REVISTA MEXICANA DE ANÁLISIS DE LA CONDUCTA 27, 145-164 NÚMERO 2 (SEP.)
MEXICAN JOURNAL OF BEHAVIOR ANALYSIS NUMBER 2 (SEP.)

ANALYSES OF SOCIAL LEARNING PROCESSES AFFECTING ANIMALS' CHOICES OF FOODS AND MATES[1]

ANÁLISIS DE LOS PROCESOS DE APRENDIZAJE SOCIAL QUE AFECTAN ELECCIONES ALIMENTICIAS Y SEXUALES EN ANIMALES

BENNETT G. GALEF, JR[2]
McMASTER UNIVERSITY

ABSTRACT

Social interactions can profoundly influence the stimuli to which an individual animal is exposed and, consequently, can determine the direction in which learning by individuals proceeds. My laboratory has been examining a few of the many ways in which social influences can bias development of behavioral repertoires of animals. Here, I briefly review our work of the last 30 years on social effects on the food choices of Norway rats and mate preferences of Japanese quail. I show that both the foods that rats ingest and the members of the opposite sex that quail select as sex partners can be profoundly biased by interaction with or observation of conspecifics and analyze behavioural processes that support social learning in these two model systems.

Key words: social learning, food choice, mate choice, Norway rat, Japanese quail, mate-choice copying.

---

1. The research described here was funded for 30 years by the Natural Sciences and Engineering Research Council of Canada and McMaster University Research Board. I thank the many students, colleagues and research assistants who have made this research program a reality, particularly Mertice Clark, Steven Wigmore, Moni Stein, Debbie Kennett, Mathew Beck, Russ Mason, Laurel McQuoid and Elaine Whiskin.

2. Correspondence concerning this article should be addressed to Bennett G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, Ontario, Canada L8S 4K1. Electronic mail may be sent to galef@mcmaster.ca.

RESUMEN

Las interacciones sociales pueden influir profundamente sobre los estímulos a los cuales un animal individual está expuesto, y por consiguiente pueden determinar en qué dirección el aprendizaje individual procede. Mi laboratorio ha examinado algunas de las muchas maneras en las cuales influencias sociales pueden sesgar el desarrollo de los repertorios conductuales animales. Aquí reviso rápidamente nuestro trabajo de los últimos 30 años sobre los factores sociales que influyen en las elecciones alimenticias de la rata de Noruega y las preferencias sexuales de la codorniz japonesa. Demuestro que tan los alimentos que las ratas ingieren como los individuos del sexo opuesto que la codorniz elige como parejas sexuales pueden ser profundamente sesgados por interacciones con, o la observación de, miembros de la misma especie; analizo los procesos conductuales que soportan el aprendizaje social en estos dos sistemas modelos.

Palabras clave: aprendizaje social, elección alimenticia, elección sexual, rata de Noruega, codorniz japonesa, imitación de elección sexual.

Satisfying analysis of the processes underlying social behavior both in animals and in humans have proven considerably more difficult than might have been anticipated, in part because of the difficulty of knowing what variables to measure and how to measure them. However, in studies of social influences on learning dependent variables with high face validity are easy to both specify and calibrate. As a possible consequence of this mastery of dependent variables, considerable progress has been made during the past decade in analyzing behavioural processes supporting social learning in animals.

Here, I briefly review two research programs currently in progress in my laboratory. The first is concerned with social influences on food choices of Norway rats' (*Rattus norvegicus*) and the second with social influences on mate choices of Japanese quail (*Coturnix japonica*). The results of both series of studies demonstrate not only that social learning can profoundly affect biologically meaningful activities of animals but also provide some insight into the behavioral process supporting such social learning. I conclude that analyses of social behavior are not only possible, but also necessary, if we are to fully understand behavioral contributions to the survival, reproduction, and possibly, even the evolution of animals both nonhuman and human.

WHY STUDY SOCIAL LEARNING IN ANIMALS?

The last decade has seen a phenomenal increase in interest in animal social learning (Galef, 1998). Psychologists, behavioral ecologists, anthropologists, primatologists, evolutionary biologists, neural network modelers, even economists, have been increasingly active in the field. In studies of social influences on

learning measuring the consequences of social interaction is relatively straightforward. Perhaps as a consequence of the ease of specifying and quantifying dependent variables in studies of social learning, behavioural analyses of instances of social learning have often achieved levels of understanding comparable to those typical in investigations of behavioral processes supporting individual learning.

Studies of social learning are not only tractable, such studies are also necessary if we are to understand fully the development of behavioral repertoires in animals. Animals, especially young animals, living outside the laboratory must learn many things rapidly, if they are to survive: A fledgling bird or weaning mammal venturing from its nest for the first time has to learn to avoid predators before it is eaten by one. It has to find water before it dehydrates. It has to learn to select and ingest a nutritionally balanced diet before it exhausts its internal reserves of any critical nutrient.

Naive, young animals faced with such problems would be well advised to take advantage of opportunities to interact with knowledgeable adults. Survival to adulthood demonstrates unequivocally that adults have learned to avoid predators, to find water, to select safe, nutritious substances to ingest, and so on. Most important, adults have done all of these things in the same environment where juveniles with whom they interact are struggling to acquire the behavioural repertoire needed for survival. Consequently, at least in principle, juveniles do not have to learn independently to overcome each of the many challenges posed by the environment they share with their parents and any other adults with whom they come in contact. Attending to the behaviour of older or more knowledgeable others can facilitate acquisition of necessary responses to environmental demands by speeding the laborious process of trial-and-error learning at a time when error can be particularly costly. Hence, from a biological or ecological perspective, as well as from a psychological one, social learning would seem to be worth studying (Galef, 1996a).

SOCIAL INFLUENCES ON THE FOOD PREFERENCES OF NORWAY RATS: A MODEL SYSTEM

My students and I have spent the last 30 years using the acquisition of adaptive patterns of food choice by Norway rats (*Rattus norvegicus*) as a model system in which to explore ways in which a developing animal can incorporate into its own behavioral repertoire the behavior of more knowledgeable conspecifics. The food choices of Norway rats provide particularly appropriate material for investigations of social learning in animals because there is a reasonable amount of field data consistent with the hypothesis that wild Norway rats living outside the laboratory show important social influences on their feeding behavior (Galef, 1976; Steiniger, 1950).

Colonies of free-living rats Norway rats are highly social animals. They live in colonies that inhabit burrow systems from which colony members emerge to forage and to which they return between foraging bouts (Calhoun, 1966). There are sound theoretical reasons to believe that members of social species that, like Norway rats, forage from a fixed location would benefit from social exchange of information about foods (Ward & Zahavi, 1973). If, for example, one member of a colony of rats were to discover a new source of food, eat some and then return to its burrow, it would be advantageous to other colony members, particularly to ignorant juveniles, if they could extract information from the returning successful forager that might facilitate their own identification and location of the newly discovered food (Galef, 1990).

Multiple Processes for Social Learning about Food

My coworkers and I have explored a variety of mechanisms, each able to bias the feeding behavior of young rats (for review see Galef, 1996b): (1) Foods eaten by a lactating rat flavor her milk, and experience of flavors in mother's milk causes weanlings to prefer to eat the foods that their mother ate while lactating (Galef & Clark, 1972; Galef & Henderson, 1972; Galef & Sherry, 1973). (2) The simple physical presence of an adult rat, even an anesthetized one, at a feeding site causes juveniles to approach that site and to begin to eat whatever foods are to be found there (Galef & Clark, 1971a, 1971b). (3) Adult rats mark both foods and feeding sites with residual chemical cues that make marked sites and foods more attractive to juveniles than unmarked ones (Galef & Beck, 1985; Galef & Heiber, 1976; Galef & Muskus, 1979). (4) Adult rats lay scent trails from feeding sites to harborage sites that others follow to food (Galef & Buckley, 1996). The very multiplicity of behavioral processes involved in Norway rats' learning from others about foods and feeding sites suggests that in rats, as in honey bees (von Frisch, 1967; Lindauer, 1961; Seeley, 1995), socially acquired information contributes significantly to foraging efficiency.

A case history

Suppose a foraging rat eats a food at some distance from its burrow, rejoins its colony, and interacts with burrow-mates that, sometime later, leave the burrow to find food. We wanted to know what effect, if any, such interaction between a successful forager and burrow-mate, occurring at some distance from a feeding site, has on the burrow-mate's subsequent choice of foods. Simple observation of free-living animals in uncontrolled environments would never provide a convincing answer to the question, so we designed a laboratory procedure that captured the important elements of the natural situation (Galef & Wigmore, 1983).

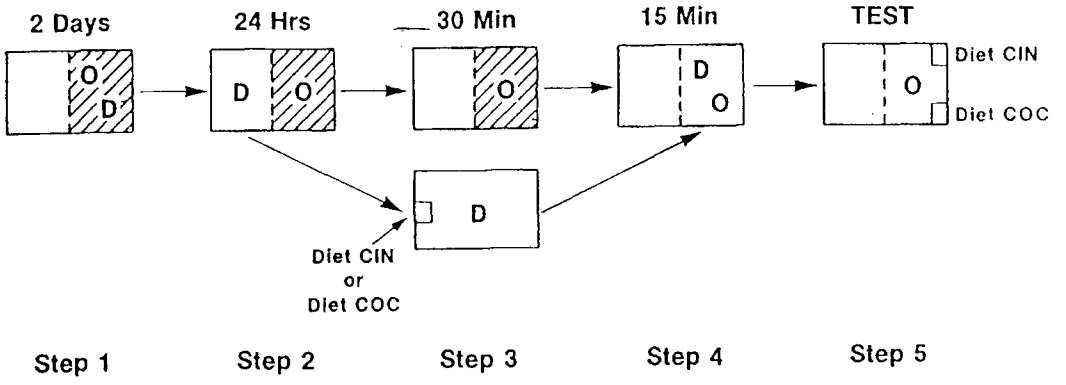

Figure 1. Schematic of procedure used to study social influence on diet choice in Norway rats. Diet Cin = cinnamon-flavored diet; Diet Coc = cocoa-flavored diet. Reprinted by Permission of the American Psychological Association.

The basic procedure

We housed and tested our subjects (referred to below as either demonstrators or observers) in pairs in cages divided into two equal parts by a screen partition (see Figure 1). To begin the experiment, we allowed each pair 2 days to become familiar with one another and with the apparatus. Next, we food deprived one of the pair members (the demonstrator) so that it would eat when given access to food. Then, we moved the demonstrator to a separate room and fed it either a cinnamon- or cocoa-flavored diet for 30 min, and, immediately afterwards, placed the demonstrator back with its pair mate (the observer) for 15 min. Last, we removed each demonstrator from the experiment and offered each observer, for 23 hr, a choice between weighed samples of cinnamon- and cocoa-flavored diets.

We found that during the 23-hr choice test, those observer rats whose demonstrators had eaten cinnamon-flavored food ate far more cinnamon-flavored than cocoa-flavored food, whereas those observers whose demonstrators had eaten cocoa-flavored food ate far more cocoa-flavored than cinnamon-flavored food (Galef & Wigmore, 1983). Clearly, the flavor of the food fed to demonstrators affected the food choices of their observers.

Robustness of the phenomenon

A frequent problem with presumed laboratory analogues of behavioral events, such as social learning of a food preference, assumed to occur in nature, is that in the laboratory a behavior of interest occurs only under a restricted set of

experimental conditions. Social learning of food preferences, to the contrary, is surprisingly robust to parametric variation.

Over the years, my students and I have repeated the basic experiment dozens of times: with many different diets (Galef, 1983), with wild rat demonstrators and observers as well as domesticated ones, with demonstrator-observer pairs familiar with one another and with pairs that had never met prior to their interaction during Step 4 of the procedure (see Figure 1), with old demonstrators and observers and young ones, with male demonstrator-observer pairs and female ones (Galef, Kennett & Wigmore, 1984). In every case, we saw profound influence of demonstrator rats on their observers' later food choices. In fact, in 15 years, we have not discovered any circumstance where one might reasonably expect observers to acquire information from demonstrators as to the diets those demonstrators have eaten, in which observers did not exhibit a preference for their respective demonstrators' diets. Social influence on the food choices of rats is clearly not dependent on a restricted set of experimental parameters for its expression.

How information is communicated

To look at the mode of communication from demonstrator to observer, we had to gain some control over their interaction. To do so, we used a procedure that differed from that illustrated in Figure 1 in only one important respect; during the 15 min when demonstrator and observer interacted (Step 3 in Figure 1), they were separated by a 1/2-in (1.25-cm) screen.

We found (Galef & Wigmore, 1983) that separating demonstrator and observer with a screen while they interacted did not interfere with communication between them. Observers continued to prefer the food that their respective demonstrators had eaten in Step 5. However, social influence of demonstrators on observers' food choices broke down totally, when we separated them while they interacted with a transparent Plexiglas rather than a screen partition. Clearly, some sort of non-visual contact, perhaps olfactory, perhaps gustatory, perhaps 'linguistic', is necessary if food choices of observer rats are to be influenced by interaction with conspecific demonstrators.

Excluding gustatory cues

If, after a demonstrator rat has eaten and before it interacts with an observer, it is anesthetized, taped to a Petri dish, and left separated from its observer by a screen so that no physical contact between demonstrator and observer is possible (see Figure 2), the observer still prefers the food that its demonstrator ate. Successful extraction of information from an unconscious demonstrator that an observer cannot touch tells us two things: First, the message is emitted in a passive way by the demonstrator, not produced by a demonstrator in response to

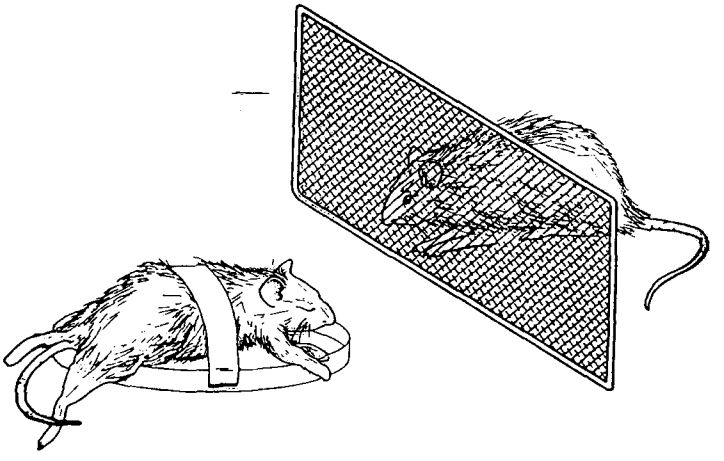

Figure 2. Illustration of anesthetized demonstrator and observer separated by a screen partition. Reprinted by permission of the American Psychological Association.

the presence of an observer. Second, no physical contact between demonstrator and observer is required for information transfer to occur.

The important cue is, as we know from the Plexiglas-barrier experiment, not visual, yet it can be transmitted over some distance. Therefore, it is not gustatory. The important cue is emitted by unconscious rats, which rules out the 'linguistic' hypothesis. We are left with only olfactory cues to carry the message from demonstrator rats to their observers.

Evidence of a role of olfactory cues

Consistent with the hypothesis that olfactory cues carry the message passing from demonstrator to observer, when we rendered observers anosmic (that is unable to smell) before they interacted with their respective demonstrators, the observers failed to exhibit a preference for their demonstrators' diets during a subsequent 22-hr choice test (Galef & Wigmore, 1983).

Also, not only rats but humans as well can tell what diet a rat has been eating using olfactory cues emitted by recently fed rats. When we fed six rats cocoa-flavored diet and another six rats cinnamon-flavored diet, then present all 12 rats in random sequence to a human observer instructed to sniff the rats' breath, the human observer identified the diet the rat had eaten with 85 to 90 percent accuracy (Galef & Wigmore 1983).

Causes of Change in Preference

It's not, of course, too surprising that an observer, either human or rodent, who sniffs a rat's breath can tell which of two foods the sniffed rat has recently eaten.

The more difficult question is why, in a proximal sense, an observer rat that has determined that a conspecific has, for example, just eaten cinnamon-flavored food should suddenly exhibit an enhanced tendency to eat cinnamon-flavored food.

Fear of novelty

Rats, particularly wild rats, are often quite hesitant to eat unfamiliar foods (Barnett, 1963; Galef, 1971). Consequently, at least under some circumstances, simple prior exposure to a food will substantially increase rats' intake of it. If rats are unwilling to eat unfamiliar foods, and if simple exposure to the smell of a food on a demonstrator rat increases an observer rat's familiarity with a food that its demonstrator has eaten, then observers might develop enhanced preferences for their respective demonstrators' diets as a result of simple familiarity with the odor of the diet a demonstrator had eaten. If this were the case, demonstrators would be acting simply as passive carriers of food particles or food odors.

However, results of a number of studies carried out over the years offer no support whatsoever for the hypothesis that changes in observer rats' food preferences result from simple exposure of an observer rat to the smell or to the taste of the diet eaten by its demonstrator (e.g. Galef, 1989; Galef & Stein, 1985; Galef & Kennett & Stein, 1985).

For example, when we gave one group of naive rats access to cinnamon-flavored diet and another group of rats access to cocoa-flavored diet for 30 min/day for 5 consecutive days, and further, offered both groups of rats a choice between cinnamon- and cocoa-flavored diets for the remaining 23 1/2 hr of each day, we saw no effect of this 1/2-hr, daily exposure to and eating of either cinnamon- or cocoa-flavored diet on subjects' food choices (Galef, 1989). If we then gave the same rats 30 min/day to interact with demonstrator rats fed either cinnamon-or cocoa-flavored diet, we saw massive effects of the diet fed demonstrators on the food choices of observers during daily 23 1/2 hr choice tests (Galef, 1989). Simple exposure to a diet did not affect the food preferences of observers. Exposure to a demonstrator that had eaten a diet did affect observers' food preferences. Changes in observers' food preferences, thus, seem to require more than simple exposure to a diet. Changes in observers' food preferences require exposure to food-related cues in the social context that is provided by the presence of a demonstrator.

If, in fact, changes in observers' food preferences depend on exposure to food-related cues in a social context, we are left with two important questions: First, where do the food-related olfactory cues emitted by demonstrators and detected by their observers that permit observers to identify the foods their respective demonstrators ate come from? Second, what are the contextual cues, the social cues, that make exposure to food-related cues effective in altering observers' food preferences?

The source of diet-identifying cues

The method that we used ~~to~~ answer the first of these two questions (Galef, Kennett & Stein, 1985; Galef & Stein, 1985) was very similar to that illustrated in Figure 1 except in the ways in which we exposed demonstrators to their respective diets and in the conditions under which demonstrators and observers interacted.

Before a demonstrator and observer interacted, we anesthetized the demonstrator and placed it in a wire-mesh tube that we inserted into a cardboard bucket rather like those in which Kentucky Fried Chicken is sold (Figure 3). We then placed an observer in the bucket and allowed it to interact for 1/2 hr with its demonstrator.

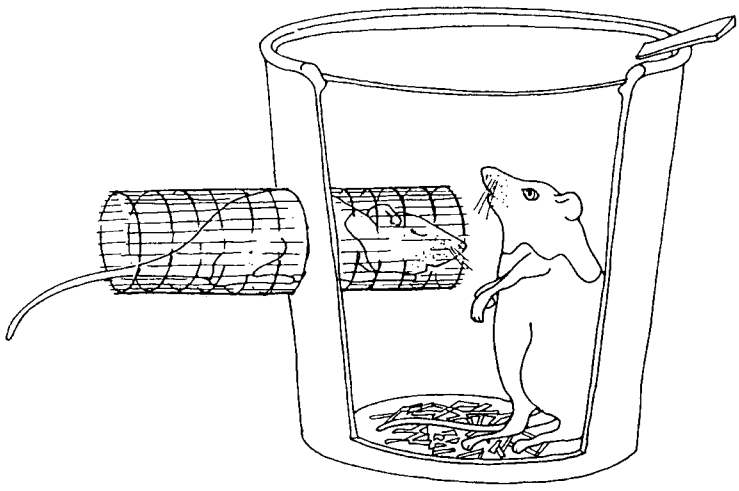

Figure 3. Illustration of apparatus used to examine the sources of diet-identifying and contextual cues. Reprinted by permission of the Psychonomic Society.

We made demonstrator rats carriers of food odors in a number of different ways: Each demonstrator assigned to the *Fed-demonstrator condition* first ate either cinnamon- or cocoa-flavored diet for 30 min, was then anesthetized and placed in a tube that we then inserted into the bucket. We placed an observer in the bucket, allowed the observer to interact with its demonstrator, and then offered the observer, in its home cage, a choice between cinnamon-and cocoa-flavored diets. Our procedures didn't interfere with social transmission of food preference, and observers assigned to the Fed-demonstrator condition preferred their respective demonstrators' diets.

We anesthetized demonstrators assigned to the *Powdered-demonstrator condition*, rolled their faces in either cinnamon- or cocoa-flavored food, and then treated them as we had treated demonstrators assigned to the Fed-demonstrator condition. Observers that interacted with a powdered demonstrator, again exhibited a preference for the food with which their demonstrators had been powdered.

Clearly, particles of food clinging to the fur and vineries of a rat provide diet-identifying cues sufficient to allow observers to identify the food their demonstrators have eaten.

Demonstrators assigned to the *Tube-fed demonstrator condition* were first anesthetized, then stomach-loaded with either coffee- or vinegar-flavored solution (We used solutions rather than solid foods with this group because of practical problems with tube feeding solids to rats). After interacting with their demonstrators, observers chose between coffee- and vinegar-flavored solutions and once again exhibited a significant increase in preference for their respective demonstrators' diets. Clearly, diet-identifying cues escaping from the digestive tract of a demonstrator rat also carry a signal sufficient to allow an observer to identify its demonstrator's diet.

Finally, *Surrogate demonstrators* were cotton-batting-stuffed, rat-sized lengths of surgical gauze one end of which was powdered with either cinnamon- or cocoa-flavored diet, then presented to observers in the buckets. Observers exposed to surrogate demonstrators did not exhibit a preference for the diet with which we had powdered them, thus again indicating that simple exposure to a diet does not enhance preference for it, whereas exposure to the same diet in the context provided by a demonstrator rat does enhance preference for it.

The source of contextual cues

A group of *Powdered-face demonstrators* that received exactly the same treatment as did Powdered-demonstrators described in the preceding section provided a baseline. We treated demonstrators assigned to the *Dead-powdered-face condition* just as we treated demonstrators assigned to the Powdered-face condition except that we sacrificed the former animals by anesthetic overdose before we placed them in tubes. We anesthetized demonstrators assigned to the *Powdered-rear condition*, just as we had anesthetized demonstrators assigned to the Powdered-face condition, then rolled their rear-ends, rather than their heads, in cinnamon- or cocoa-flavored diet before placing them in the tubes with their rear ends inside the bucket and their heads outside of it.

We found that demonstrators assigned to the Powdered-face condition had a significant influence on the food preferences of their observers, but that demonstrators assigned to Dead-powdered-face and Powdered-rear conditions did not. We concluded that the most potent contextual or social cues causing observers to prefer foods eaten by their demonstrators emerge from the anterior of live rats (Galef & Stein, 1985).

Rat breath

Given the preceding result, it seemed reasonable to ask whether constituents of rat breath provided the contextual or social cues that make diet-identifying cues

emitted by demonstrator rats effective in changing their observers' food preferences. Because rats breathe only through their noses, not though their mouths, when you compare chemical contents of a sample of air taken from the nose of a rat with chemical contents of a sample of air taken from the mouth of that rat, any differences between the two samples is a component of rat breath. The results of mass spectrographic analyses of sulfur compounds in rats' breath (Galef, Mason, Preti & Bean, 1988) revealed significant quantities of carbon disulfide. We subsequently found that observer rats exhibited substantial enhancement of their preference for cocoa- or cinnamon-flavored diets following exposure to a cotton-batting surrogate rat powdered with cocoa- or cinnamon-flavored-diet and moistened with carbon-disulfide solution, but not following exposure to a similarly powdered surrogate moistened with distilled water (Galef, Mason, Preti & Bean, 1988). Thus, carbon disulfide appears to be an important component of the social context that allows demonstrator rats to alter the food preferences of their observers.

Human demonstrators

Human beings, like rats, have trace amounts of carbon disulfide on their breaths. Consequently, it might be expected that if the combination of a food odor and a very small amount of carbon disulfide is sufficient to produce a change in the flavor preferences of rats, human demonstrators who ate a food and then breathed on a rat should increase the rat's preference for the food the human demonstrator had eaten. In fact, observer rats breathed upon by humans that had eaten either cinnamon-flavored or cocoa-flavored rat food prefer food of the flavor that their human demonstrators ate (Figure 4).

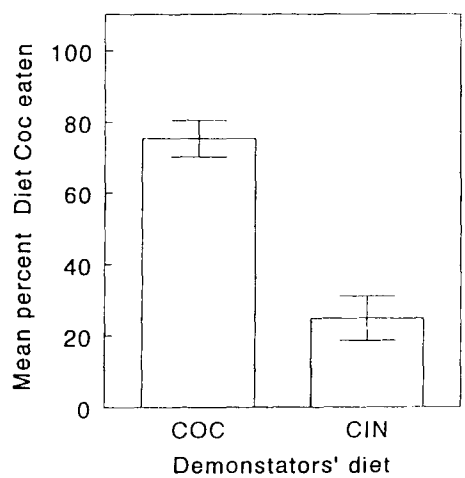

Figure 4. Amount of cocoa-flavored diet, as a percent of total amount ingested during 22 hr, eaten by observer rats after interacting with human demonstrators fed either cinnamon- or cocoa-flavored rat diet. Cin = cinnamon-flavored diet; Diet Coc and Coc = cocoa-flavored diet. Flags = + 1 SEM.

Survival Value of Social Learning about Foods

The last point that I would like to make with regard to social influences on food choice in rats is that social learning can have adaptive value, increasing the probability of survival of naive individuals wise enough to use conspecifics as sources of information when selecting items to ingest. Omnivores such as rats must, by definition, learn to construct a nutritionally adequate diet by sampling among myriad potentially ingestible substances. Weanling omnivores face an especially critical challenge; they have limited internal reserves and must learn rapidly to ingest a nutritionally adequate mix of foods if they are to survive. As you might expect, a weanling rat trying to solve for itself the complex puzzle of selecting appropriate substances to ingest can run into difficulties (Galef, 1991; Galef & Beck, 1990).

We placed young rats in enclosures where they had continuously available four different foods (Beck & Galef, 1989; Galef, Beck & Whiskin, 1991). Three of these four foods were relatively palatable but low in protein, one was protein-rich, but relatively unpalatable. The pups did abysmally and would surely have died of protein deficiency, if we had not terminated the experiment. On the other hand, a second group of pups treated identically to the first group, but sharing their individual enclosures with adult rats that previously trained to eat the protein-rich food, grew normally. There is survival value in learning socially what food one's elders are eating.

SOCIAL INFLUENCES ON THE MATE CHOICES OF FEMALE JAPANESE QUAIL

Japanese quail (*Coturnix japonica*) are wonderful animals for laboratory investigations of sexual behavior. Mature quail will court and mate essentially whenever they are given an opportunity to do so. Consequently, it is possible do experiments on factors affecting mate-choice in Japanese quail that would be impossible with most other avian or mammalian species.

The Basic Experiment

We used an enclosure divided into three sections by two screen partitions (Figure 5). The central area of the enclosure contained a transparent Plexiglas holding cage which we could raise from another room to release a quail held captive in the holding cage. A television camera allowed us to watch the birds and to score their behavior without disturbing them.

Each experiment consisted of 3, 10-minute phases: the first was a *pre-test* to determine a focal animal's preference between two members of the opposite sex. During the pre-test we simply confined one quail (*the focal subject*) in the holding

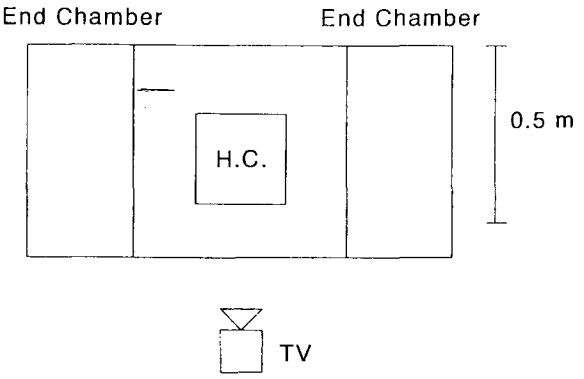

Figure 5. Overhead schematic of the apparatus used to study social influence on mate choice in Japanese quail. H.C. = holding cage; TV = television camera. Reprinted by permission of Academic Press.

cage and placed one member of the opposite sex (*target subject*) in each of the two end compartments of the enclosure (see Figure 5). We then raised the holding cage, allowing the focal animal to move freely about the central compartment of the enclosure, and recorded the time that the focal animal spent on the side of the central compartment closer to each of the two target subjects.

The second phase of each experiment was an *observation phase* during which the focal animal was confined in the holding cage and given the opportunity to observe one of the two target subjects remain alone and the other interact with a *model subject* which was of the same sex as the focal animal.

The third and last phase was a *post-test* during which the focal animal got to choose for a second time between the same two target subjects that it had chosen between during the pre-test.

In the first experiment (Galef & White, 1998), we simply determined whether a focal female quail would increase her preference for a target male that she had seen court and mate with a model female during the observation phase. Twenty-eight focal females chose between 28 pairs of target males during the pre-test. During the observation phase, half these focal females watched their non-preferred male, that is the male they had spent less time with during the pre-test, court and mate with a model female. The remaining focal females were treated exactly as were the first group except that, during the observation phase, we did not place a model female with the focal female's non-preferred target male.

The results were exceptionally clear. During the post-test, focal females that saw their non-preferred target male court and mate with a model female during the observation phase showed a highly significant increase between pre-test and post-test in the time that they spent with the target male that they had seen court and mate. Focal females that did not see their non-preferred male court and mate during the observation phase showed no change between pre-test and post-test in the time that they spent with him (Galef & White, 1998).

Changes in Female Perception or in Male Behavior

In other experiments (Galef & White, 1998, 1999a), we compared the behavior of focal females that, during the observation phase, either watched their respective non-preferred target males mate with a model female or had an opaque wall blocking their view of their non-preferred target male while he mated with a model female. We found that focal females that could not see their non-preferred target male while he mated with a model female did not show an increase between pre-test and post-test in the time that they spent near him. We concluded that mating does not change the subsequent behavior or appearance of males so as to make them more attractive to focal females. Focal females have to see a non-preferred target male interacting with a female, if their tendency to remain near that male is to increase.

Necessary Conditions for Female Change in Preference

What is it that the focal female has to see a non-preferred male do for his attractiveness to her to be increased? Does she have to see him mate, or just court, or just standing near a female? We changed the apparatus so that during the observation phase the model female, like the focal female, was held in a transparent Plexiglas cage. This second holding cage, located in an end-chamber of the apparatus, had one opaque wall. When the cage holding the model female was positioned so that the opaque wall was located between the focal female and the model female, the focal female saw a male courting, but no female; when the wall was located between the non-preferred male and the model female, the focal female saw a male and female together, but no courtship or mating; when the opaque wall faced the back of the cage, the focal female saw the male and female court, but not mate.

The results of such experiments were again quite clear (Galef & White, 1998). If focal females watched their respective non-preferred target males court, but couldn't see what the male was courting, the focal female's preferences were unaffected. If a focal female saw a target non-preferred male and model female simply standing near one another or saw a non-preferred target male court a female but not mount her, the focal female showed a significant increase in her attraction to that non-preferred male. In both the latter cases focal females showed an increase in preference for their non-preferred target males that was as great as that shown by focal females that had watched their non-preferred males actually court and mount a model female. We concluded that simply seeing a male and female in the same area is sufficient to cause a female to increase her preference for that area or for the male in it.

Further studies in which the location of target males was reversed between the observation and post-test phases of the experiment showed that focal females actually show an increase in preference for a particular male as a result of seeing

him mate, not just a preference for the place where he mated (Galef & White, 1998, 1999a).

SOCIAL INFLUENCES ON MATE CHOICES OF MALE JAPANESE QUAIL

The effects of observing mating are sex-specific (White & Galef, 1999b); focal males that saw the target females that the had preferred during the pre-test mate during the observation phase were significantly less attracted to those target females during the post-test than they had been during the pre-test (White & Galef, 1999b).

Necessary Conditions for Change in Male Preference

We carried out the same sort of analysis with male quail that we had with female quail to discover what males had to see to learn to avoid a female. We found that the necessary conditions for changing the mate choices of male quail are slightly different from those for changing mate choice in females. As in female quail, change in the response of male focal subjects resulted from seeing a target animal mate, not from changes in a target animal's appearance or behavior as a result of mating (White & Galef, 1999b). However, a focal male quail had to see a preferred target female courted by a male (not just standing near a male) before he lost interest in her (White & Galef, 1999a, 1999b).

Affiliation or Mate Choice?

It has become conventional in the literature on mate choice to equate a tendency on the part of two animals of opposite sex to affiliate with one another with their choosing one another as mates (Wagner, 1998). Obviously, that is not entirely satisfactory. We used tethered males and untethered females to look at the correlation between affiliative tendency and choice of partners for copulation (White & Galef, in press).

We first allowed females to chose between two males in a pre-test of affiliative preference. We then allowed the same females to choose for 10 min between the same males as partners for copulation after we tethered the males at opposite ends of an enclosure. We found that, regardless of the measure of female mate choice that we used (first male the female allowed to copulate with her, last male the female allowed to copulate with her, or male that a female copulated with most frequently), the male that a female spent longer near in the pre-test of affiliation was the male with whom she preferred to copulate during the mate-choice test (White & Galef, in press).

We also found that males free to copulate with both their preferred and non-preferred females, as determined by an affiliative-preference pre-test, preferred to copulate with the female they remained closer to during the test of affiliative preference (White & Galef, in press).

A Role for Social Learning in the Evolution of Male Characteristics

In the studies described thus far, focal animals saw members of the opposite sex engage in some aspect of courtship and mating and changed their preferences for the particular individual that they saw mating. In the last set of experiments we conducted (White & Galef, submitted), we asked whether a focal female that observed a male mate with a model female changed her preference not just for the individual male she saw mating, but for all males that were similar in appearance to him. We anticipate that behavioral ecologists will see such experiments as relevant to the question of whether social influence might play a role in the spread of mutant, sexually selected genes through a population.

Basic method

We used a modified version of both the original apparatus (Figure 6) and original procedure. The experiment was carried out in two rather than three stages. First, we confined a focal female in a holding cage that had two opaque walls oriented so that the focal female could see into the auxiliary cage (Figure 6), but could not see into the two end compartments of the main enclosure each of which contained a target subject. For 10 min, the focal female observed either a male in the auxiliary enclosure mating with a model female, a male standing alone in the auxiliary enclosure, or an empty auxiliary enclosure. Then we lowered an opaque partition between the auxiliary enclosure and the central compartment of the main enclosure, freed the focal female from the holding cage, and gave her a 10-min choice test between target males, one confined in each end compartment of the apparatus.

Pseudo-mutant males

In the course of our earlier studies, we had brought 100s of quail into our laboratory, and some of them were feather color mutants. These mutants would have one or two unmelanated primaries on each wing, or a small unmelanated spot on the breast. It is an easy matter to create "pseudo-mutant" quail by using glue to place some feathers taken from an albino quail on a normal quail.

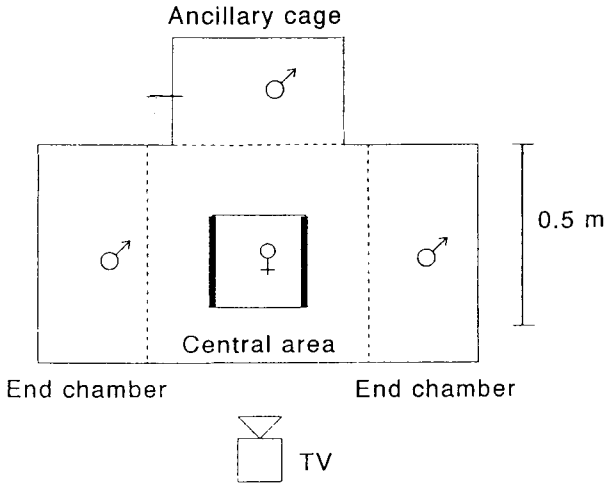

Figure 6. Overhead schematic of apparatus used to study generality of socially-learned preference of focal females for pseudo-mutant male Japanese quail. Reprinted by permission of Academic Press.

Use of pseudo-mutant males in the experiment

During the first stage of the present experiment, focal females saw a pseudo-mutant male either mating with a model female or standing alone in the auxiliary compartment. During the second stage, all focal females chose between a pseudo-mutant target male and normal-looking target male that had three of his feathers replaced with normal quail feathers. Neither of the target males that the female chose between during the second phase of the experiment were the same male that the focal female had seen in the auxiliary compartment during the first stage of the experiment.

We found (White & Galef, submitted) that those focal females that had seen a pseudo-mutant male mating with a model female, were more likely to affiliate with another pseudo-mutant male than were those focal females that had seen an empty auxiliary cage or a pseudo-mutant male standing alone in the auxiliary cage. Thus, we have provided evidence of a social or cultural process that could substantially accelerated the rate of spread of mutant genes through a population.

CONCLUSION

My conclusion is a simple one following directly from the evidence provided above. Social learning can have profound effects on the development of behavioral repertoires in animals. It can guide animals to select appropriate foods or appropriate mates. It may even play a role in evolution, accelerating the spread of mutant genes through a population. Behavioral analyses of social behavior are

not only possible, but also necessary, if we are to understand the survival, reproduction, and perhaps, even the evolution of animals both nonhuman and human.

REFERENCE

Barnett, S. A. (1958). Experiments on "neophobia" in wild and laboratory rats. *British Journal of Psychology, 49*, 195-201.

Beck, M., & Galef, B. G.,Jr. (1989). Social influences on the selection of protein-sufficient diet by Norway rats. *Journal of Comparative Psychology, 103*, 132-139.

Calhoun, J. B. (1962). *The ecology and sociology of the Norway rat.* Bethesda, MY: U.S. Department of Health Education and Welfare.

Galef, B. G., Jr. (1971). Social effects in the weaning of domestic rat pups. *Journal of Comparative and Physiological Psychology, 75*, 358-362.

Galef, B. G., Jr. (1972). Mother's milk and adult presence: Two factors determining initial dietary selection by weaning rats. *Journal of Comparative and Physiological Psychology, 78*, 220-225.

Galef, B. G., Jr. (1976). Mechanisms for the social transmission of acquired food preferences from adult to weanling rats. In L. M. Barker, M. R. Best, & M. Domjan (Eds.), *Learning mechanisms in food selection* (pp. 123-150). Waco, TX: Baylor University Press.

Galef, B. G., Jr. (1983). Utilization by Norway rats (*R. norvegicus*) of multiple messages concerning distant foods. *Journal of Comparative Psychology, 97*, 364-371.

Galef, B. G., Jr. (1991). A contrarian view of the wisdom of the body as it relates to food selection. *Psychological Review, 98*, 218-224.

Galef, B. G., Jr. (1996a). An adaptationist perspective on social learning, social feeding and social foraging in Norway rats. In D. A. Dewsbury (Ed.), *Contemporary issues in comparative psychology* (pp. 55-79). Sunderland, MA: Sinauer Associates.

Galef, B. G., Jr. (1996b). Social influences on the food preferences and feeding behaviors of vertebrates. In E. D. Capaldi (Ed.), *Why we eat what we eat: The psychology of eating* (pp. 237-232). Washington, DC: American Psychological Association.

Galef, B. G., Jr. (1998). Recent progress in studies of imitation and social learning in animals. In M. Sabourin, F. Craik & M. Robert (Eds.), *Advances in psychological science: Vol. 2. Biological and cognitive aspects* (pp. 275-299). Hove, East Sussex, England: Psychology Press.

Galef, B. G., Jr., Attenborough, K. S., & Whiskin, E. E. (1990). Responses of observer rats to complex, diet related signals emitted by demonstrator rats. *Journal of Comparative Psychology, 104*, 11-19.

Galef, B. G., Jr. & Beck, M. (1990). Diet selection and poison avoidance by mammals individually and in social groups. In E. M. Stricker (Ed.), *Handbook of neurobiology* (Vol. 11, pp. 329-349). New York: Plenum Press.

Galef, B. G., Jr., Beck, M., & Whiskin, E. E. (1991). Protein deficiency magnifies social influence on the food choices of Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology, 105*, 55-59.

Galef, B. G., Jr. & Buckley, L. L. (1996). Use of foraging trails by Norway rats. *Animal Behaviour, 51*, 765-771.

Galef, B. G., Jr., & Clark, M. M. (1971a). Parent-offspring interactions determine time and place of first ingestion of solid food by wild rat pups. *Psychonomic Science, 25*, 15-16.

Galef, B. G.,Jr., & Clark, M. M. (1971b). Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. *Journal of Comparative and Physiological Psychology, 25*, 341-357.

Galef, B. G., Jr., & Heiber, L. (1976b). The role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. *Journal of Comparative and Physiological Psychology, 90*, 727-739.

Galef, B. G., Jr., & Henderson, P. W. (1972b). Mother's milk: A determinant of feeding preferences of weaning rat pups. *Journal of Comparative and Physiological Psychology, 78*, 213-219.

Galef, B. G., Jr., Kennett, D. J., & Wigmore, S. W. (1984). Transfer of information concerning distant food in rats: A robust phenomenon. *Animal Learning and Behavior, 12*, 292-296.

Galef, B. G., Jr., Kennett, D. J., & Stein, M. (1985). Demonstrator influence on observer diet preference: Effects of simple exposure and the presence of a demonstrator. *Animal Learning & Behavior, 13*, 25-30.

Galef, B. G., Jr., & Sherry, D. F. (1973). Mother's milk: A medium for the transmission of cues reflecting the flavor of mother's diet. *Journal of Comparative and Physiological Psychology, 83*, 374-378.

Galef, B. G., Jr., & Stein, M. (1985). Demonstrator influence on observer diet preference: Analysis of critical social interactions and olfactory signals. *Animal Learning & Behavior, 13*, 31-38.

Galef, B. G., Jr. & White, D. J. J. (1998). Mate-choice copying in Japanese quail, *Coturnix coturnix japonica. Animal Behaviour, 55*, 545-552.

Galef, B. G.,Jr., & Wigmore, S. W. (1983b). Transfer of information concerning distant foods: A laboratory investigation of the "information-centre" hypothesis. *Animal Behaviour, 31*, 748-758.

Galef, B. G., Jr. & Muskus, P. (1979). Olfactory mediation of mother-young contact in Long-Evans rats. *Journal of Comparative and Physiological Psychology, 93*, 708-716.

Lindauer, M. *Communication among social bees.* Cambridge, MA: Harvard University Press.

Seeley, T. D. (1995). *The wisdom of the hive.* Cambridge, MA: Harvard University Press.

Steiniger, von F. (1950) *Beitrage zur Soziologie und sonstigen Biologie der Wanderratte. Zeitschrift fur Tierpsychologie, 7*, 356-370.

Von Frisch, K. (1967). *The dance language and orientation of bees.* Cambridge, MA: Belknap Press.

Wagner, W. E. (1998). Measuring female mating preferences. *Animal Behaviour, 55*, 1029-1041.

Ward, P. & Zahavi, A. (1973). The importance of certain assemblages of birds as 'information-centres' for food finding. *Ibis, 115*, 517-534.

White, D. J. & Galef, B. G., Jr. (1999a). Mate-choice copying and conspecific cueing in Japanese quail, *Coturnix coturnix japonica. Animal Behaviour, 57*, 465-473.

White, D. J. & Galef, B. G., Jr. (1999b). Social effects on mate choices of male Japanese quail, Coturnix japonica. *Animal Behaviour, 57*, 1005-1012.

White, D. J. & Galef, B. G., Jr. (in press). Affiliative preferences are stable and predict mate choices in both sexes of Japanese quail, *Coturnix japonica. Animal Behaviour.*

White, D. J. & Galef, B. G., Jr. (submitted) 'Culture' in quail: Social influences on mate choices of female *Coturnix japonica*