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Social Influences on Food Choices of Norway Rats and Mate Choices of Japanese Quail

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Here I review the two major lines of research in which my laboratory has been engaged for the past 35 years. The first of these research programs concerns the description and analysis of social learning processes influencing food choices of Norway rats (*Rattus norvegicus*). The second involves social interactions affecting mate choices of Japanese quail (*Coturnix japonica*). Study of these model systems has shown that at least two biologically important behaviors, food choice and mate choice, can be shaped by social interactions and that the social interactions that bias behavioral development are open to reductionist analysis in terms of the behavior of interacting individuals.

I have spent most of my 40 years as an experimental psychologist studying learning processes in animals. However, rather than study classical or operant conditioning, as have most others interested in animal learning, I have spent my time examining a few of the very many ways in which social interactions can bias acquisition of behavior in adaptive directions.

The reason for my interest in social learning is quite straightforward. Many of the things that animals, especially young animals living outside the laboratory, have to learn, they have to learn rapidly. A fledgling bird or weaning mammal, venturing from the site where it has been sustained and protected by adults of its species must learn to avoid predators before being eaten by one. It needs to learn to select a nutritionally balanced diet before it exhausts its internal reserves of any critical nutrient and without ingesting harmful quantities of toxins. It has to learn to find water before it becomes dehydrated. Naive young animals faced with such problems would be well advised to take advantage of opportunities provided by interaction with conspecific adults.

Adults, almost by definition, are individuals that have learned how to avoid predators, select appropriate substances to ingest, find water and harborage sites, etc. Most important, adults are occupying the environment where juve-

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niles with whom they interact are struggling to achieve independence. Consequently, to the extent that juveniles can make use of the behavior of adults to guide development of their own behavioral repertoires, juveniles may be able to acquire adaptive responses without going through all of the potentially costly process of independent trial-and-error learning (Galef, 1995). So, from a biological or ecological perspective, as well as from a psychological one, social learning would seem to be worth studying.

Social Influences on the Food Choices of Norway Rats

The feeding behavior of Norway rats (*Rattus norvegicus)* provides particularly appropriate material for investigations of social learning in animals. Free-living Norway rats are highly social animals. They live in colonies inhabiting fixed burrow systems from which colony members emerge to forage and to which they return between foraging bouts (Calhoun, 1962).

There are a number of theoretical arguments suggesting that members of social species that, like rats, forage from a fixed location (so-called central-place foraging species), can benefit from an exchange of information about locations where foods are to be found (e.g., Ward & Zahavi, 1973). For example, if one member of a rat colony discovers a new food, eats it and then returns to its burrow, other colony members might profit if they could extract information from the returning, successful forager that would facilitate their own exploitation of the new food (Galef & Beck, 1990).

My coworkers and I have explored a variety of social mechanisms each biasing the feeding behavior of young rats to make it congruent with that of their elders (for review, see Galef, 1976, 1996). I shall first describe very briefly five such social influences on the feeding behavior of juvenile rats, to indicate that such influences are quite complex, before discussing in greater detail a sixth mechanism for social learning about foods.

First, flavor cues that reflect the flavor of a lactating rat's diet are present in her milk and allow her suckling young to identify some of the foods that she ingests during the nursing period (Galef & Sherry, 1973). Experience of such food flavors in mothers' milk biases pups' food preferences at weaning so that weaning rats prefer foods with flavors that they have experienced in maternal milk (Galef & Clark, 1972; Galef & Henderson, 1972). Second, the simple physical presence of an adult rat, even an anesthetized one, at a potential feeding site induces hungry juveniles to approach that site and to begin eating whatever foods are to be found there (Galef & Clark, 1971a, 1971b).

Third, while eating, adult rats mark both foods and feeding sites they exploit with residual chemical cues, and marked foods and feeding sites are far more attractive to juveniles than are unmarked sites or foods (Galef & Beck, 1985; Galef & Heiber, 1976; Galef & Muskus, 1979). Fourth, adult rats lay scent trails as they travel from a feeding site back to their burrow, and juveniles follow trails adults have created leading to food (Galef & Buckley, 1996). Fifth and last, young rats that snatch some unfamiliar food from the mouth of a conspecific and eat it, as

young rats frequently do, subsequently prefer that food, whereas pups that take a similar sample of food from the ground and eat it do not (Galef, Marczinski, Murray, & Whiskin, 2001). The multiplicity of behavioral processes involved in rats' learning socially about foods and feeding sites is important because such redundancy in social-learning mechanisms suggests that, in rats, as in the honey bees von Frisch and his successors have studied for decades, social learning contributes significantly to foraging efficiency (von Frisch, 1967; Lindauer, 1961; Seeley, 1995).

In the studies that I shall describe in some detail, we used the method illustrated in Figure 1. The procedure was intended as a laboratory analogue of a natural situation in which a rat leaves its home burrow to forage, returns to its burrow and then interacts with a burrow mate. We wanted to know whether interaction between a returning, successful forager and a burrow mate taking place at a distance from a feeding site would influence the burrow mate's later feeding behavior.

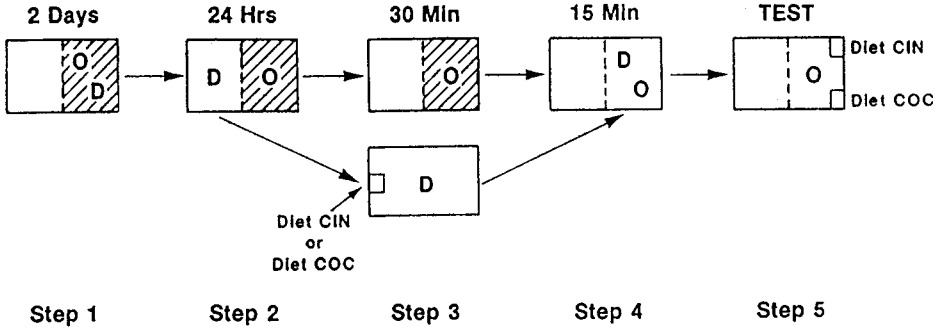

Figure 1. Schematic of procedure used to study social influence on diet choice in Norway rats. Diet Cin = cinnamon-flavored diet; Diet Coc = cocoa-flavored diet, D = demonstrator, O = observer. Hatching indicates that pellets of Purina chow were present. Reprinted by permission of the American Psychological Association.

As can be seen in Figure 1, during the experiment, subjects were housed and tested in pairs in cages divided in two equal parts by a screen. I shall refer to the members of pairs of subjects in all that follows as either "demonstrators" or "observers." I use the terms "demonstrator" and "observer" simply to distinguish one animal from the other. I intend no implication that the demonstrator is actively demonstrating or the observer observing. Indeed, our data suggest that demonstrators are essentially passive and observers extract information from their demonstrators much as they extract information from other aspects of the environment.

To allow demonstrators and observers to become familiar with both apparatus and pair-mate, we first left pairs together for 2 days with ad libitum access to Purina Laboratory Chow pellets (as indicated by the cross-hatching in Figure 1). In Step 2, we moved each demonstrator to the opposite side of the screen partition from its observer, and deprived the demonstrator of food for 24 h to ensure that the demonstrator would eat when we gave it access to food. At the end of the 24-h period of food deprivation of the demonstrator, and in preparation for testing of the observer, we removed all food from the observer's side of the cage. We then moved

the demonstrator to an enclosure in a room separate from the observer and fed the demonstrator, for 30 min, either cinnamon-flavored diet or cocoa-flavored diet. After the demonstrator had eaten for 30 min, we placed it in the observer's side of the cage, and allowed demonstrator and observer to interact for 15 min. Last, we removed the demonstrator from the experiment and, for 22 h, offered the observer two weighed food cups: one containing cinnamon-flavored diet and one containing cocoa-flavored diet. At the end of the observers' 22-h choice test, we simply weighed each food cup, and determined the percentage of each observer's total intake that was cocoa-flavored diet.

The results of this first experiment are presented in Figure 2. It shows the mean amount of cocoa-flavored diet, as a percentage of total amount eaten, ingested during the 22-h choice test by observer rats whose demonstrators had eaten either cocoa-flavored or cinnamon-flavored food while separated from their respective observers for 1/2 h (Step 3 in Figure 1). As can be seen in Figure 2, observer rats whose demonstrators had eaten cocoa-flavored diet ate a greater percentage of cocoa-flavored diet than did observer rats whose demonstrators had eaten cinnamon-flavored diet. The data presented in Figure 2 are sufficient to show that observer rats exhibit an increase in their relative intakes of foods that their respective demonstrators have eaten.

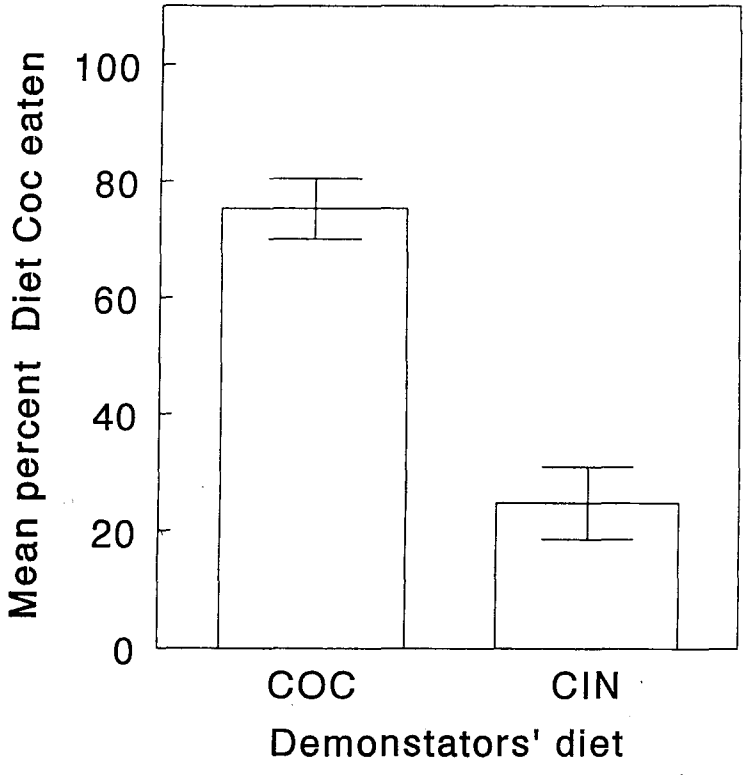

Figure 2. Mean (± SEM) amount of cocoa-flavored diet (Diet Co) eaten by observer rats that interacted with demonstrator rats fed either cinnamon- (Diet Cin) or cocoa-flavored diet as a percentage of total intake over 23 hr. Diet Cin = cinnamon-flavored diet. Reprinted by permission of the American Psychological Association.

One problem with many purported laboratory analogues of behavioral events presumed to occur in nature, is that the laboratory analogue is often not particularly robust. That is, often, an effect is to be observed in the laboratory under a fairly restricted set of parametric conditions. So it is important to demonstrate that transmission of information from demonstrator rats to observer rats concerning foods previously eaten by the demonstrators, is a robust phenomenon.

My students and I have repeated the basic experiment just described dozens of times with: (a) a variety of different diets, (b) wild rat demonstrators and observers as well as domesticated rat demonstrators and observers, (c) demonstrator-observer pairs familiar with one another and pairs that had never met prior to their interaction during Step 4 of the procedure (see Figure 1), (d) old demonstrators and observers and young ones, and (e) male demonstrator-observer pairs and female ones (Galef, Kennett, & Wigmore, 1984). In every case, we have seen a profound influence of demonstrator rats on their observers' later food choices. In fact, we have been unable to discover any circumstance where one might reasonably expect observers to extract information from demonstrators as to the diets those demonstrators have eaten, in which observers have not exhibited an enhanced preference for their respective demonstrators' diets. The phenomenon of demonstrator influence on observer diet preference seems to be a general one in rats, and for that matter, in mice (Valsecchi & Galef, 1989), Mongolian gerbils (Galef et al.,1998) and pine voles (Solomon, Yaeger, & Beeler, 2002) as well. It is not dependent on a restricted set of experimental parameters for its expression. So, observers can and extract information from observers concerning diets eaten by the demonstrators somewhere other than the place where information exchange occurs. How does an observer rat learn what food its demonstrator has eaten?

To look at the processes involved in information extraction by observer rats, we had to gain some control over the interaction of demonstrators and observers. We used a procedure very similar to that illustrated in Figure 1 except in one important respect. During the 15 min of interaction between demonstrator and observer (Step 4), they were separated by a screen partition. As can be seen in Figure 3, we found that separating demonstrator and observer with a screen while they interacted did not interfere in any way with communication between them (Galef & Wigmore, 1983).

We have developed several converging lines of evidence each consistent with the hypothesis that olfactory cues passing from demonstrator rats to their observers are sufficient to allow transmission of flavor preference to occur. First, as can be seen in Figure 3, an observer rat can extract information from a demonstrator, even if separated from that demonstrator by a screen barrier during their period of interaction. However, as can also be seen in Figure 3, communication between demonstrator and observer breaks down totally when they are separated by a transparent Plexiglas barrier rather than by a screen barrier. Obviously, some sort of non-visual contact, perhaps olfactory, gustatory, or acoustic, is needed if observer rats are to acquire information from their respective demonstrators.

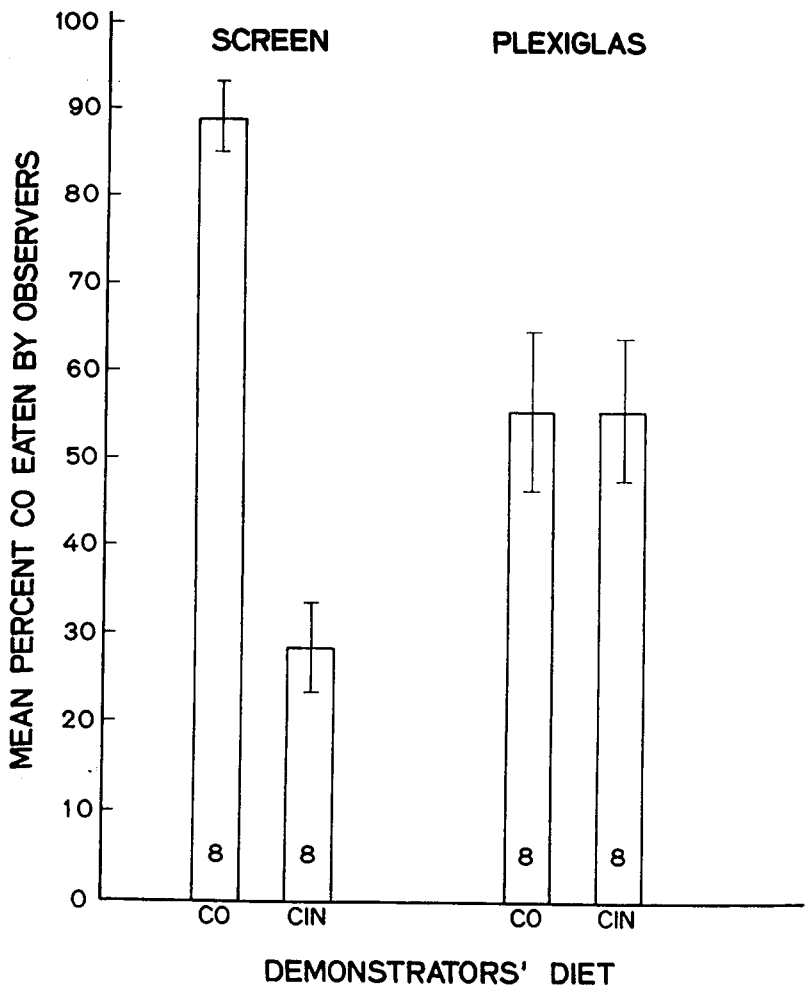

Figure 3. Mean (± SEM) amount of cocoa-flavored diet (Diet Co) eaten by observer rats that interacted with demonstrator rats fed either cinnamon- (Diet Cin) or cocoa-flavored diet as a percentage of total intake over 23 hr. Screen = subjects separated by hardware cloth; Plexiglas = subjects separated by a transparent Plexiglas barrier. Reprinted by permission of the American Psychological Association.

One line of evidence consistent with the view that olfactory cues are sufficient to transmit information from a demonstrator rat to its observer is as follows. If, after a demonstrator has eaten, and before it interacts with an observer, the demonstrator is anesthetized, taped to a Petri dish, and placed facing the screen partition with its nose 2 in from that screen, with an observer on the opposite side of the screen (so that no physical contact between demonstrator and observer is possible; Figure 4), the message still gets through. Observers still exhibit an enhanced preference for their respective demonstrators' diets (Galef & Wigmore, 1983).

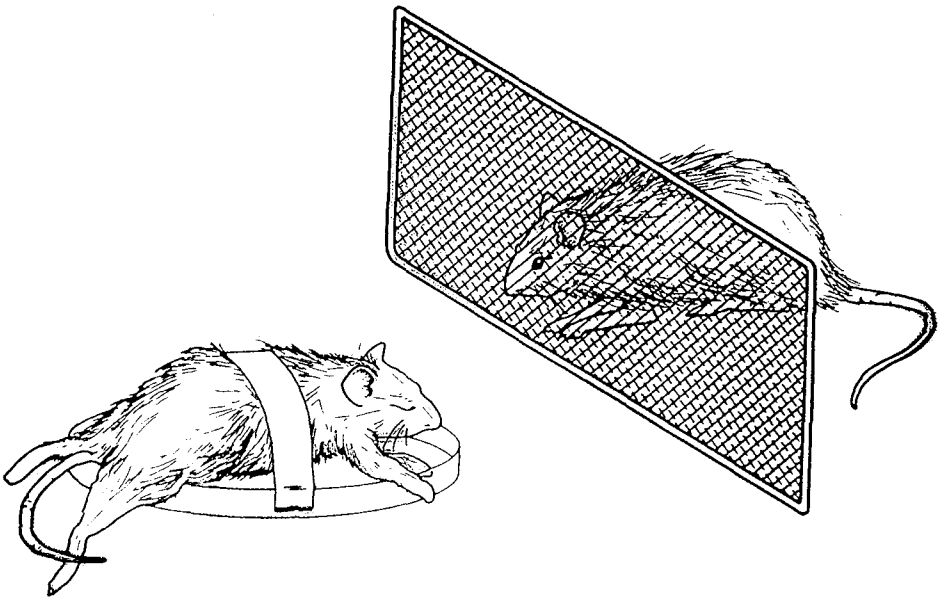

Figure 4. Illustration of anesthetized demonstrator rat taped to a Petri dish and placed 4 in from a screen barrier separating it from an observer rat.

Unconscious demonstrators can neither detect the presence of observers nor behave. Consequently, the finding that an unconscious demonstrator emits signals sufficient to affect its observer's food choices indicates that observers extract information from demonstrators; demonstrators don't actively communicate with observers (Galef, 1986; King, 1994).

In the present experiment, no physical contact between demonstrator and observer was possible, and obviously none was needed for observers to extract the necessary information from their demonstrators. As we know from the Plexiglas-barrier experiment, the important cue passing from demonstrator to observer is not visual, yet it can be transmitted over some distance. Hence, it is not gustatory. The important cue is emitted by unconscious rats, which rules out the auditory hypothesis. We are left with only olfactory cues to carry the message from demonstrator rats to their observers.

Second, if one renders an observer rat anosmic (i.e., unable to smell) before it interacts with its demonstrator, the observer fails to exhibit a preference for its demonstrator's diet during the 22-h test. Control observer rats (observers whose nasal passages had been rinsed with saline solution) showed a significant bias towards eating the same diet as had their respective demonstrators. Observers whose nasal passages had been rinsed with a zinc sulfate solution that produces a transient anosmia (Alberts & Galef, 1971), did not exhibit a preference for their respective observers' diets (Galef & Wigmore, 1983; Figure 5). So, sensitivity to olfactory cues is necessary for information transfer from demonstrator to observer to occur.

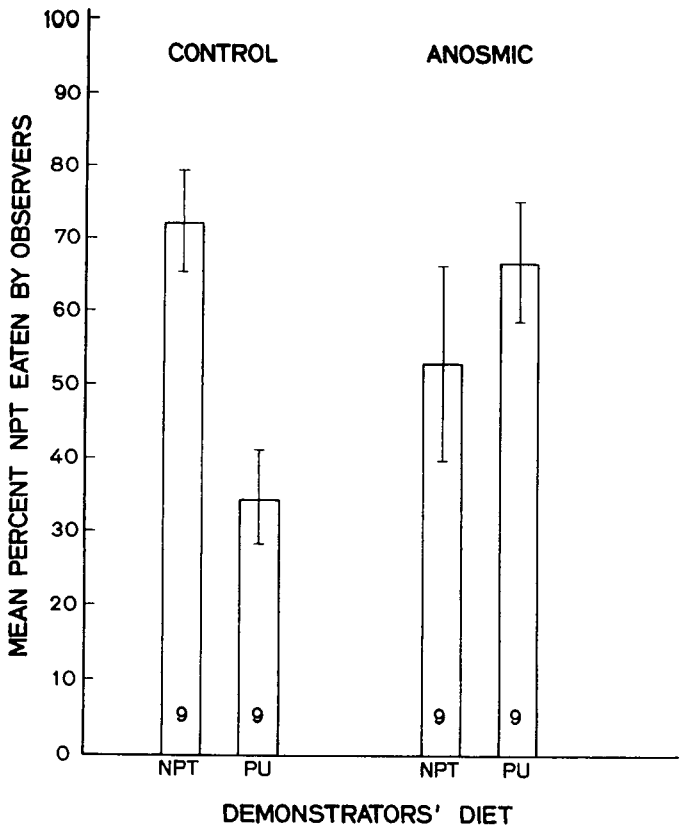

Figure 5. Mean (± SEM) amount of cocoa-flavored diet (Diet Co) eaten by observer rats that interacted with demonstrator rats fed either cinnamon- or cocoa-flavored diet as a percentage of total intake over 23 hr. Control = subjects whose nasal passages had been rinsed with saline solution. Anosmic = subjects whose nasal passages had been rinsed with zinc sulfate. Reprinted by permission of the American Psychological Association.

Last, but not least, not only rats but also humans can tell what diet a rat has been eating using olfactory cues emitted by recently fed rats. If you take a dozen rats and feed half of them cocoa-flavored diet and the rest cinnamon-flavored diet, then present all 12 rats to a human observer instructed to sniff the rats' breath, he or she can, with 85 to 90 percent accuracy, tell which rat has eaten which diet (Galef & Wigmore, 1983). We have not, however, noticed any craving for cinnamon- or cocoa-flavored rat diet in our human observers, which brings us to the next issue that needs to be addressed.

It is not, of course, too surprising to find that an observer, whether human or rodent, that 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 just eaten cinnamon- or cocoa-flavored food should suddenly exhibit enhancement of its tendency to eat whichever food its demonstrator has eaten.

Norway rats, particularly wild Norway rats, are often unwilling to eat unfamiliar foods (Barnett, 1958; Galef, 1971), and simple previous exposure to a food will, at least under some circumstances, substantially increase intake of it. If rats dislike unfamiliar foods, and if exposure to the smell of food particles clinging to a demonstrator rat increases familiarity of the observer rat with a food that its demonstrator has eaten, then we have a plausible explanation for the effect of demonstrator rats on observers rats' diet preferences. Observers might simply develop an enhanced preference for their respective demonstrators' diets as a result of simple exposure to the smell of the diet carried on a demonstrator. If so, the demonstrator would be acting simply as a passive carrier of food particles and food odors.

However, the results of a number of studies offer no support for the hypothesis that changes in observer rats' food preferences result from simple exposure of observers to the smell or taste of a diet (e.g., Galef 1989; Heyes & Durlach, 1990). For example, we gave one group of rats access to cinnamon-flavored diet and another access to cocoa-flavored diet for 30 min/day for 5 days while offering members of both groups a choice between cinnamon- and cocoa-flavored diets for the remaining 23.5 h of each day. As can be seen in Figure 6, we saw no effect of this 1/2-h, daily exposure to a diet on subjects' food choices. However, when 2 days later we gave the same rats 30 min/day to interact with demonstrator rats fed either cinnamon- or cocoa-flavored diet, we found massive effects on the observers' diet choices. The observers preferred to eat whichever food their respective demonstrators had eaten even though observers were thoroughly familiar with the taste and smell of both diets, having eaten both for a week (Galef, 1989; Figure 6).

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. So changes in observers' food preferences seem to require more than simple exposure to a diet; such changes seem to require exposure to food-related cues in the social context provided by the presence of a demonstrator.

If changes in observers' food preferences depend on exposure to food-related cues in a social context, we are left with two critical questions. First, what is the origin of the food-related olfactory cues emitted by demonstrators and detected by their observers that permit observer rats to identify the foods that their respective demonstrators have eaten? Second, what are social cues that make exposure to food-related cues effective in altering observers' food preferences?

The method we used to answer the first of these questions was similar to that used in the first experiment described above, except in how we exposed demonstrators to diets and in the conditions under which demonstrators and observers interacted (Galef, Kennett, & Stein, 1985; Galef & Stein, 1985). As shown in Figure 7, when a demonstrator and its observer interacted, the demonstrator was anesthetized and held in a wire-mesh tube inserted into a cardboard bucket. An observer was placed in the body of the bucket and allowed to interact with its demonstrator for 30 min.

We introduced demonstrator rats to foods in a number of different ways (see Figure 8). Demonstrators assigned to the Fed-demonstrator Group ate either cinnamon- or cocoa-flavored diet for 30 min. We then anesthetized the demonstra-

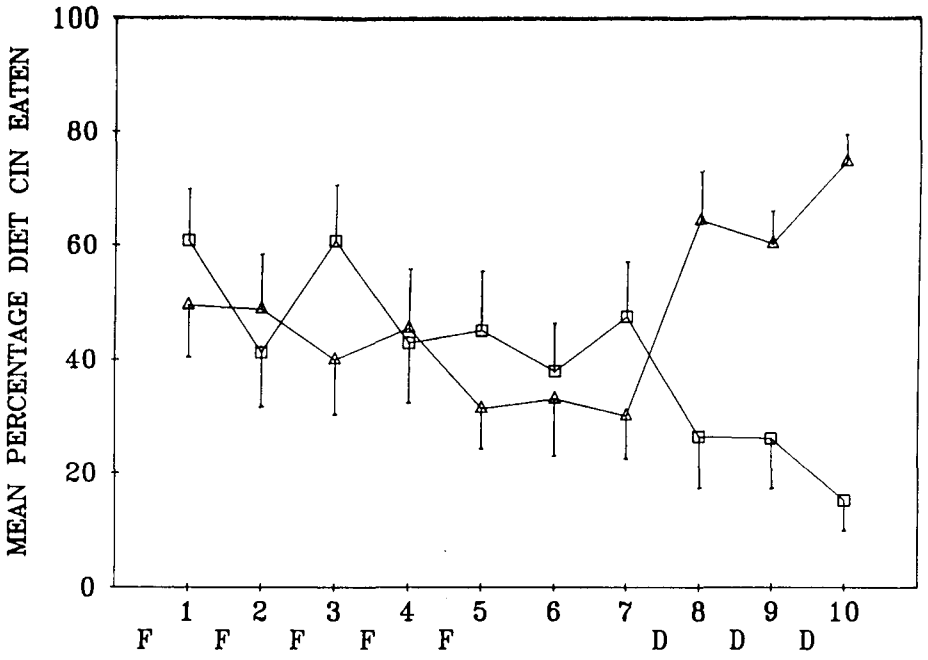

Figure 6. Mean (± SEM) amount of cinnamon-flavored diet (diet cin) eaten daily by observers first fed diet cin and then interacting with a demonstrator fed cocoa-flavored diet (diet coc) or first fed diet coc and then interacting with a demonstrator fed diet cin. F = 30 min exposure/day to a food cup containing either diet cin or diet coc. D = exposure for 30 min/day to a demonstrator rat fed either diet cin or diet coc. Reprinted by permission of Academic Press.

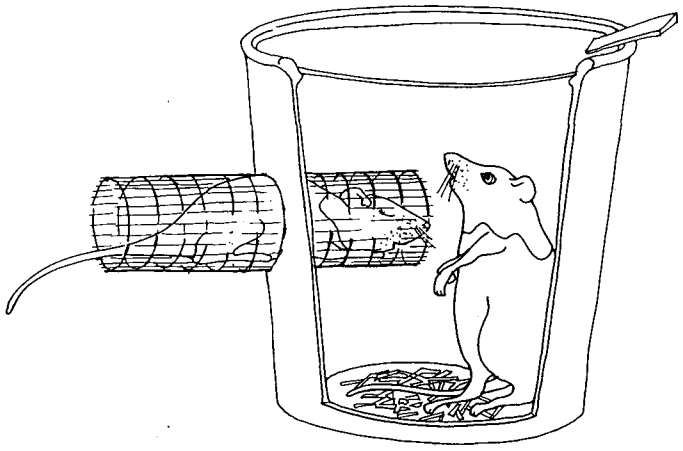

Figure 7. Illustration of apparatus used to examine the sorces of diet-identifying and contextual cues. Reprinted by permission of the Psychonomic Society.

Concordance in Diet Choice Between Demonstrator and Observer

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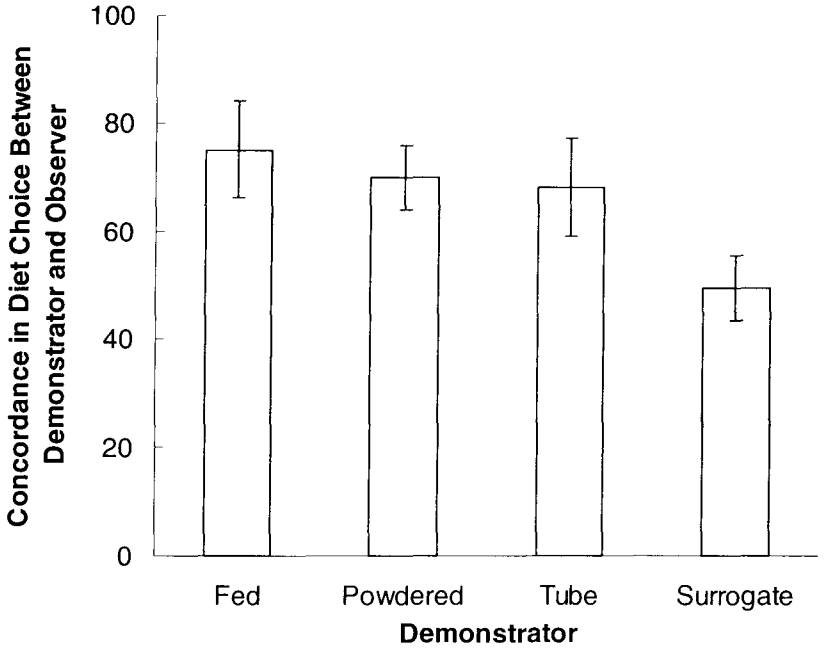

Figure 8. Mean (± SEM) concordance between demonstrator and observer rats in diet applied to demonstrator and diet eaten by observer. Dashed line indicates chance. See text for explanation of groups.

tors, and placed them in the wire-mesh tubes and placed the tubes in the buckets. We then placed an observer in each bucket, allowed observers to interact with their respective demonstrators for 30 min, and finally tested the observers individually in their home cages for 22 h for their preferences between cinnamon- and cocoa-flavored foods.

To facilitate comparison among the many groups in this experiment and the next one, I have presented the data in both Figures 8 and 9 in terms of the percentage of subjects' intake that was of the food associated with their respective demonstrators. So, if all observers in a group ate only the food associated with their respective demonstrators (i.e., if all observers with cinnamon demonstrators ate only cinnamon-flavored diet and all observers with a cocoa demonstrator ate only cocoa-flavored diet), the group would have received a score of 100. If, to the contrary, all observers in a group ate only the food not associated with their respective demonstrators, those observers would have received a score of 0, and if there was no influence of demonstrators on food choices of observers in a group, that group would have received a score of 50.

As shown in Figure 8, observers assigned to the Fed-demonstrator Group showed a preference for their respective demonstrators' diets. Clearly, our procedures did not interfere with social learning of a food preference.

We anesthetized demonstrators assigned to the Powdered-demonstrator Group, then rolled their faces in either cinnamon- or cocoa-flavored food, and then placed the powdered demonstrators in tubes. An observer was placed in the bucket, allowed to interact with a demonstrator for 30 min and then tested for its preference

between cinnamon- and cocoa-flavored foods. As is also shown in Figure 8, observers that interacted with a powdered demonstrator, like those assigned to the Fed-demonstrator Condition, showed a preference for whichever food had been placed on their demonstrators. So particles of food clinging to the fur and vibrissae of a rat can provide adequate diet-identifying cues to observers.

Demonstrators assigned to the Tube-fed Demonstrator Condition were first anesthetized and then stomach-loaded with 2 ml of either coffee- or vinegar-flavored solution (we used solutions rather than solid foods because of practical problems in force feeding solids to rats). Following stomach loading, we placed the anesthetized demonstrators in the tubes and the observers in the buckets, and allowed observers to interact with the tube-fed demonstrators before giving the observers a choice between coffee- and vinegar-flavored solutions. Once again observers exhibited a significant preference for their respective demonstrators' diets. So diet-identifying olfactory 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.

Last in Figure 8 are subjects assigned to the Surrogate-demonstrator Condition. Surrogate demonstrators were cotton-batting-stuffed, rat-sized lengths of surgical gauze one end of which we powdered with either cinnamon- or cocoa-flavored diet, then presented to observers in the tube inserted into the apparatus. Observers were again placed in the bucket and allowed to interact with surrogate demonstrators for 30 min. As can be seen in Figure 8, observers exposed to surrogate demonstrators did not show a preference for the diet with which we had powdered the surrogates. This last result simply reinforces the point that simple exposure to a diet does not enhance preference for that diet, whereas exposure to the same diet in the context provided by the presence of a conspecific demonstrator does enhance preference for a diet.

What are these contextual, social cues? Figure 9 provides some relevant information. We used as one baseline condition a group of Powdered-face Demonstrators that received exactly the same treatment as did Powdered Demonstrators in the last experiment. The demonstrators were anesthetized, their faces were rolled either in cinnamon- or in cocoa-flavored diet, and the demonstrators were then presented for 30 min to observers held in cardboard buckets. Observers assigned to the Surrogate-demonstrator Condition were treated exactly as were observers assigned to the surrogate demonstrator condition in the last experiment. They, like the members of the Powdered-face group, served as a baseline against which to evaluate the remaining two groups: Observers assigned to the Dead-powdered-face and Powdered-rear Conditions. Dead-powdered-face demonstrators were treated exactly as were powdered-face demonstrators except that dead-powdered-face demonstrators were sacrificed by anesthetic overdose, rather than simply anesthetized, before we placed them in the apparatus. We anesthetized demonstrators assigned to the Powdered-rear Condition, just as we had anesthetized demonstrators assigned to the Powdered-face Condition. However, we rolled the rear ends rather than the heads of demonstrators assigned to the Powdered-rear Condition in cinnamon- or cocoa-flavored diet before placing them in tubes with their rear-ends inside the bucket and their heads outside of it.

As can be seen in Figure 9, observers assigned to the Powdered-face Condition exhibited significantly greater influence of demonstrators on their food preferences than did observers assigned to either the Dead-Powdered-Face or Powdered-Rear Conditions. What all this tells us is that the most potent contextual or social cues, causing observers to prefer foods eaten by their demonstrators, emerge from the anterior of live rats.

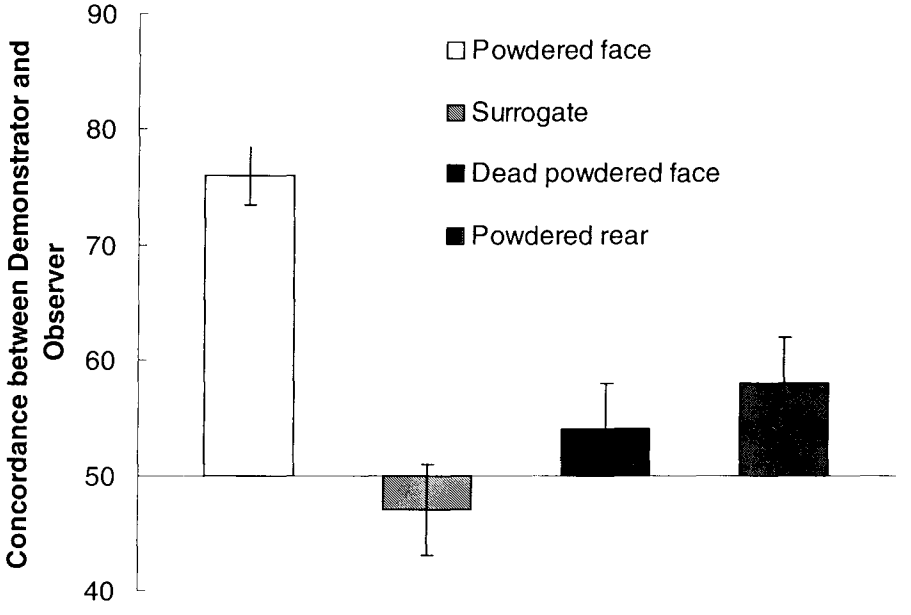

Figure 9. Mean (± SEM) concordance between demonstrator and observer rats in diet applied to demonstrator and diet eaten by observer. Dashed line indicates chance. See text for explanation of groups.

In thinking about possible differences between live, anesthetized rats, that emit very effective contextual cues, and recently sacrificed rats, that do not, it was obvious that one of the major differences between live and dead rats is that only live rats breathe. Similarly, the anterior end of a live rat emits rat breath, while their posterior end does not. So, it seemed reasonable to ask whether constituents of rat breath might provide the contextual or social cues that make diet-identifying cues emitted by demonstrator rats effective in altering their observers' food preferences.

Normally, rats breathe only through their noses, not though their mouths. Consequently, when the chemical contents of a sample of air taken from the nose of a rat and the chemical contents of a sample of air taken from the mouth of that rat are compared, any differences between the two samples should reveal the chemical components of rat breath. Results of mass spectrometry carried out in collaboration with the Monell Chemical Senses Center revealed carbon disulfide and carbonyl sulfide as important components of rat breath (Galef, Mason, Preti, & Bean, 1988).

As can be seen in Figure 10, adding a few drops of a dilute solution of carbon disulfide (a compound found in rat breath) to a surrogate rat powdered with food made that piece of cotton batting almost as effective as an anesthetized demonstrator rat in altering observers' food preferences. On the other hand, adding distilled water to a surrogate rat powdered with diet did not have a similar effect. Carbon disulfide appears to be an important component of the social context that allows demonstrator rats to alter the food preferences of their rat observers.

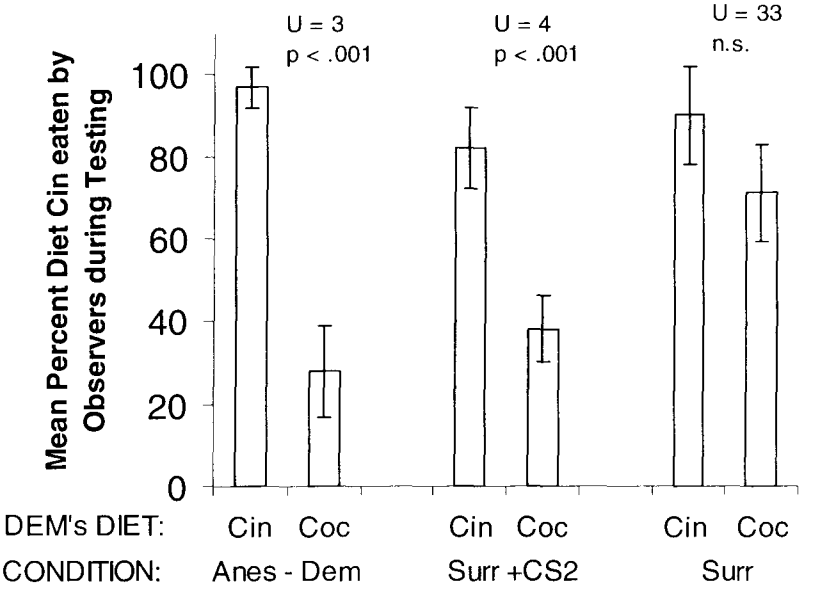

Figure 10. Mean (± SEM) amount of cinnamon-flavored diet (Diet Cin) eaten, as a percentage of total amount ingested, by observers that interacted with either an anesthetized demonstrator (Anes-Dem), a surrogate rat moistened with distilled water (Surr), or a surrogate rat moistened with dilute CS2 solution (Surr + CS_2). Reprinted by permission of Pergmon Press.

Human beings also have trace amounts of carbon disulfide on their breaths. Consequently, one might expect that, if the combination of a food odor and carbon disulfide suffices to produce a change in flavor preferences of rats, human demonstrators who eat a food and then breathe on a rat should increase the rat's preference for the food that its human demonstrators ate. In fact, rats with human demonstrators that ate cinnamon-flavored rat diet, preferred cinnamon-flavored rat diet; rats with human demonstrators that ate cocoa-flavored rat diet, preferred cocoa-flavored rat diet (Galef & Burton, 2002).

Social interactions are more than powerful determinants of food choice. Socially acquired information can also increase the probability of survival of individuals wise enough to exploit conspecifics as sources of information when selecting items to ingest. Like all young mammals, weaning rat pups face a life-threatening puzzle as their dam's milk supply gradually wanes and they must make the transi-

tion to solid food. To survive, weanling omnivores, such as rats, must learn to select a nutritionally adequate mix of foods from among myriad potential foods present in the environment, before their relatively limited internal reserves of various macro- and micro-nutrients are exhausted. As might be expected, a weanling rat trying to solve for itself the complex puzzle of selecting an appropriate diet to ingest can run into difficulties (Galef, 1991; Galef & Beck, 1990).

We placed young rats in enclosures where they were exposed for 24 h/day to four different foods (Beck & Galef, 1989; Galef, Beck, & Whiskin, 1991). Three of these four foods (cinnamon-, cocoa-, and thyme-flavored foods) were low in protein, one (nutmeg-flavored food) was protein rich.

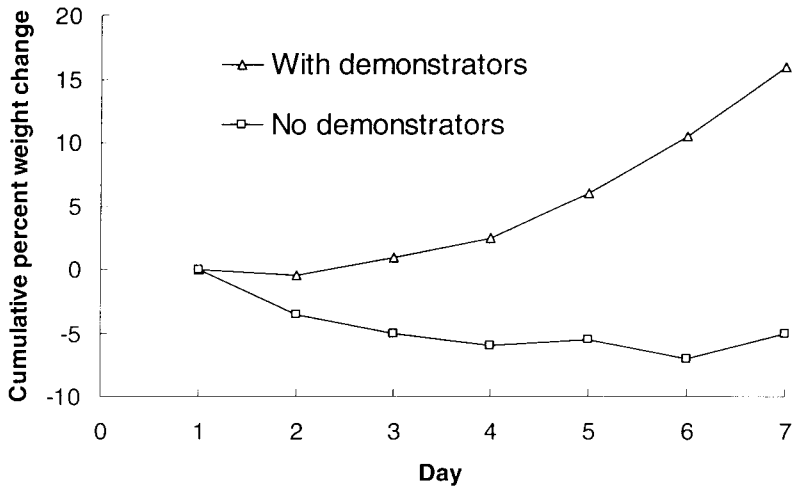

Figure 11. Mean cumulative percent weight change of weanling subjects during a week spent either in isolation or with a trained demonstrator in the apparatus illustrated in Figure 12. Reprinted by permission of the American Psychological Asssociation.

As can be seen in Figure 11, the isolated pups failed to solve even this fairly trivial puzzle and lost weight. Indeed, they would surely have died of protein deficiency, had we not terminated the experiment when we did. The second curve in Figure 11 shows the change in body weight of a second group of pups treated almost identically to the first group except that the pups in this second group each shared its enclosure with an adult rat trained to eat the protein-rich, nutmeg-flavored food. Pups with access to social information grew relatively normally. Clearly, there can be survival value in learning socially what food one's elders are eating.

Social Influences on the Mate Choices of Japanese Quail

It is not just the feeding behavior of animals that is open to social influence. Indeed, there is convincing evidence that other critical aspects of survival and reproduction, for example, predator avoidance (e.g. Curio, 1988; Mineka & Cook, 1988) and sexual behavior (Dugatkin, 1996; Galef & White, 2000) can be shaped in important ways by interactions with conspecifics.

Japanese quail, *Coturnix japonica*, the birds we have used as subjects in our studies of social influence on mate choice, are wonderful animals for laboratory investigations of sexual behavior. Mature individuals maintained on a long day-night cycle are willing to court and mate pretty much whenever given the opportunity to do so. Consequently, experiments can be conducted on factors affecting mate-choice in Japanese quail that would be impossible with most other avian and mammalian species.

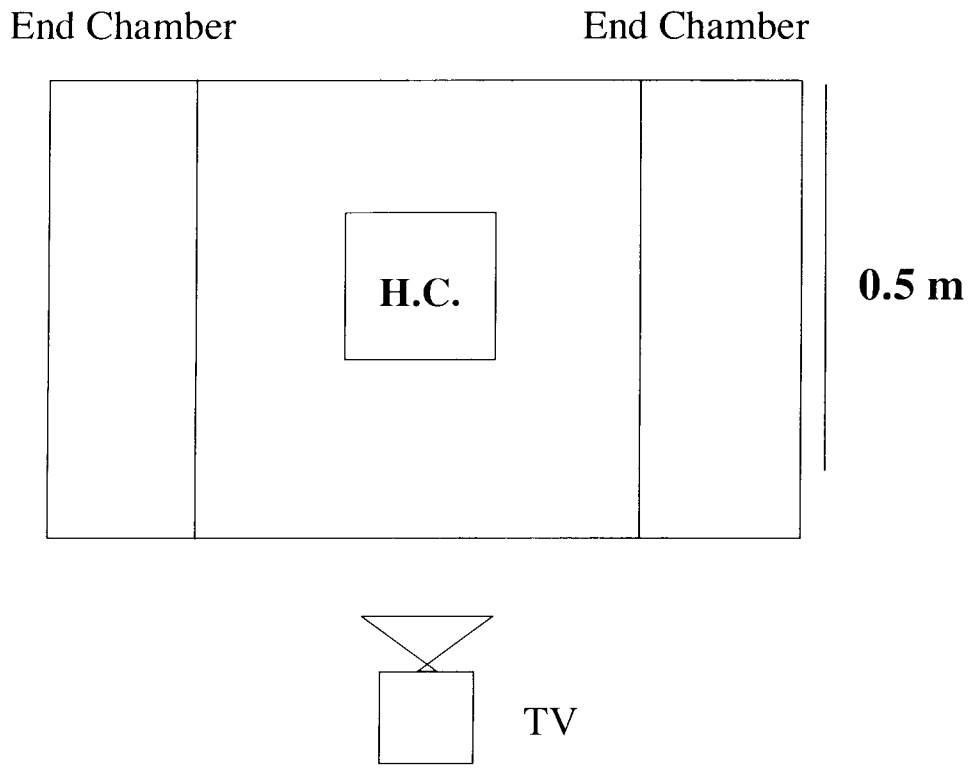

Figure 12. Overhead schematic of the apparatus used to study sociall influence on mate choice in Japanese quail. H.C. = holding cage; TV = television camera. Reprinted by permission of Academic Press.

The apparatus that we have used to look at mate choice is illustrated in Figure 12. It is simply a cage divided into three sections by two screen partitions.The central compartment of the apparatus contains a holding cage constructed of transparent Plexiglas that can be raised by a string and pulley arrangement that is operated from a room adjacent to that holding the apparatus. Raising the holding cage releases a restrained quail to move freely about the central compartment. Closed-circuit television allows us to watch the birds and to score their behavior without disturbing them.

Each of the first several experiments described below consisted of three 10-min phases. The first phase was a pretest that we used to determine a "focal" animal's preference between two members of the opposite sex that we call "target"

subjects. To begin a pretest, we confined a focal animal in the holding cage and placed one target subject in each of the two end compartments of the apparatus. We then raised the holding cage, allowing the focal animal to move freely about the central compartment. For the next 10 min, we recorded how much time the focal animal spent closer to each of the two target subjects.

The second phase of each experiment was an observation phase throughout which the focal animal was confined in the holding cage and given the opportunity to observe one target subject remain alone and the other target subject mate with

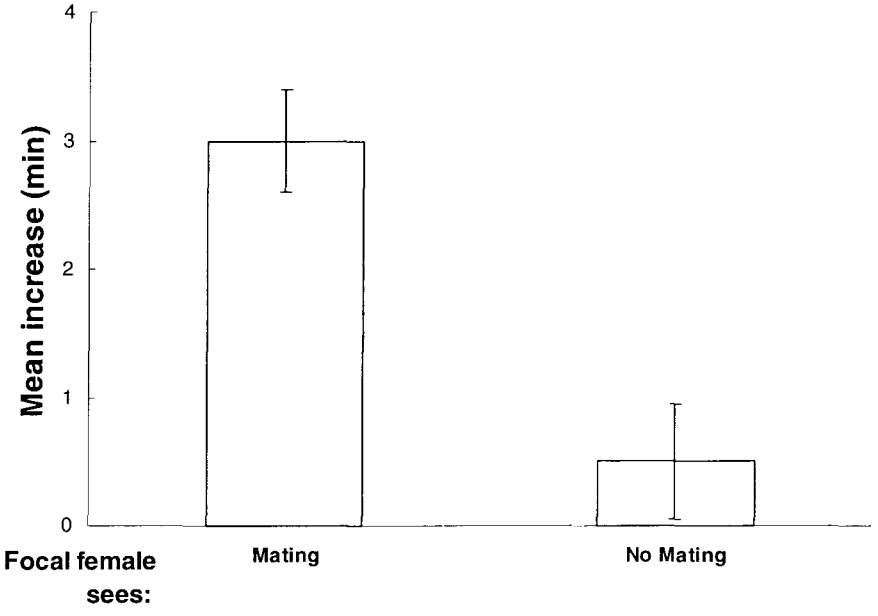

Figure 13. Mean (+ SEM) change from pre-test to post-test in time that focal females assigned to experimental and control conditions spent closer to a target male. Reprinted by permission of Academic Press.

what we call a "model" subject. (A model subject was another quail of the same sex as the focal subject.) The third and last phase of the experiment was a posttest during which the focal animal chose for a second time between the same two target subjects that it had chosen between during the pretest.

In our first experiment (Galef & White, 1998), we simply determined whether a focal female quail would show a change between pretest and posttest in the amount of time she spent closer to the target male that she had seen court and mate with a model female during the observation phase. During the observation phase, focal females that we had assigned to the Experimental Condition watched while one of their target males courted and mated with a model female. We treated focal females assigned to the Control Condition exactly as we treated focal females assigned to the Experimental Condition except that during the observation phase we did not place a model female with either target male.

As can be seen in Figure 13, females that had seen a target male court and mate with a model female during the observation phase showed a highly significant

increase between pretest and posttest in the time that they spent nearer to the target male that they had seen mating. Females in the Control Group showed no change between pretest and posttest in the time that they spent with target males.

We also compared the behavior of focal females that, during the observation phase of the experiment, either could or could not see the target male while he was courting and mating with a model female. In the latter case, during the observation phase, opaque walls blocked the focal female's view of both target males during the observation phase.

As in the preceding experiment, focal females that saw a target male court and mate showed a significant increase between pre-test and post-test in the time they spent with that target male. On the other hand, focal females that could not see target males while they courted and mated with model females during the observation phase, did not show any increase between pretest and posttest in time spent with males that had mated. We conclude that courting and mating per se do not change the subsequent behavior or appearance of target males so as to make them more attractive to focal females. Rather it is seeing a target male court and mate that increases his attractiveness to a focal female (Galef & White, 1998; White & Galef, 1999b).

We have also looked at effects on the mate choices of focal male quail of seeing target female quail mate. After all, if females like popular males, perhaps males would like popular females. The experiments (White & Galef, 1999c) were identical to those just described examining social effects on mate choices of females with two exceptions. First, when studying mate choices of males, during both pretest and posttest, we allowed focal males to choose between target females. Second, in these studies, we allowed each focal male to watch one of his target females mate with a model male during the observation phase.

As behavioral ecologists might have anticipated, the results with male focal subjects were exactly the opposite of those with female focal subjects (White & Galef, 1999c; Figure 14). After a focal male watched a target female mate with a model male during the observation phase, he spent significantly less time near her.

Once again, we found that mating does not change the behavior or appearance of females to make them less attractive to focal males. A male had to see a female engage in courtship and mating if her attractiveness to him was to change (White & Galef, 1999c).

I have been referring to mate choices of focal male and female quail I have provided data only on affiliative preferences of focal males and females, not on their actual choice of partner for copulation. It has become conventional in the literature on mate choice to equate affiliative preference with mate-choice, although that is not altogether satisfactory (Wagner, 1998).

We used tethered males to look at the correlation between affiliative preferences and choices of true sex partners (White & Galef, 1999a). We found an extraordinary correlation between the target male that a female chose to remain near during a test of affiliation and the target male with whom a target subject chose to copulate. We first allowed a focal female to chose between two target males for 10-min in a test of affiliative preference identical to the pretests in the experiments described above. We then permitted the same focal female to choose for 10 min be-

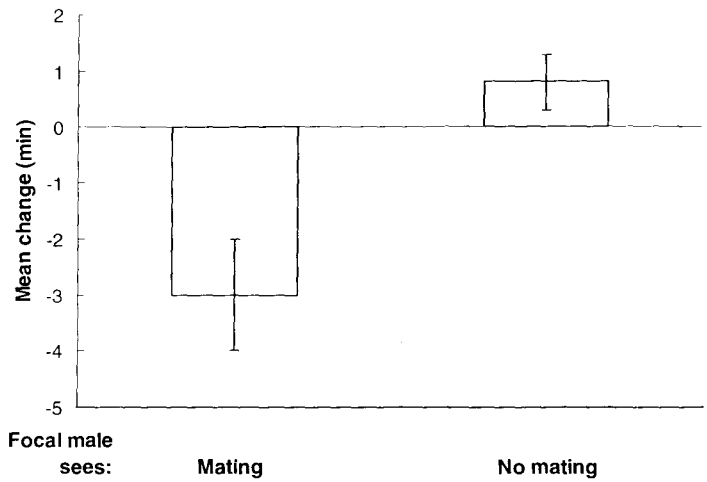

Figure 14. Mean (± SEM) change from pre-test to post-test in time that focal males assigned to experimental and control conditions spent closer to a target female. Reprinted by permission of Academic Press.

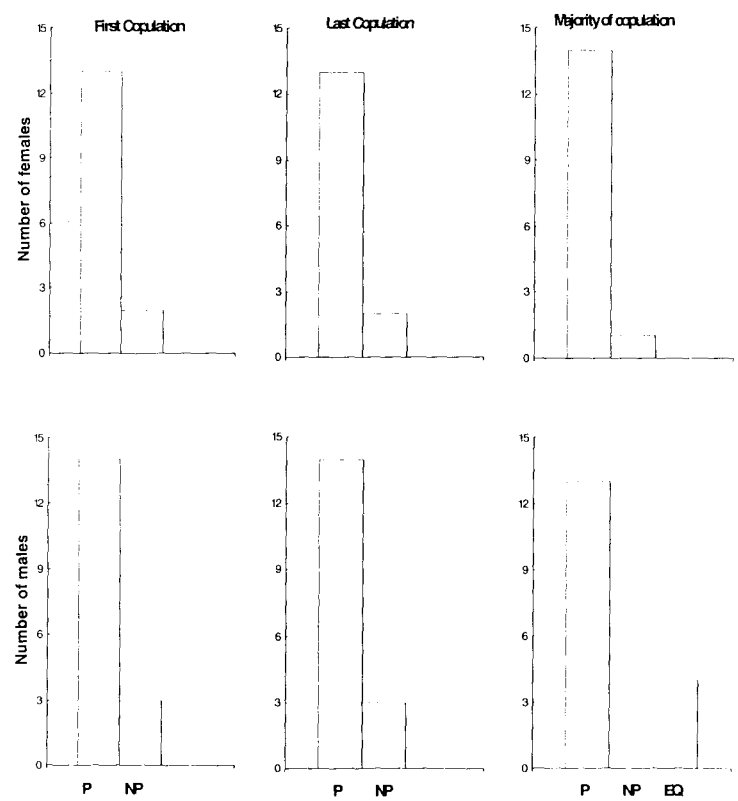

Figure 15. Number of focal females and focal males that copulated first, last, and more frequently with the tethered target male that they preferred (P) and did not prefer (NP) during a previous test of affiliative preference. Reprinted by permission of Academic Press.

tween the same two target males, now tethered at opposite ends of an alley as partners for copulation. Regardless of the measure of female mate choice (first male the female allowed to mate with her, last male the female allowed to mate with her, or male that a female allowed to mate with her more frequently), the target male a female preferred in the affiliation test was the male with whom she preferred to mate (White & Galef, 1999a; Figure 15). As can also be seen in Figure 15, males free to copulate with both target females from a 10-min test of affiliative preference, copulated more often with the target female they preferred during the test of affiliative preference (White & Galef, 1999a).

The main conclusions from this first set of experiments with Japanese quail are quite straightforward. First, females increase their tendency to stay near males they have seen court and mate (Galef & White, 1998). Second, males show a decrease in their tendency to stay near females that they have seen mate (White & Galef, 1999c). Third, in both sexes the partner preferred for affiliation and for mating are very highly correlated (White & Galef, 1999a).

Presumably, female quail increase their preferences for male quail they have seen copulating because some cost or probability of error is associated with choosing high quality males, and copying the mate choices of others either increases accuracy of choice or reduces costs of sampling (Gibson & Hooglund, 1992). Male quail, on the other hand, show decreased attraction to females seen mating presumably because a male is unlikely to fertilize the eggs of a female that has recently been inseminated by another. Indeed, evidence in the literature indicates consistently that for several hours after a female bird has mated with a male, copulations with other males are unlikely to fertilize her eggs. However, as time passes, the probability of a second partner fertilizing a female's eggs rises, and by roughly 24 h after copulating with a first male, the probability of a female's eggs being fertilized by a second male again approaches baseline (Birkhead, 1988; Birkhead & Fletcher, 1995; Birkhead & Moller, 1998).

Given the very different reasons why male and female birds are believed to attend to the mating histories of potential partners, it might be predicted that males' aversions to females seen mating would dissipate rapidly because, after 24 h, a female seen mating would be as good as new. On the other hand, females' enhanced preferences for males seen mating should last for a relatively long time; if a male is a better choice as partner on Tuesday, he should continue to be a better choice on Thursday. The experiments to test these predictions (White & Galef, 2000) were exactly like the first two experiments with quail described above with one exception. We introduced a 48-h delay between the observation phase, when a focal animal observed one of two target animals mate, and the posttest, when the focal animal chose for the second time between the same two target animals chosen between during the pretest.

The results were as predicted. As can be seen in Figure 16, females that saw a target male mate during the observation phase preferred him both immediately afterwards and 48 h later. Males who saw a target female mate did not like her immediately after seeing her mate, but 48 h later appeared to have forgotten about her previous affair. Not only do male and female quail respond in opposite

ways to seeing members of the opposite sex mate; they also seem to respond differently to that social information as a function of the time since it was acquired (White & Galef, 2000). We suggest that both the direction and duration of the responses of male and female Japanese quail to seeing a member of the opposite sex mate may reflect the action of adaptive, domain-specific, information-processing systems (Tooby & Cosmides, 1992).

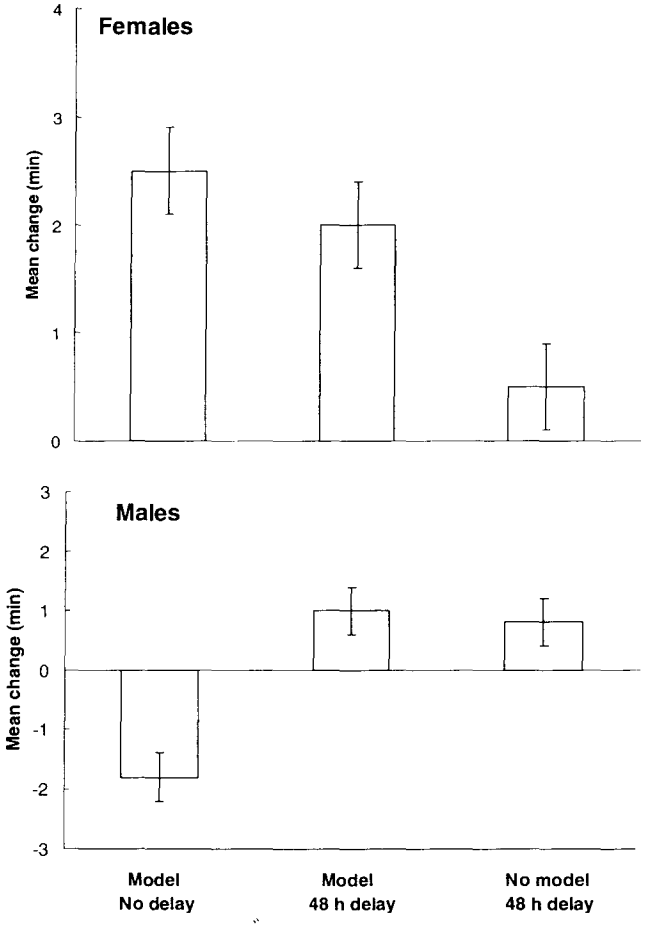

Figure 16. Mean (± SEM) change in time between pre-test and post-test that focal males and females assigned to no-delay, 48-hr delay and control conditions spent nearer to a target female. Reprinted by permission of Academic Press.

Of course, just because males and females change their responses to members of the opposite sex that they have actually observed court and mate, that does not mean that other kinds of social interaction do not have an impact on the distribution of mating success in quail. Previous researchers in the area of mate choice have discussed two general types of behavioral process either of which can result in the observed tendency of females to mate with the same partner thus producing considerable skew in the mating success of males: (1) mate-choice copying (defined

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