

## Diving for Food: Analysis of a Possible Case of Social Learning in Wild Rats (*Rattus norvegicus*)

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Many members of some colonies of wild rats living along the banks of the Po River dive for and feed on molluscs living on the river bottom. No members of nearby colonies, having equal access to molluscs, exploit them as a food source. It has been suggested that these field observations indicate that social transmission processes are responsible for the spread of mollusc predation within predaceous colonies. The results of the present laboratory analysis of the development of diving behavior in wild and domesticated rats indicate that differential exposure of various colonies to shaping procedures occurring in nature and differences in resource distribution within colony home ranges are probably more important than social transmission processes in producing the intercolony variability in diving behavior observed in nature.

Gandolfi and Parisi (1972, 1973; Parisi & Gandolfi, 1974) reported field observations indicating that although many members of some colonies of rats living along the banks of the Po River dive for and feed on molluscs inhabiting the river bottom, no members of nearby colonies, which have equal access to molluscs within their home ranges, prey upon them.<sup>1</sup> Gandolfi and Parisi (1973, p. 73) interpret their observations of extreme intercolony variability in mollusc predation as supporting the hypothesis that predation on submerged molluscs spreads through many colonies 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 a diving individual, then one would expect the observed bimodality in frequency of individuals diving in various colonies. While the hypothesis that the habit of diving in shallow water for food spreads by social learning is

an attractive one, evidence adequate to support it would be extremely difficult to collect in the uncontrolled natural situations in which mollusc predation by rats was originally observed.

The series of experiments described below was undertaken to assess the potential contribution of social transmission processes (Galef, 1976) to the development in rats of the habit of diving for food in shallow water. Although the experiments reported here involve laboratory analogues of the natural situation, and therefore cannot be uncritically extrapolated to the more complex natural environment, they do allow a preliminary assessment of the necessity for invoking social learning as a mechanism to explain the observed distribution of the expression of the habit of diving for food in colonies of rats.

### Experiment 1

The present experiment was undertaken to explore the possibility that naive rats (either wild or domesticated, young or ma-

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<sup>1</sup> It should be made clear that Gandolfi and Parisi's main interest lay not in the study of intercolony variability in diving behavior but in the study of intercolony variability in motor patterns involved in opening molluscs. In the absence of access to appropriate prey species I have not been able to study the latter problem.

ture) will come to dive for food in shallow water as a direct result of freely interacting with conspecifics exhibiting diving behavior.

Method

Subjects

Subjects were (a) 14 male-female sibling pairs of adult wild rats (more than 3 mo of age), the second and third generation laboratory-bred descendants of rats trapped on a sanitary landfill in West Flamboro, Ontario, (b) 14 male-female sibling pairs of adult Long-Evans rats, purchased from the Canadian Breeding Farms, St. Constant, Quebec, and (c) six 2-day post-partum, second generation laboratory-bred wild rats and their litters, culled to six pups/litter shortly after birth.

Apparatus

Subjects were housed and tested in one of four diving enclosures of the type illustrated in Figure 1. Each diving enclosure was composed of three modules: (a) a living cage (1 × 1 × .3 m) constructed of galvanized sheet metal, angle iron, and hardware cloth and containing two wooden nest boxes (30 × 30 × 15 cm); (b) a diving area consisting of a caged patio (45 × 75 × 30 cm, constructed of the same materials as the living cage), a glass-walled diving pool (15-gal, 30 × 30 × 60 cm aquarium), and a hardware-cloth ladder joining the water surface and patio; and (c) a tunnel (8 × 8 × 100 cm), constructed of hardware cloth, providing access between the living cage and diving areas.

Drinking water was available ad lib in the living cage, and food (powdered Purina Laboratory Chow) was available there for 3 hr/day. Additional food, squares (2.4 g) of Neilson's Jersey Milk chocolate (William Neilson Co. Ltd., Toronto) covered with small pieces of aluminum foil (to increase visibility on television) and wrapped in Saran Wrap and transparent tape (to prevent the chocolate from dissolving in water) was available at the bottom of the diving pool.

DIVING ENCLOSURE

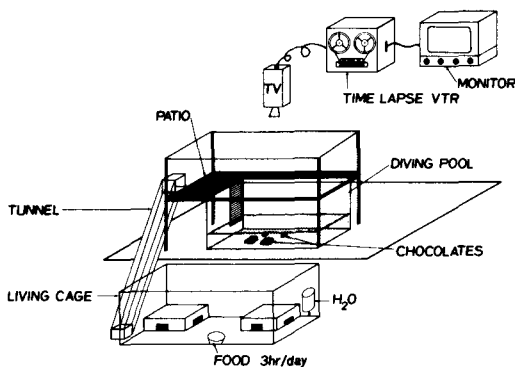


Figure 1. The diving enclosure used in Experiments 1, 2, and 4.

Procedure

*Experimental subjects.* An individual adult rat (a *trained adult*) was introduced into each diving enclosure and provided with Purina chow for 3 hr/day in the living cage module. At the time of introduction of the subject into the diving enclosure, the diving pool was dry and five wrapped chocolates were present on its floor. Once a day for the duration of the experiment the experimenter examined each diving pool and replaced any missing chocolates. Over the next 10-17 days the water level in each diving pool was gradually increased to a depth of 15 cm. It was maintained at this level until completion of the experiment. Once the pool was flooded to 15 cm the trained adult was left undisturbed until it had taken at least four chocolates/day for 7 consecutive days from the floor of the diving pool. On the following day a naive sibling of opposite sex to the trained adult (a *naive adult*) was shaved along its dorsum for identification and introduced into the diving enclosure. Treatment of both members of each experimental pair for the subsequent 36 days is described in Table 1 as Days 1 through 36.

The dams of three litters of wild rats were trained to dive for food in the same way as were the trained adults

Table 1  
Treatment of Subjects in Experiment 1

Subject	Pretreatment	Days			
		1-21	22-24	25-32	33-36
Experimental					
Trained	training	present	removed	returned	removed
Naive	absent	present	present	present	present
Control					
"Trained"	no training	present	removed	returned	removed
Naive	absent	present	present	present	present
Food <sup>a</sup>	3 hr/day	3 hr/day	none	3 hr/day	none

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

described above. The series of manipulations described in Table 1 as Days 1 through 36 was initiated when each dam's litter reached 21 days of age.

*Control subjects.* To determine whether any diving behavior exhibited by naive experimental subjects was promoted by social interaction with trained cagemates, it was necessary to observe the diving behavior of naive animals treated identically to naive subjects in experimental groups but lacking the opportunity to interact with a cagemate trained to dive for food. One member of each sibling pair of control animals was arbitrarily designated a "trained" adult. This subject was introduced into the apparatus illustrated in Figure 1 and was maintained on Purina chow on a 3 hr/day feeding schedule for 2 wk. No chocolates were placed on the floor of the dry diving pool to which "trained" subjects in control groups had access, but one wrapped chocolate/day was placed in each "trained" adult's living cage to ensure familiarity with chocolate as food.

At the end of this 2-wk period, the diving pool was abruptly flooded to 15 cm, five wrapped chocolates were placed on the floor of the diving pool, and an experimentally naive sibling of opposite sex to the "trained" subject was shaved and introduced into the enclosure. The treatment of pairs of control subjects for the next 36 days is described in Table 1 (Day 1 through 36).

The three wild rat dams in the control condition were treated identically to dams in the experimental condition except that the water level in their diving pools was abruptly raised from 0 to 15 cm 16 days following birth of their litters, they were given one chocolate/day in their living cages, and no chocolates were introduced into the diving pools to which they had access until after the diving pools were flooded.

The behavior of all subjects in the diving pools and on the patios was recorded on a time-lapse videotape recorder (Hitachi Model SV-513C) and reviewed daily. It was possible for the observer to determine whether each rat entering the water or diving to retrieve a chocolate was a naive or trained subject.

### *Results and Discussion*

The main results of Experiment 1 are presented in Table 2 which indicates the number of wild and domesticated naive rats that recovered one or more chocolates from the diving-pool floor during the 36 days each naive rat was present in the diving enclosure. As is clear from inspection of the upper half of Table 2, adult animals not explicitly trained to dive for food did not learn to do so as the result of interacting with a diving conspecific.

The failure of naive adult rats in the experimental condition to learn to dive cannot be attributed to a failure on the part of their trained cagemates to demonstrate diving behavior. Trained rats in experimental groups retrieved an average of 4.6 choco-

Table 2  
*Number of Rats Not Trained to Dive Diving During the 36 Days of Experiment 1*

Rat	Dive	Not dive
Naive experimental		
Adult wild	0	10
Adult domesticated	0	10
Juvenile wild	4	14
Naive and "trained" control		
Adult wild	0	4 (4)
Adult domesticated	0	4 (4)
Juvenile wild	3	15 (3)

*Note.* The numbers in parentheses describe the behavior of the "trained" rats in the control condition.

lates/day from the diving-pool floor on each of the 29 days they co-occupied 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 they very rarely entered the water themselves.

The results of Experiment 1 suggest that interaction with, or observation of, a diving conspecific is not in itself sufficient to directly induce an adult wild or domesticated rat to dive for food.

As would be expected, given the absence of acquisition of diving behavior by naive adult subjects in the experimental group, no naive or "trained" adult subject in the control group learned to dive during the 36 days of the experiment (see the lower half of Table 2).

While some<sup>2</sup> juvenile wild rats did learn to dive for food, the fact that approximately equal numbers of pups in experimental and control conditions did so (see Table 2) does not offer support for a social learning model

<sup>2</sup> I was able to determine the number of pups in a litter diving for food in the following manner. I watched on closed-circuit television until a pup was observed to dive and retrieve a chocolate, and then I removed the wet pup (presumably the diver) from the living enclosure. This procedure was repeated until no further diving occurred. Pups in litters containing divers were classified as nondiving pups if they failed to dive during the week following removal of the last diving pup.

of the spread of diving behavior. Pups in the two litters whose members exhibited diving behavior did so only some weeks after developing the habit of fleeing to the ladder leading from the patio to the diving pool and clinging to it, often with their entire bodies submerged, in response to disturbance by caretakers.

Observation, both of rats not explicitly trained to dive and of trained rats early in the training process, suggested that a major impediment to their acquisition of diving behavior was a reluctance to enter the water. Although naive juveniles would swim spontaneously on occasion (1.2 times/48 hr), naive adults rarely (2 observations in 720 rat days) entered the water. Such observations suggest that a willingness to enter the water and to swim on the water surface might be a necessary precursor to the social learning of diving behavior.

To determine whether rats that were willing to swim could be socially induced to dive for food, I initiated an experiment in which naive adult wild rats that had been trained to swim but not to dive were allowed to interact in the diving enclosure illustrated in Figure 1 with a sibling that 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 trained cagemates had demonstrated diving behavior. This informal result suggested that swimming rats might spontaneously exhibit a tendency to dive and retrieve objects from under water.

## Experiment 2

The present experiment was undertaken to confirm the informal observation reported above, i.e., that rats trained to swim will spontaneously dive and retrieve objects from beneath the water. If this observation were replicated, it would suggest that rats that have learned to swim do not require interaction with diving conspecifics to learn to dive for food. To the contrary, acquisition of swimming behavior would be shown to be sufficient in itself to promote acquisition of diving behavior.

## Method

### Subjects

Subjects were six litters of third generation laboratory-born wild rats and six litters of Long-Evans rats, each culled to six pups/litter shortly after birth.

### Apparatus

Each litter of pups was maintained in a swimming enclosure a part of which is illustrated in Figure 2. The swimming enclosure was composed of three modules: (a) a living cage and (b) a tunnel identical to those described in Method of Experiment 1 and (c) a patio-swimming-pool module (illustrated in Figure 2) similar to the diving-pool module depicted in Figure 1 but modified so as to reinforce swimming but not diving behavior. As can be seen in Figure 2, the swimming pool required subjects to cross a small body of water (60 cm in length) to acquire food. Although the subjects were free to dive in the swimming pool, they received no extrinsic reinforcement for doing so.

### Procedure

*Experimental subjects.* Three litters of wild rat pups and three litters of domesticated rat pups served as experimental subjects. Each 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 was then gradually filled with water over a 1-wk period until a depth of 20 cm was achieved.

A litter was left undisturbed in the swimming enclosure for 30–37 days, at which time each member of the litter was introduced into a diving enclosure like that illustrated in Figure 1. At the time of introduction of each subject into its diving enclosure, the water in the diving pool was 15 cm deep, and three chocolates were 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 remained in its diving enclosure.

Instances of diving were recorded if one or more chocolates disappeared from the floor of a diving pool, and retrieved chocolates were replaced daily.

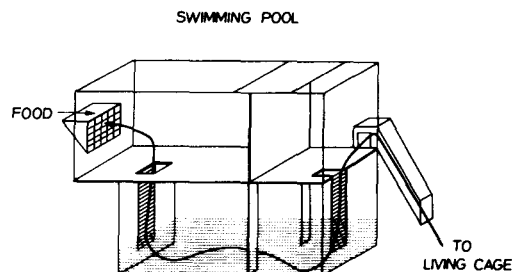


Figure 2. The swimming pool used in Experiment 2.

*Control subjects.* Three litters each of wild and domesticated rats served as control subjects. Control subjects were treated identically to experimental subjects except that no water was ever introduced into their swimming pools prior to their transfer to the diving enclosure.

### Results and Discussion

The main results of Experiment 2 are presented in Figure 3 which shows the percentage of wild and domesticated rats diving for chocolates on each of the 7 test days in the diving enclosure. As is clear from examination of the upper panel of Figure 3, wild rats trained to swim exhibited a high probability of diving, while those lacking swimming experience exhibited considerable reluctance to do so. Although domesticated rats trained to swim are less likely to dive than wild rats, they too show an enhanced probability of diving as a result of swimming experience (lower panel of Figure 3).

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, then social interaction could serve only to direct rats already prepared to dive to one locale rather than another. It is, however, also possible that the development of swimming itself might be socially influenced. If it is, then social factors might indirectly result in the spread of diving behavior by facilitating the spread of swimming behavior.

### Experiment 3

The present experiment was undertaken to determine whether social interactions are important in the initiation of swimming behavior in young rats.

### Method

#### Subjects

Subjects were 13 litters of third and fourth generation laboratory-bred wild rats, culled to six pups/litter 2 days after birth and simultaneously cross-fostered to Long-Evans dams of approximately ( $\pm 24$  hr) the same postpartum age as their natural mothers. (It proved impossible for wild rat females to survive reintroduction into their home colonies after a 3-4-wk absence. Cross-fostering of pups to domesticated females was, therefore, necessary to preserve our breeding stock.) An additional 13 litters of Long-Evans pups, culled to six pups/litter 2 days after birth, and their natural mothers also served as subjects.

#### Apparatus

The apparatus used to examine the role of social interaction in the development of swimming behavior is illustrated in Figure 4. It consisted of a  $1 \times 1 \times .3$  m living cage (see Figure 1) attached to a  $1.7 \times .3 \times .3$  m swimming alley, constructed of plywood, lined with commercial swimming-pool liner, and covered with transparent Plexiglas. Access to the swimming alley from the living cage was through a short tunnel and across hardware-cloth ramps. A Plexiglas barrier, which blocked passage to the swimming alley by the dam but not the pups, could be introduced into the tunnel at the point marked A in Figure 4.

Food (powdered Purina Laboratory Chow) was available ad lib in a container mounted on a hardware-cloth stand at the opposite end of the swimming alley from the living cage.

#### Procedure

*Experimental litters (six wild and six domesticated).* A mother and litter were introduced into the living cage on Day 2 postpartum, and the dam was trained to swim

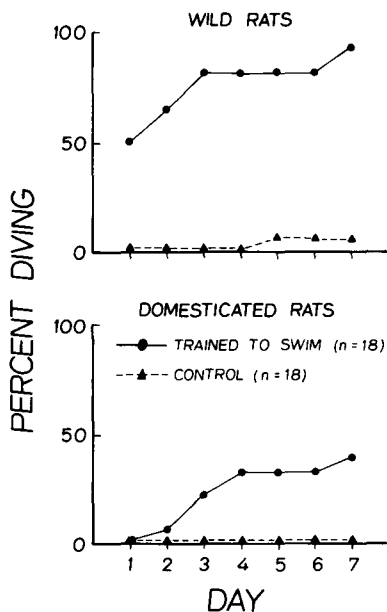


Figure 3. Percentage of wild (upper panel) and domesticated (lower panel) rats diving for chocolates in the diving enclosure after either receiving or not receiving swimming training.

SWIMMING ALLEY

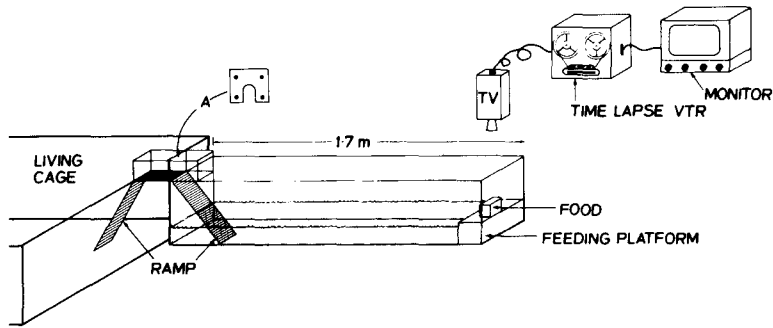


Figure 4. The swimming alley used in Experiment 3.

for food over a period of from 2 to 10 days by gradually raising the water level in the swimming alley from 0 to 15 cm. Water was available in the living cage ad lib, and food (powdered Purina Laboratory Chow) was presented there for 3 hr/day. Mother and litter were left undisturbed until the pups were observed to feed from the food cup at the far end of the swimming alley from the living cage, at which time the experiment was terminated. Behavior at the feeding site in the swimming alley was continuously monitored by closed-circuit television in conjunction with time-lapse videotape recording.

*Control litters (seven wild and seven domesticated).* Control litters were treated similarly to experimental litters except that (a) the partition that allowed pups but not dams access to the swimming alley was placed in the tunnel, (b) powdered Purina Laboratory Chow was available ad lib in the living cage of control litters until they reached 21 days of age, when they were placed on a 3-hr feeding schedule (this procedure was necessary to equate the growth rate of control litters with that of experimental litters whose dams had ad lib access to food in the swimming alley), and (c) the dam and partition were removed from the cages of control litters on Day 28. Initiation of swimming in control litters was determined by examination of the surface and the weight of the food cup in the swimming alley.

Results and Discussion

The main results of Experiment 3 are presented in Figure 5 which indicates the mean age of pups, both wild and domesticated, in experimental and control litters, at which one of their members first reached the food dish at the far end of the swimming alley from the living cage. As is clear from examination of the figure, and as statistical tests confirm, wild rat pups start to swim at an early age regardless of whether they are in the presence of a swimming adult rat, and Long-Evans rats will swim at a considerably

earlier age in the presence than in the absence of a swimming adult (Mann-Whitney  $U = 0, p < .001$ ).

The results of the present experiment, while indicating that social interaction can accelerate the acquisition of swimming in some strains of rat, are not consistent with the hypothesis that social interaction is necessary for its spread. All litters of rats, regardless of whether they were exposed to swimming conspecifics, came to exhibit swimming behavior prior to reaching maturity. Taken together with the results of Experiment 2, the results of the present experiment suggest that swimming behavior, and therefore diving behavior, will develop

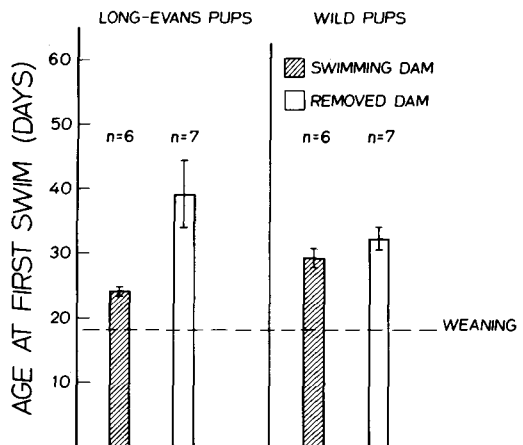


Figure 5. Mean age of first incidence of swimming behavior in litters of wild and domesticated pups either exposed or not exposed to a swimming mother. (Flags indicate  $\pm 1 SE$ .)

in the absence of social induction. In general, the results of Experiments 1, 2, and 3 suggest that attempts to explain long-term intercolony differences in frequency of diving behavior in terms of social learning processes may not prove successful.

#### Experiment 4

If the observation that many members of some colonies of rats dive for molluscs whereas no members of other colonies do so cannot be explained in terms of social transmission processes within diving colonies, then the explanation must be sought elsewhere. The results of Experiments 2 and 3 above 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 (1972, 1973; Parisi & Gandolfi, 1974) field observations indicating that in natural settings no members of many colonies exhibit diving behavior, the results of Experiments 2 and 3 suggest that in the field, members of most colonies acquire the diving response but that its subsequent performance is inhibited in some way in nondiving colonies. 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. Thus, nondiving colonies of rats in the natural habitat might simply be those that have access to alternative foods, and diving colonies might be those lacking access to alternative sources of nutrients (for a similar discussion of intertroop variability in the feeding behavior of primates, see Gaulin & Kurland, 1976; Strum, 1976).

In the present experiment the frequency of expression of diving behavior in rats is examined as a function of the availability of alternative means of acquiring food. If the occurrence of food-diving is influenced by the availability of alternative resources, then one might predict that rats trained to dive for food would be less likely to do so when alternative foods were available ad lib than when they were available on a restricted basis.

#### Method

##### Subjects

Subjects were two male and three female, third generation laboratory-bred wild rats.

##### Procedure

Each subject was placed in a diving enclosure like that illustrated in Figure 1 and trained, in 10 to 12 days, to dive for three chocolates/day in 15 cm of water. Each subject was maintained on a 3 hr/day feeding schedule (powdered Purina Laboratory Chow offered in the living cage). After each rat had dived for and retrieved three chocolates/day for 7 consecutive days, Purina chow was made available ad lib in the rat'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 for 14 days.

The experimenter recorded the number of chocolates eaten by each subject each day and replaced any missing chocolates daily throughout the 51 days of the experiment.

#### Results and Discussion

The main results of Experiment 4 are presented in Figure 6 which shows the mean percentage of available chocolates eaten by each subject during each of the 51 days of the experiment. As is evident from inspection of Figure 6, rats that have acquired the habit of diving for food will not do so if an ade-

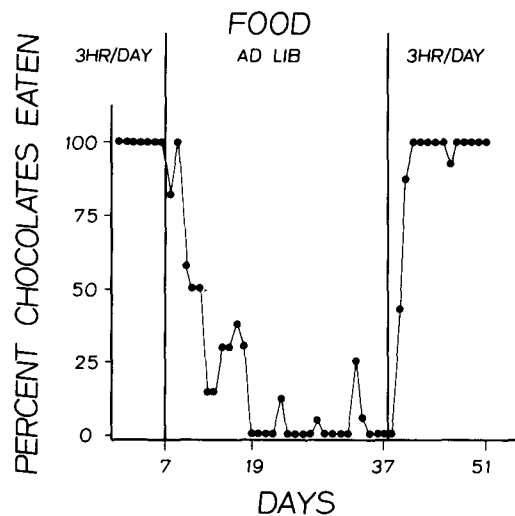


Figure 6. Percentage of chocolates retrieved from the diving-pool floor by wild rats trained to dive while food was available on land on a 3 hr/day schedule and while food was available ad lib.

quate 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. (After habituation to both diets, wild rats ( $n = 3$ ) ingest, on average, three times as much grated Jersey Milk chocolate as powdered Purina Laboratory Chow.) The results suggest that most rats living near water may, in fact, have acquired the habit of diving for food but that they exhibit diving behavior only if they lack adequate alternative rations within their home ranges.

### General Discussion

The range of feeding behaviors exhibited by free-living Norway rats is considerably greater than would be predicted from observation of conspecifics maintained under standard laboratory conditions. Colonies of rats have, for example, been reliably reported to compete successfully with trout in a fish hatchery for food thrown on the water surface, to prey on fingerling fish (Cottam, 1948), to stalk and kill sparrows (Steiniger, 1950), and, as discussed above, to dive for gastropod and bivalve molluscs (Grandolfi & Parisi, 1972).

In the ecological literature such idiosyncratic colony feeding patterns are frequently treated as "local traditions," the implication being that the discovery of the means of exploiting an unusual food source is made by one or a few individuals in the exploiting colony and that it is then acquired by other colony members as the result of observational learning, imitative behavior, or some other social transmission process (Galef, 1976). Unfortunately, unobtrusive observations in natural settings are not, in most cases, sufficient to determine either the circumstances under which an unusual behavior is initiated or the reasons for its spread through a population. The observation that many members of a single geographical subpopulation of a species exhibit some behavior not generally exhibited by members of that species is consistent with the interpretation that the behavior spreads by social learning. Such an observation is not, however, evidence that social learning

is actually involved in the spread of the behavior in the subpopulation in which it is observed.

The results of the present series of studies of the factors responsible for the expression of the habit of diving for food in Norway rats, taken together with the field observations of Grandolfi and Parisi, allow a preliminary assessment of the role of three markedly different mechanisms, any of which might be responsible for the observed intercolony variability in mollusc predation by rats.

### *Natural Shaping*

The term "natural shaping" is used below to refer to a series of events occurring in the natural habitat that is analogous to the method of reinforcement of successive approximations frequently employed in laboratory situations to bring to high probability a behavior that would otherwise rarely or never appear in the behavioral repertoire of the shaped individual (see Skinner, 1953, p. 92 for a discussion of the method of laboratory shaping).

It was observed in Experiment 1 that adult naive rats (which had chocolates available at the bottom of the diving pool only under 15 cm of water) failed to acquire the habit of diving, while trained adult experimental subjects (which had chocolates available in the diving pool as the water level gradually increased from 0 to 15 cm) invariably learned to dive. These observations suggest that rat colonies living along portions of the Po River where fluctuations in water level first expose molluscs and then gradually resubmerge them could learn to dive for food as the result of a natural shaping process. On the other hand, colonies living along portions of the river where water levels were relatively constant and the river banks steep might never experience a natural shaping process sufficient to support the development of diving behavior.

Grandolfi and Parisi's (1973, p. 71) observations suggest that natural shaping processes are probably involved in the development of diving behavior in those colonies living in areas where wide fluctuations in water level frequently expose mollusc-bearing mud flats. However, diving behavior was also



observed in other areas on the Po where water levels are consistently high and molluscs are not exposed (Parisi & Gandolfi, 1974, p. 92). These field observations suggest that natural shaping may be sufficient to account for some observed instances of diving but not for others. Thus, the simplest mechanism sufficient to explain the development of diving behavior is not adequate to do so in all cases.

### *Social Learning*

The results of Experiments 1, 2, and 3 offer scant support for hypotheses suggesting that social learning is a necessary substrate for the spread of diving behavior within those colonies that exhibit it. Both swimming behavior and its sequela, diving behavior, appear in individual rats in the absence of the opportunity to observe conspecifics exhibit those behaviors.

Before rejecting the hypothesis that social learning is an important element in the spread of diving behavior in natural situations, one must consider the possibility that differences between our laboratory situations and field conditions serve to obscure possible contributions of social learning to the development of diving behavior in individual rats. If, for example, molluscs in the Po River are clumped in relatively small areas beneath a vast expanse of water and if rats tend to dive in the vicinity of other diving rats, such "local enhancement" effects (Thorpe, 1956) might be critical for the spread of effective exploitation of molluscs within a colony. Individual rats diving at randomly selected locations in the river might fail to find molluscs and extinguish their diving behavior unless directed to appropriate locations for finding molluscs by more knowledgeable conspecifics.

Also, the results of Experiment 3 indicate that social interaction with swimming conspecifics has different effects on rats of different genotype. Social interaction with trained swimmers, which considerably accelerated the initiation of swimming behavior in domesticated rats, had no comparable effect on the initiation of swimming behavior in wild rats. It seems probable that Italian wild rats differ in genotype both from

the wild rats of southern Ontario and from domesticated strains. It, therefore, remains possible that the effects of social interaction on the development and spread of diving behavior in the strain in which it was observed in the field are more profound than in those strains that I have studied.

### *Bioenergetic Variables*

The results of Experiment 4 suggest that the availability or absence of alternative food sources within a colony's home range might be sufficient to account for colony differences in diving behavior observed in the field.

Gandolfi and Parisi (1973, p. 69) similarly report that at those locations where predation on molluscs occurs, it represents "one of the main sources if not the main source of food for rats." They further report (Parisi & Grandolfi, 1974, p. 102) that "the time dedicated by rats to Mollusc capture depends greatly on the availability of other foods." Thus, both the field and laboratory data are consistent with the view that predation on molluscs may be a feeding strategy available to all colonies along the Po but one that is exhibited only in those areas or at those times when alternative foods are not available on land.

### *Conclusion*

Taken together, the results of the present series of studies are consistent with a variety of hypotheses concerning observed intercolony variability in exhibition of the habit of diving for food. While the evidence suggests that both natural shaping and bioenergetic variables have robust effects on the probability of an individual rat either learning or continuing to dive for food, it does not offer strong support for the hypothesis that social learning plays an important role in the spread of diving behavior. Although the data presented here 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 investigation of environmental variables that may affect the frequency of occurrence of the behavior need to be un-

dertaken before the social learning hypothesis is accepted. In particular, it would be valuable to know whether adult rats 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 helpful to know whether introduction of an alternative food source into the home ranges of diving colonies along the Po would inhibit further diving. The results of such studies in the natural habitat, taken together with those described above, should permit the determination of the relative contribution of social and nonsocial factors to the intriguing intercolony variability in feeding behavior described by Gandolfi and Parisi.

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