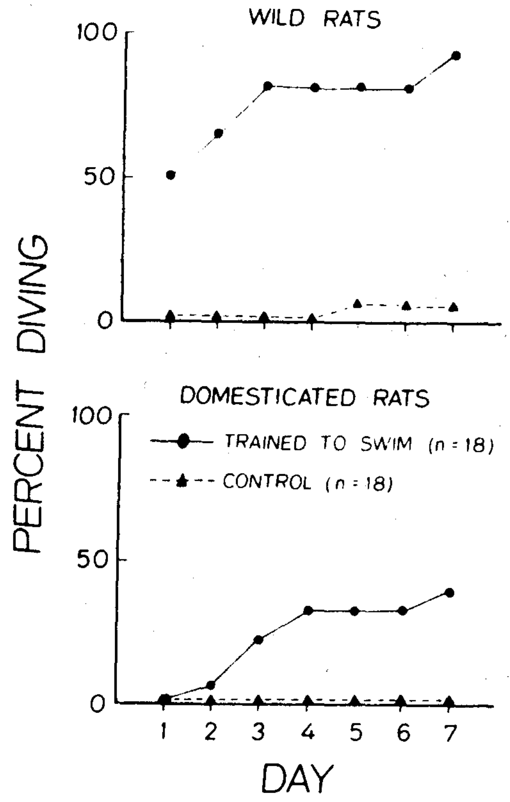

FIG. 6.10. Percentage of wild and domesticated rats diving for chocolates in the diving enclosure, on each of 7 days after either receiving or not receiving swimming experience in the swimming enclosure. (Galef, 1980). Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher and author.)

which shows the percentage of wild and domesticated experimental and control subjects retrieving one or more chocolates from beneath 15 cm of water in the diving enclosures on each of 7 consecutive days of testing. As can be seen in Fig. 6.10, 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 that social factors could play in the spread of diving behavior through a population. If rats learn to swim independently, and if swimming rats dive, social interaction could only serve to direct rats already prepared to dive to one 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 Fig. 6.11. It consisted of a living cage attached to a 2-meter-long *swimming alley*. Food was 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 continuously available in the living cage, and food was present there for 3 hours each day. Control litters were treated identically to experimental litters except that a partition with a small hole in it, which allowed pups but not dams access to the swimming alley, was placed in the tunnel between the living cage and swimming alley.

Figure 6.12 indicates the mean age of litters on the day one of their members first 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 whether they are in the presence of a swimming adult rat or not, whereas Long–Evans rats will swim at a considerably earlier age 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 just described 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 situation members of most rat colonies may acquire diving behavior, but that its subsequent performance is inhibited in some way in nondiving colonies.

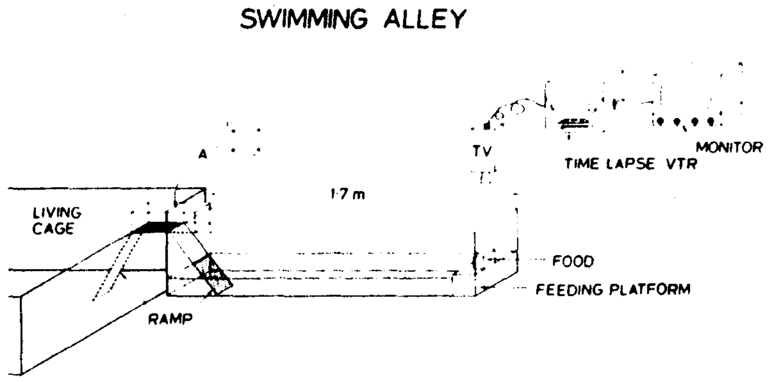

FIG. 6.11. The swimming alley. (Galef, 1980. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher and author.)

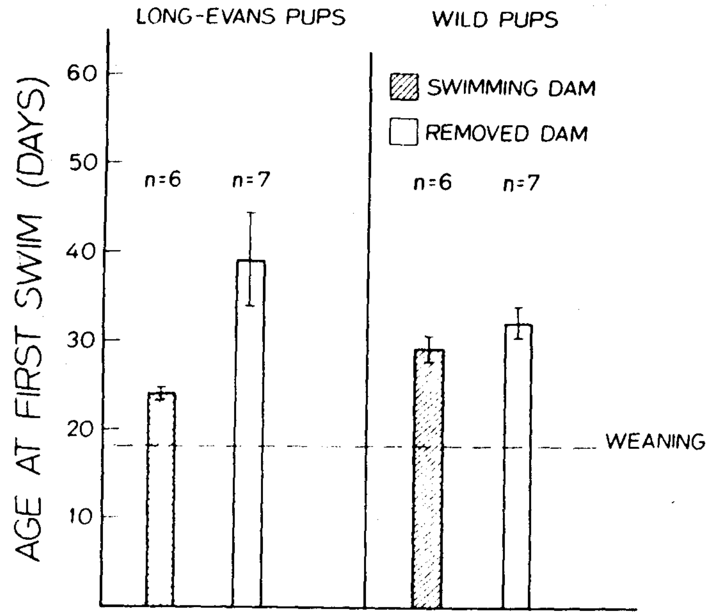

FIG. 6.12. Mean age at first incidence of swimming to the feeding platform in the swimming alley by rat pups reared either by a swimming or nonswimming mother. (Galef, 1980. Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher and author.)

Clearly, the habit of diving for food is only one element in the feeding repertoires of the rats that 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 three chocolates per day in 15 cm of water while maintained on a 3-hr/day feeding schedule (Purina Laboratory Chow offered in its living cage). After each subject had learned to dive for chocolates, Purina Chow was made available ad lib in its 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.

Fig. 6.13 shows the mean percentage of available chocolates eaten by subjects on each day of the experiment. As can be seen in the figure, even rats that 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 Purina Laboratory Chow in a simple choice situation. The present result thus suggests that most rats living near water may, in fact, have acquired the habit of diving for food, but that they

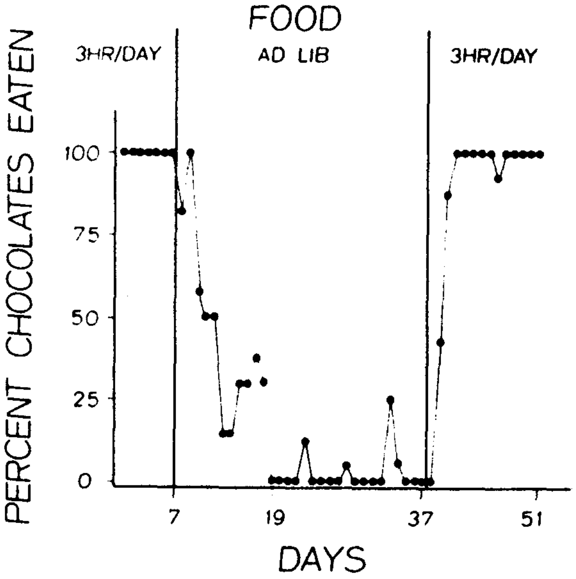

FIG. 6.13. Percentage of available chocolates retrieved from the diving-pool floor by wild rats on a 3 hr/day feeding schedule and while on ad lib food. (Galef, 1980). Copyright 1980 by the American Psychological Association. Reprinted by permission of the publisher and author.)

only exhibit diving behavior if they lack adequate alternative rations within their home ranges.

Although the data presented cannot be interpreted as showing that social learning of the behavior of diving in shallow water for food is unimportant in natural settings, they 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 living along 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.

Field observations are, in fact, consistent with the hypothesis that relative availability of alternative food sources within a colony's home range accounts for much of the intercolony variability in diving behavior. For example, Gandolfi and Parisi (1973) have reported that at those locations where predation on molluscs was observed, molluscs represent "one of the main sources if not the main source of food for rats" (p. 69). Gandolfi and Parisi (1974) have also found that "the time devoted by rats to mollusc capture depends greatly on the availability of other foods" (p. 102). Thus, laboratory data call attention to aspects of the field data that were not salient to the field observers themselves, field data that suggest that a nonsocial mechanism may underlie the observed intercolony variability in diving behavior observed in nature.

CONCLUSION

The message inherent in the preceding examples 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. For example, recent observations are consistent with the view that one of the most frequently cited examples of culturally transmitted behavior in animals, the washing of sweet potatoes in salt water by the macaques of Koshima Island (Kawai, 1965; Kawamura, 1959), may be maintained and propogated by processes other than intraspecific social ones. Green (1975) has reported that the long-time caretakers of the Koshima Island monkeys, when showing the troop to researchers and tourists, preferentially present sweet potatoes to those troop members known to exhibit washing behavior. As sweet potatoes are only available to the island monkeys in this context, differential reinforcement by the caretaker rather than "culture" may be responsible for the maintenance of washing behavior in the troop. Green further suggests that, because the troop is spatially organized in matrilineal groups, the propagation of sweet potato washing along family lines may have been guided by the enhanced probability of relatives of "washers" remaining close to them and therefore coming close to the provisioner, the source of sweet potatoes and reinforcement for washing. The importance of a human agency in the propagation and maintenance of this "traditional" behavior remains to be determined.

Some of the intriguing differences in behavior to be found in different populations of a species may be the result of social processes, others are probably not. The only way to determine which is which is, as Thorndike proposed, to examine phenomena of interest in controlled settings.

Experimental animal psychology in North America began with analysis of the processes underlying acquisition of a pattern of behavior observed in free-living animals. In the intervening 80 years, the techniques and theory of experimental psychology have matured immensely; yet we know little more today of the determinants of the development of naturally occurring behaviors of interest than we did in 1894. It is time to return to study of some of the intriguing questions that were the proximal stimulus for the initiation of animal psychology as an experimental discipline.

ACKNOWLEDGMENTS

Preparation of this chapter was greatly facilitated by funds from the Natural Science and Engineering Research Council of Canada and the McMaster University Research Board. I thank the faculty and staff of the Department of Psychology of the University of Colorado at Boulder both for their warm hospitality and for provision of resources during the preparation of the manuscript. I also thank Jerry Rudy, Mertice Clark, and Jeffrey Alberts for their most helpful discussions of earlier drafts.

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