# Direct and Indirect Behavioral Pathways to the Social Transmission of Food Avoidance[a]

BENNETT G. GALEF, JR.

*Department of Psychology*
*McMaster University*
*Hamilton, Ontario L8S 4K1*
*Canada*

## INTRODUCTION

During the past fifteen years my students and I have been examining the role of social factors in diet selection by wild and domesticated Norway rats. The results of our studies provide evidence of a number of discrete behavioral processes permitting a rat choosing between novel diets to make use of the learned feeding preferences of others of its social group. As a general rule, an individual rat tends to select for ingestion the same foods that others of its social group are eating.

In any two-choice situation there are, *a priori*, two motivational pathways that might lead an organism to ingest more of one diet than of another available to it. The subject might be directly motivated to ingest the selected food because of attraction to it or the animal might be indirectly motivated to ingest the selected diet because it is avoiding the available alternative.

Similarly, if an organism is observed to avoid ingestion of one of two accessible diets, such avoidance could be either directly or indirectly motivated: directly motivated in the sense that the animal avoids ingestion of the unselected food because of some aversion to it or indirectly motivated in the sense that the animal ingests little of one item in consequence of its greater liking for the other.

The somewhat surprising fact I will be focusing on below is that in 15 years of experimentation, while uncovering four independent socially mediated behavioral processes resulting in indirect avoidance of foods by rats, my co-workers and I have not been able to find any evidence of social influence acting directly to induce a food aversion. In each of our analyses of social transmission of diet selection, socially induced avoidance of one diet has been the indirect result of socially, directly induced preference for an available alternative.

Below, I first review data from my own laboratory that lead me to the conclusion that socially induced diet avoidance in rats tends to be indirect rather than direct. Second, I describe experiments by others indicating that direct social transmission of diet aversion occurs in at least one species, the red-wing blackbird. Last, I briefly discuss approaches to the question of why there might be interspecific differences in

the types of information socially transmitted about foods and implications of such interspecific differences for the study of social learning.

## SOCIAL TRANSMISSION OF DIET PREFERENCE AT A DISTANCE FROM A FEEDING SITE

As a first illustration of the issue with which I'm concerned, I'll describe in some detail recent work in my laboratory on the use by rats of aggregation sites as "information centers"[1] at which members of a social group exchange information concerning foods they have ingested while on foraging expeditions away from the aggregation site itself. Our experimental procedures were designed to mimic a situation in which a foraging rat (a demonstrator) ingests a food at some distance from its burrow, returns to its burrow, and then interacts with a familiar burrow-mate (an observer). We were interested to know whether, as a result of such interaction, the observer could acquire information concerning the food the demonstrator had eaten and whether the observer would use this information when selecting a diet.[2]

Treatment of subjects during the experiment was as follows (FIGURE 1). (Step 1) Demonstrator and observer were first maintained together with *ad lib* access to Purina Laboratory Chow pellets for a two-day period of familiarization with both apparatus and pair-mate. (Step 2) The demonstrator was moved to the opposite side of a screen partition from the observer and food deprived for 24 hr to ensure that the demonstrator ate when given the opportunity to do so. (Step 3) Chow was then removed from the observer's side of the cage (in preparation for testing) and the demonstrator was moved to an enclosure in a separate room and allowed to feed for 30 min on either cocoa-flavored diet or cinnamon-flavored diet. (Step 4) The demonstrator was returned to the observer's cage and demonstrator and observer were allowed to interact for 15 min. (Step 5) The demonstrator was removed from the experiment and the observer was offered, for 60 hr, two weighed food-cups, one containing cinnamon-flavored diet and one containing cocoa-flavored diet.

The results of this experiment are presented in FIGURE 2, which shows the mean amount of cocoa-flavored diet (as a percentage of total amount eaten) ingested by observers whose demonstrators had eaten either cocoa-flavored or cinnamon-flavored diet during the 30 min they were removed to a separate room (Step 3 in FIGURE 1). As can be seen in FIGURE 2, those observers whose demonstrators ate cocoa-flavored diet ate a greater percentage of cocoa-flavored diet than did those observers whose
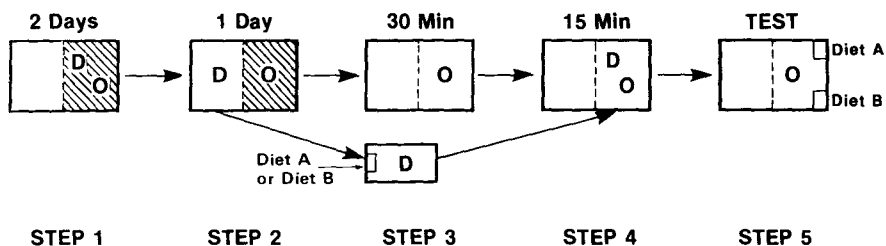


FIGURE 1. Schematic diagram of a procedure for investigating the ability of rats to communicate information concerning distant diets. D = demonstrator; O = observer; cross-hatching indicates Purina Laboratory Chow in cage. (From Galef and Wigmore.[2] Reproduced by permission of Baillière Tindall.)
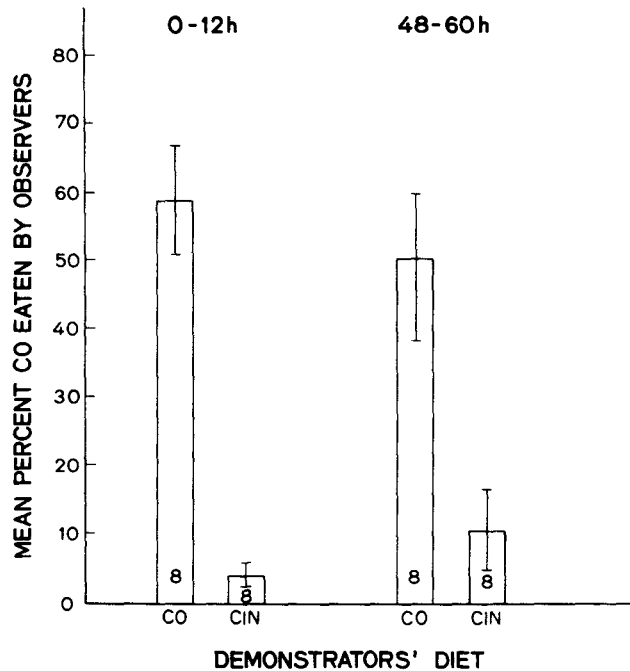
**FIGURE 2.** Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by observers whose demonstrators had eaten either cocoa- or cinnamon-flavored diet. CO = cocoa-flavored diet; CIN = cinnamon-flavored diet. Bars indicate ± 1 S.E. Left-hand panel, 1st 12 hr intake; right-hand panel intake from the 48th-60th hr. (From Galef and Wigmore.[2] Reproduced by permission of Baillière Tindall.)

demonstrators ate cinnamon-flavored diet. Both the present data and similar findings by Strupp and Levitsky[3] and Posadas-Andrews and Roper,[4] clearly indicate that a demonstrator rat can influence conspecific observers to select the diet that the demonstrator ate at a distant time and place. Such preference for a demonstrator's diet may result in a reduced tendency to eat alternative diets, but as discussed above, this avoidance of alternative diets is only an indirect consequence of a socially induced preference for a demonstrator's diet.

What about food aversion? Can one rat communicate information about a distant diet to a naive conspecific that would cause that individual to directly develop an aversion to that diet. Suppose a rat leaves its burrow system, ingests some novel food that happens to be toxic, returns to its burrow, and while ill, interacts with a burrow mate. Will the burrow-mate of the sick individual subsequently avoid ingesting the food that made its companion ill?

There is some reason to believe that the naive individual might subsequently avoid ingesting the ill rat's diet. Coombes and Lavin[5] and their colleagues have reported data indicating that signals emitted by an ill rat can serve as unconditional stimuli in a taste aversion learning situation. If a naive rat ingests an unfamiliar diet and then interacts with a fellow who has been rendered ill by injection of a mildly toxic lithium chloride solution, the naive rat subsequently exhibits reluctance to ingest the novel diet it ate prior to interaction with the ill conspecific.
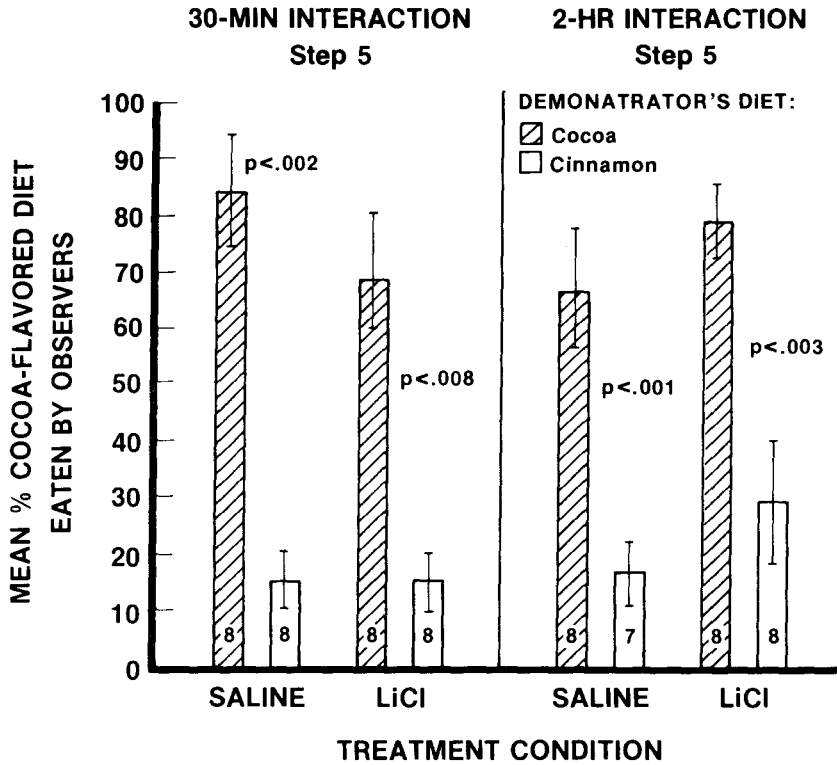
**FIGURE 3.** Mean amount of cocoa-flavored diet ingested by observers as a percentage of total amount eaten. Left-hand panel; observer and demonstrator interacted for 30 min; right-hand panel, observer and demonstrator interacted for 2 hr during Step 4 of FIGURE 1. (From Galef et al.[6] Reproduced by permission of the American Psychological Association.)

Our finding[2] that an observer can extract information from a demonstrator concerning the diet the demonstrator has recently eaten, taken together with Coombes et al.'s[5] observation that an ill rat can serve as an unconditional stimulus for taste-aversion learning, suggests that a rat made ill following ingestion of a novel food might provide two potentially useful signals to a conspecific: First, a signal containing information sufficient to permit identification of that food the signal-emitter has recently eaten, and second, a signal capable of inducing a learned aversion. Exposure to these two signals in temporal contiguity might produce in their recipient avoidance of the specific diet recently ingested by an ill conspecific.

We, therefore, repeated the experiment described in FIGURE 1, but with an important modification. Between the time the demonstrator was removed to a separate enclosure and fed either cinnamon- or cocoa-flavored diet (Step 3) and the time it was placed in its observer's cage (Step 4), it received an intraperitoneal injection. Demonstrators in experimental groups were injected with toxic LiCl solution, while demonstrators in control groups were injected with a benign saline solution.

The results of this attempt to demonstrate socially mediated direct taste-aversion

learning are shown in FIGURE 3. Observers in all groups, regardless of whether they had interacted with poisoned or saline-injected demonstrators, exhibited a substantially enhanced preference for the diet their respective demonstrator had eaten. Poisoned demonstrators were as effective in promoting intake of the diet they had eaten (and which they would subsequently avoid) as were unpoisoned demonstrators.

Thus, results of recent work on social transmission of food preference in rats are consistent with the notion that direct social influence on preference is a more robust phenomenon than direct social influence on aversion.

## SOCIAL TRANSMISSION OF DIET PREFERENCE AT A FEEDING SITE

The two studies discussed above are not the first of our experiments to reveal rats making use of information indicating that conspecifics are exploiting some food while, under similar circumstances, failing to make use of information that conspecifics have learned to avoid a diet.

In one of our earliest investigations of the role of social influence on diet selection, Mertice Clark and I[7] established colonies of adult wild rats in large enclosures and, by use of LiCl contamination, trained adults to eat only one of two simultaneously presented diets. We then looked at the food preferences of weanling young born to adults of our colonies. We found, as FIGURE 4 illustrates, that young rats ate the same food that the adults of their colony had been trained to eat. As can be seen in FIGURE 4, weanling wild rats born to a colony trained to avoid ingesting Diet A, ingested only Diet B and those born to a colony trained to avoid ingesting Diet B, ingested only Diet A.

As mentioned in the introduction, such a pattern of diet selection could be the result either of young learning to eat the food adults of their colony are eating or learning to avoid the food adults of their colony had learned to avoid. Clark and I[7] conducted a single experiment to determine which was the case. We established two different types of adult wild rat colonies. In the first type of colony, adults were again trained (by adulterating samples of Diet B offered to the colony with LiCl) to avoid ingesting the normally preferred Diet B and to eat Diet A. In the second, adults were forced to eat Diet A by making it the only food available. We waited till our adults had given birth to young and the young had grown to weaning and fed on solid food with the adults for ten days (those in the first type of colony eating no Diet B). We then removed the young to individual enclosures. In these individual enclosures each pup was allowed to choose between Diets A and B for nine days. As can be seen in FIGURE 5, there was no difference between pups from the two types of colony in rate of acceptance of Diet B. Pups from colonies of the first type (in which adults had learned to avoid ingesting Diet B) accepted Diet B as rapidly as those from colonies of the second type (in which pups had no information concerning Diet B). The fact that pups from colonies that had learned to avoid Diet B showed no greater reluctance to ingest Diet B than pups from colonies that had not learned an aversion to Diet B, suggests that pups from colonies of the first type learned nothing about avoiding Diet B as a result of social interaction.[7] Once again, through social interaction, rats are learning about what to eat, not about what to avoid.

It might well be argued that this single experiment is not sufficient to establish that pups in the first type of colony were learning nothing about the diet the adults of their colony were avoiding. In retrospect I would agree that we should have pursued the matter more diligently. However, the outcome of further analysis of factors
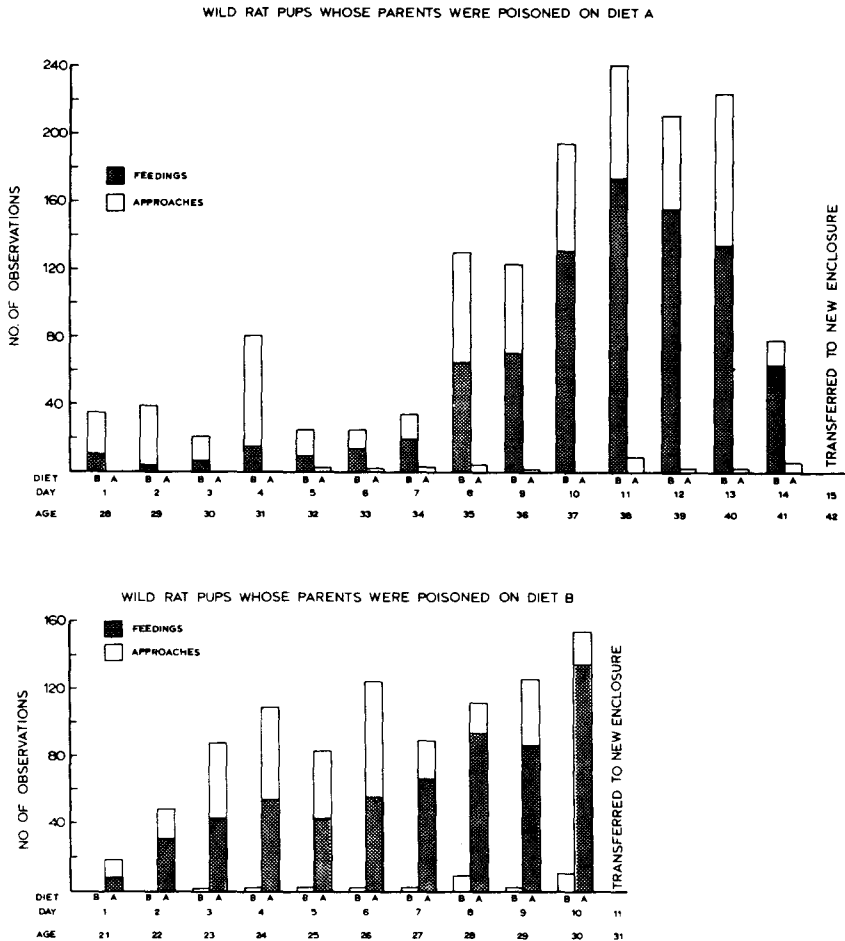
WILD RAT PUPS WHOSE PARENTS WERE POISONED ON DIET A



WILD RAT PUPS WHOSE PARENTS WERE POISONED ON DIET B



**FIGURE 4.** Number of observed approaches to and feedings on Diets A and B by wild rat pups the adults of whose colony had been poisoned when eating Diet A (upper panel) or Diet B (lower panel). (From Galef and Clark.[7] Reproduced by permission of the American Psychological Association.)

responsible for social transmission of acquired food preferences from adults to their young is entirely consistent with the view that it is only information about those foods that adults are eating that is transmitted to juveniles.

The primary behavioral process involved in the transmission of acquired adult food preferences to juveniles is a tendency of wild rat pups to approach adults, feed on the diet the adults are eating, become familiar with that diet, and subsequently exhibit a reluctance to ingest alternative foods. There is little place in such a scheme for the young to learn anything about foods that adults are not exploiting. In fact, during the time juvenile wild rats were with adults, they rarely approached adult-avoided

foods and never tasted such foods (FIGURE 4). It is difficult to imagine how pups could acquire a socially induced aversion to adult-avoided foods to which they are never exposed.[8]

A further behavioral mechanism biasing rat pups to exploit foods that the adults of their social group are eating similarly offers little opportunity for the young to acquire knowledge of food that adults are avoiding. Linda Heiber and I[9] found that adult rats deposit residual olfactory cues in areas in which they feed. These olfactory markers are sufficient to bias pups to explore and eat in areas adults are utilizing for foraging. In this case, pup avoidance of adult-avoided feeding sites appears to be the result of the absence of conspecific olfactory signals in such areas. Once again the avoidance by pups of sites that adults are not utilizing seems to be indirect rather than direct.

## ACTIVE DIRECT TRANSMISSION OF POISON AVOIDANCE: A FAILURE TO REPLICATE

In 1975 Danguir and Nicolaides[10] reported results of an experiment that suggested two rather surprising conclusions. First, that rats could directly transmit poison avoidance, and second, that the avoidance exhibited by naive individuals resulting from
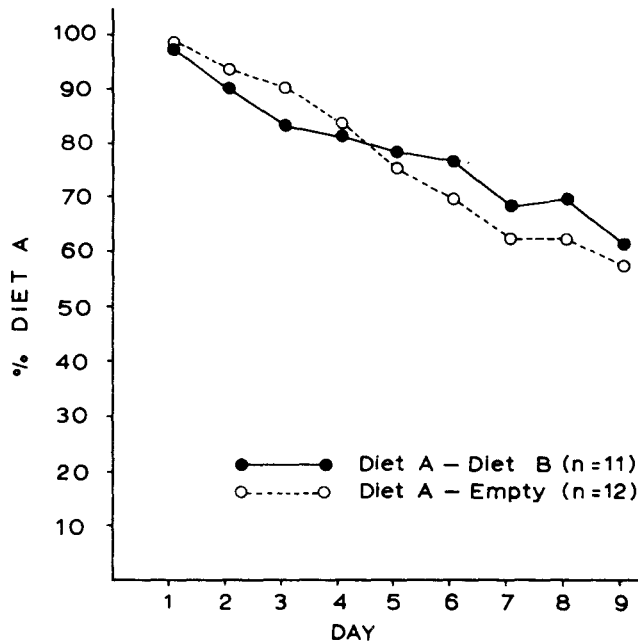
FIGURE 5. Amount of Diet A ingested, as a percentage of total intake, by pups in individual enclosures transferred from adult colonies eating only Diet A, either because it was the only diet available (Diet A- Empty Group) or because Diet B had been poisoned (Diet A-Diet B Group). (From Galef and Clark.[7] Reproduced by permission of the American Psychological Association.)

interaction with trained conspecifics was the result of active interference by knowledgeable animals in the ongoing behavior of their less knowledgeable fellows. The first conclusion was unexpected only in that it contradicted a generalization extrapolated from my own studies of social learning in rats and hence was more exciting than dismaying. The second implication of the Danguir and Nicolaides experiment, however, was contrary to generalizations based on fifty years of research on social learning processes in non-primate animals.

Reviews of the relevant literature[11,12] indicate that in a wide variety of social learning situations, the role of knowledgeable individuals in influencing the behavior of naive conspecifics is passive, not active. Rather than actively intervene in the behavior of naive individuals, knowledgeable conspecifics create, presumably unknowingly, a stimulus situation that causes naive individuals to match their behavior to that of the model. For example, an adult rat feeding at some location provides a stimulus complex that markedly biases orientation of the exploratory behavior of young conspecifics. It is the influence of such passively emitted stimuli that results in adult influence on diet preferences of their offspring. All examples of social learning in the literature, with the exception of two anecdotes,[12] can be understood in such terms. The finding that any nonprimate mammal would actively restrain a naive conspecific from approaching and ingesting a potential toxin suggested a previously unsuspected sophistication and complexity in the behavioral processes supporting animals social learning.

Danguir and Nicolaides[10] trained two members of trios of rats to avoid salt solutions by twice exposing them, when 24 hr water deprived, to a toxic 0.9 percent LiCl solution. To test for transfer of avoidance to naive trio members, trained pairs of subjects were reunited with their untrained trio mate, all were water deprived for 24 hr, and then allowed access as a group for 15 min to a single bottle containing NaCl solution. Trios in a control condition were treated identically to those in the experimental trios, treatment of which is described above, except that on the two training days trained subjects in control trios were exposed to a benign NaCl solution rather than toxic LiCl solution. The results of the experiment are presented in the left-hand panel of FIGURE 6. Naive subjects in experimental trios drank significantly less than naive subjects in control trios, indicating that the trained experimental pair had induced their naive trio-mate to avoid drinking the salt solution. This reduced intake of NaCl solution by naive members of experimental trios was attributed to overt behavior of trained individuals, which in seven of twelve cases were said both to hold down naive rats and to interpose themselves between naive rats and bottle spouts, blocking naive rats' access to NaCl solution.

There are two critical questions: first, whether naive subjects in experimental trios truly drank less NaCl solution during testing than did naive subjects in control trios. Second, if naive subjects in experimental trios did drink less than naive subjects in control trios, was this difference in intake the result of active intervention by trained members of experimental trios?

The answer to the first question was not as clear from Danguir and Nicolaides' data as one might hope. The problem arose in determining the amount of solution actually ingested by naive rats in control trios. During testing there were three animals potentially drinking from a single water bottle and it was only the intake of one of them, the naive animal, that was of interest. In the case of experimental trios, the problem was not particularly acute because trained members of such trios had learned to avoid salty solutions. Danguir and Nicolaides' observations revealed that trained members drank for only a few seconds and all intake could be safely attributed to the naive members of experimental trios. Control trios posed a greater problem. All members of each control trio were 24 hr water deprived at the time of testing. None
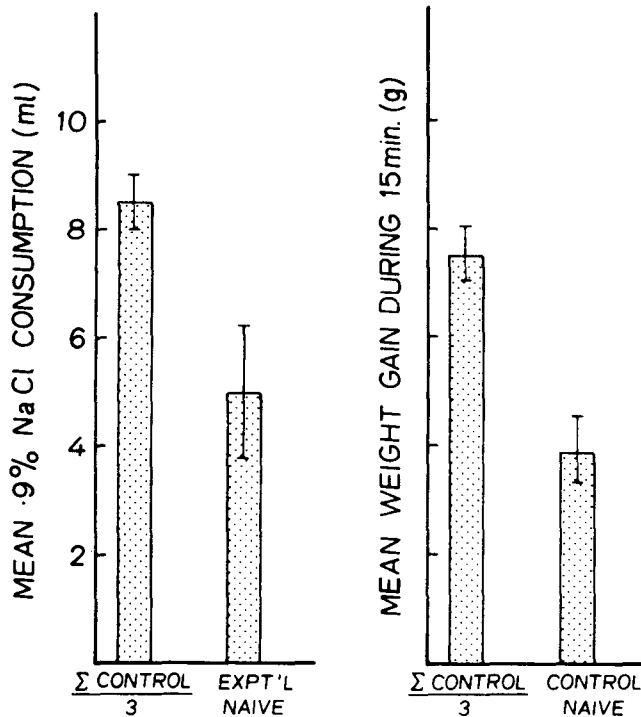
**FIGURE 6.** (Left) Prepared from data presented by Danguir and Nicolaidis.[10] Mean amount of .9% NaCl solution consumed by naive experimental subjects and naive control subjects. The latter amount was calculated by dividing the total amount consumed by control trios by 3. (Right) mean amount of .9% NaCl solution consumed by naive control subjects calculated by dividing the total weight gain of control trios by 3 and by directly measuring the weight gain of naive control subjects. (From Galef and Dalrymple.[13] Reproduced by permission of Academic Press.)

had learned to avoid ingesting salty solutions, and all drank avidly. How can one establish the proportion of the intake of a control trio attributable to its naive member? Danguir and Nicolaides determined the time each member of control trios spent in contact with the drinking spout. They found that trained and naive subjects drank an approximately equal length of time, and therefore, attributed one-third of the total intake of each control trio to its naive member. This is surely a reasonable procedure, but one open to some question.

There is reason to suspect that naive members of control trios, which had not previously experienced salt solutions, might be more hesitant to ingest such solutions than their trained fellows that had ingested NaCl solution on two previous occasions. If naive members of control trios were in fact more hesitant than their trained triomates to ingest NaCl solutions during testing, then the calculation of intake by naive control subjects employed by Danguir and Nicolaides (total amount drunk by control trios divided by 3) would have overestimated the intake of naive subjects in control trios. Apparent difference between the intakes of naive subjects in control and experimental groups could have been due to measurement artifact rather than differences in the behavior of naive subjects in control and experimental groups.

Andrew Dalrymple and I[13] attempted to replicate the Danguir and Nicolaides study as closely as possible while more directly measuring the intake of subjects in control trios. Rather than divide the intake of control trios by three to determine the intake of naive subjects in control trios, we weighed both trained and naive control subjects before and after the 15-min test session.

The right-hand panel of FIGURE 6 shows the intake of naive members of control trios calculated both by dividing the weight gain of all the members of control trios by 3 and by directly measuring individual weight gain. The two methods of calculating the intake of naive subjects in control trios produced the same difference in measured intake of naive subjects as Danguir and Nicolaides found between naive subjects in their control and experimental groups. Our data thus suggest that the apparent difference in intake of NaCl by naive subjects in control and experimental trios reported by Danguir and Nicolaidis was probably the result of measurement error in the determination of the amount ingested by naive subjects in control trios. Of course, in the absence of compelling evidence of social influence on avoidance in the situation under discussion, concern over the mechanisms by which such influence might proceed is unwarranted.

The conclusion I draw from the above is that the only instance of social learning of a direct avoidance by rats reported in the literature (and the only instance of active transmission of behavior) does not hold up under close examination.

## SOCIAL TRANSMISSION OF FOOD PREFERENCES AND AVERSIONS BY RED-WING BLACKBIRDS

Understanding of social learning phenomena would be greatly simplified if information on social learning processes could be generalized across species with confidence. If, as the preceding sections suggest, I am correct in asserting that direct social transmission of taste aversions in rats is not an important factor in their diet selection, while direct transmission of diet preference is, one might hope to find similar patterns of the role of social interaction in diet selection in other species. Unfortunately this does not seem to be the case.

In a series of recent papers[14-16] Russell Mason and his co-workers have described the results of an integrated set of experiments on social learning of food preferences and aversions in red-wing blackbirds (*Agelaius phoeniceus*). Their data provide compelling evidence of direct transmission of both learned aversions and learned preferences in their avian subjects.

Demonstration of socially transmitted diet preference resulted from allowing five pairs of naive blackbirds to observe (for 1 hr/day on four consecutive days) pairs of demonstrators in an adjacent cage eat orange food and five additional pairs of naive blackbirds to observe demonstrators eat green food. Twenty-four hours following the last observation trial, all ten naive pairs were offered a choice between orange and green foods. It was found that each of the ten naive pairs of blackbirds exhibited a preference for that diet (orange or green) that it had observed a demonstrator-pair eat on the four preceding days.[14] Thus, red-wing blackbirds, like Norway rats, can directly influence the food preference of conspecifics.

Using similar procedures, Mason and Reidinger[15] have also been successful in demonstrating direct social transmission of a feeding-related avoidance. In this case, individually housed naive blackbirds watched a conspecific eat from a container marked with either a red or white rectangle. After each demonstrator had eaten for 1 hr, it was intubated with either toxic or control solution, and then returned to the feeding

situation for a further hour. Naive birds were tested the following day, and for five days thereafter, with a simultaneous choice between two feeding containers, one labeled with a red and one with a white rectangle. Naive birds ate reliably less from the colored container from which their demonstrators had eaten if those demonstrators had been intubated with toxin, but not if they had been intubated with benign control solution. The naive observers clearly had learned to avoid a visual cue associated with the ingestive behavior of an ill conspecific.

Both of the above effects have been replicated and the aversion induced by watching a single trial in which a demonstrator becomes ill has been found more resistant to extinction than the preference induced by watching four trials in which a conspecific ate safely.[16] The evidence that red-wing blackbirds will directly learn aversions as the result of social interaction is compelling.

## CONCLUSIONS

Data reviewed in preceding sections suggest the conclusion that there are qualitative differences in the role of social influence in diet selection by Norway rats and red-wing blackbirds. In blackbirds, direct transmission of diet aversion is at least as robust as transmission of diet preference. In rats, evidence of direct transmission of diet preference is easily found, while evidence of direct transmission of diet aversion has proven elusive. This contrast in the nature of the information communicated by members of different species concerning foods leads directly to the question of why such differences might exist. While I do not believe that the question can be answered from current knowledge, simply posing the question of why social learning should be employed in different species in different ways may prove a useful exercise.

Presumably, in those species and situations in which social transmission of information occurs, it increases the fitness of those individuals making use of the behavior of conspecifics in shaping their own behavior. One is thus led to ask in what situations the use of social learning by an individual might enhance fitness. There appear to be two sets of variables affecting the probability that social learning would be fitness enhancing in a population. The first has to do with the nature of the environment in which an organism lives and the second with the ability of the individual to cope with the demands of that environment in the absence of social learning.

In a provocative recent paper Boyd and Richerson[17] have examined the environmental conditions under which natural selection would favor social learning rather than "pure" individual acquisition of behavior. The results of Boyd and Richerson's modelling suggest that individual learning is favored in environments varying greatly over time, social transmission of behavior in moderately temporally variable environments, and genetic transmission in very stable environments. Social learning was also favored over individual learning in spatially varying environments, independent of the degree of environmental heterogeneity. Although the simplifying assumptions needed to render the problem tractable to mathematical analysis make it difficult to extrapolate with confidence Boyd and Richerson's conclusions to natural situations, their work suggests that the extent of trait-relevant environmental variability may prove to be an important determinant of the efficiency of social learning.

Similarly, Johnston and Turvey,[18] in their overview of adaptive behavior, have suggested that adaptation is achieved by behavioral mechanisms differing in the time scale over which they act. Johnston and Turvey propose that different rates of relevant environmental change require adaptive responses with different feedback characteristics (back-reference periods). Although Johnston and Turvey do not consider

situations in which social learning might be an appropriate adaptive mode of response, Boyd and Richerson's analysis suggests that those environments varying spatially and those sufficiently autocorrelated to allow a back-reference period somewhat longer than that supporting individual learning might be particularly appropriate for social learning to occur.

Thus, one sort of answer to the question of why members of one species should socially transmit learned aversions and another should not, would lie in information about temporal and spatial variability in the distribution of toxins to which members of a species are exposed.

A second, and not totally unrelated, answer to the question of causes of differences in use of social learning as an adaptive response lies in consideration of alternative strategies available to an individual in coping with particular environmental challenges. The potential value to an individual of any behavioral tactic for coping with a challenge can only be evaluated in the context of alternative tactics available to that organism for dealing with that challenge. The psychological literature presents a picture of the individual wild rat as a highly specialized poison-avoider, possessing defenses in depth against the ingestion of lethal quantities of toxins: a very strong tendency to avoid ingesting novel foods, an inherent aversion to bitter foods, a tendency to sample novel foods suspiciously, and a capacity to learn toxicosis-induced taste-aversions in a single trial. Within such a behavioral complex, it is possible that social transmission of information concerning toxic foods would be of minimal benefit.

If the individual is capable of coping with the presence of toxins in its environment without the benefit of information acquired from conspecifics, there would be little selective pressure for the development of the capacity to exploit conspecifics as sources of information about potential toxins. As Lehrman[19] stated "Nature selects for outcomes not processes of development." If rats are adequately protected against ingesting deleterious substances by their individual behavioral repetoires, there would be little pressure to evolve social learning mechanisms to cope with the problem. Social learning may be more likely to evolve to fill a gap in an individual's capacity to cope with environmental challenges than as an addendum to a highly sophisticated system. If the above views of social learning is correct, one might well expect situational and species specificity of social learning to be the rule rather than the exception.

The study of individual learning has proceeded by analysis of phenomena conceptualized in abstract terms. Parallel attempts to formalize and reify social learning paradigms (e.g. observational learning, social facilitation, etc.) and to explore their properties at the level of abstraction that has characterized the study of operant and classical conditioning, have not proven particularly enlightening. The preceding discussion suggests that consideration of both ecological and organismic variables may be central to understanding of the distribution and use of social learning processes.

## ACKNOWLEDGMENTS

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