

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

**Bennett G. Galef, Jr.**  
*McMaster University*

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

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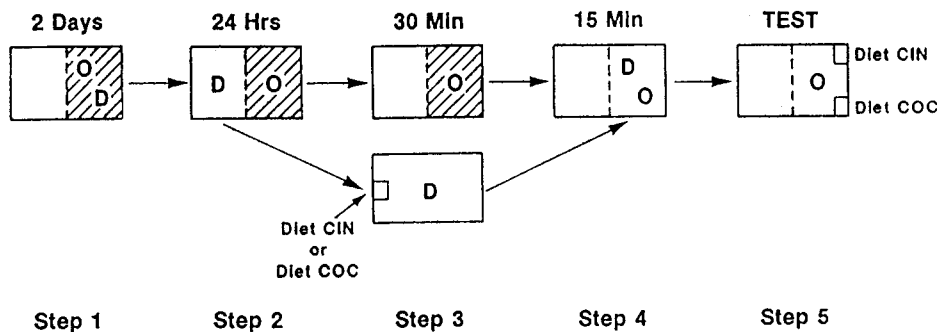
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young rats frequently do, subsequently prefer that food, whereas pups that take a similar sample of food from the ground and eat it do not (Galef, Marczinski, Murray, & Whiskin, 2001). The multiplicity of behavioral processes involved in rats' learning 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.



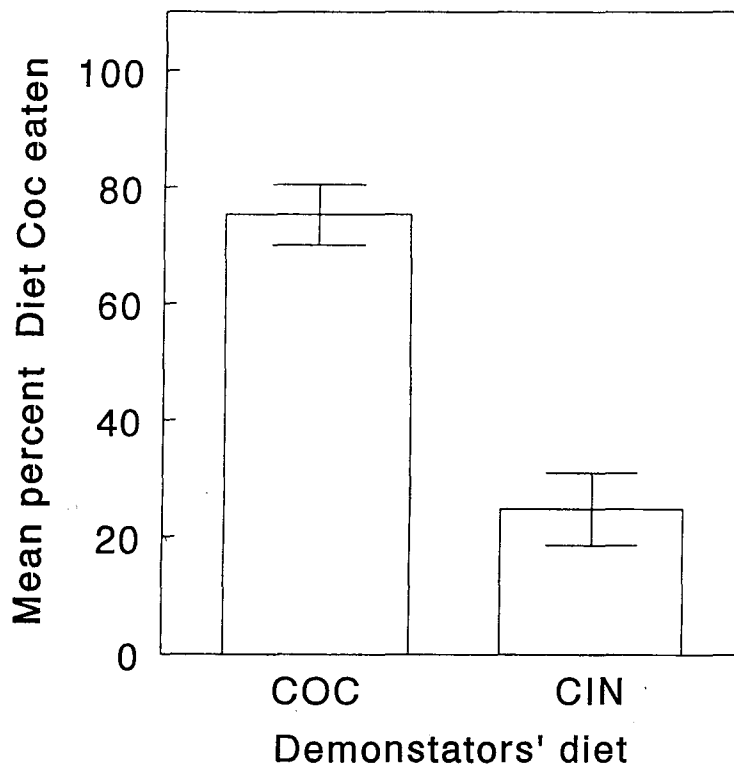
**Figure 1.** Schematic of procedure used to study social influence on diet choice in Norway rats. Diet Cin = cinnamon-flavored diet; Diet Coc = cocoa-flavored diet, D = demonstrator, O = observer. Hatching indicates that pellets of Purina chow were present. Reprinted by permission of the American Psychological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

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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.

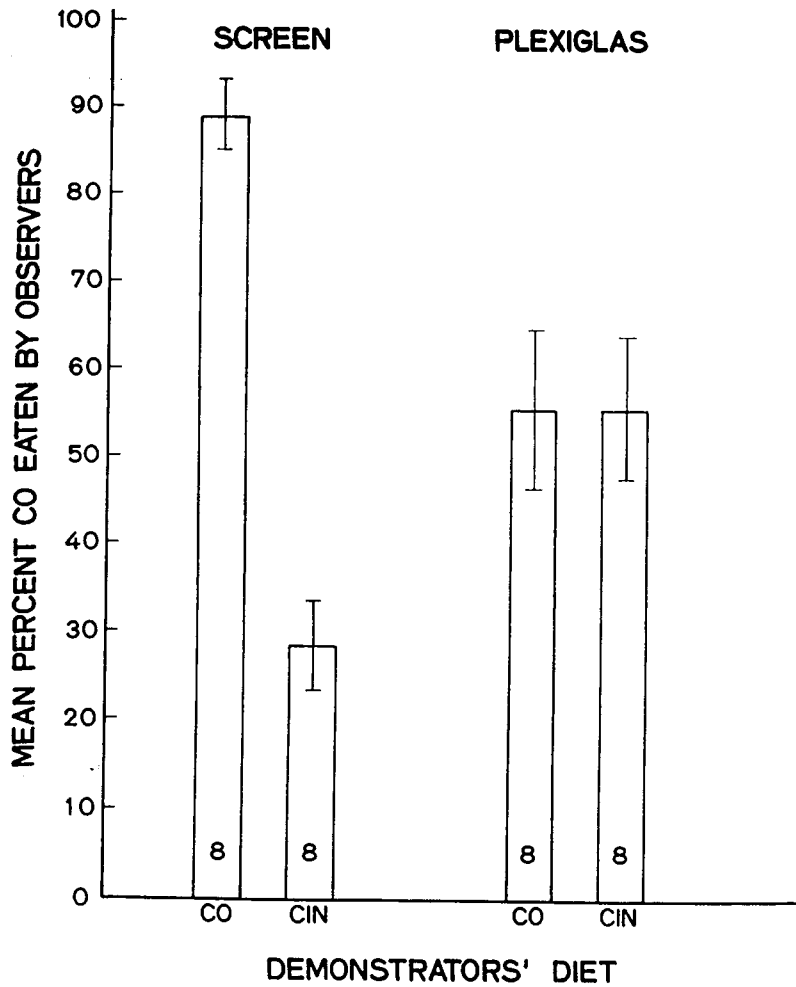


Figure 3. Mean ( $\pm$  SEM) amount of cocoa-flavored diet (Diet Co) eaten by observer rats that interacted with demonstrator rats fed either cinnamon- (Diet Cin) or cocoa-flavored diet as a percentage of total intake over 23 hr. Screen = subjects separated by hardware cloth; Plexiglas = subjects separated 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).

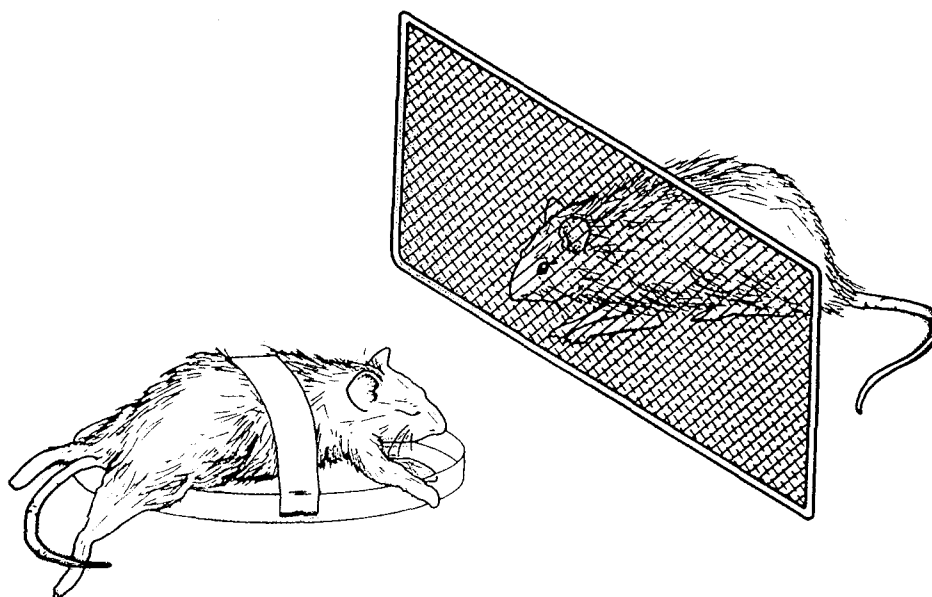


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**Figure 4.** Illustration of anesthetized demonstrator rat taped to a Petri dish and placed 4 in from a screen barrier separating it from an observer rat.

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.

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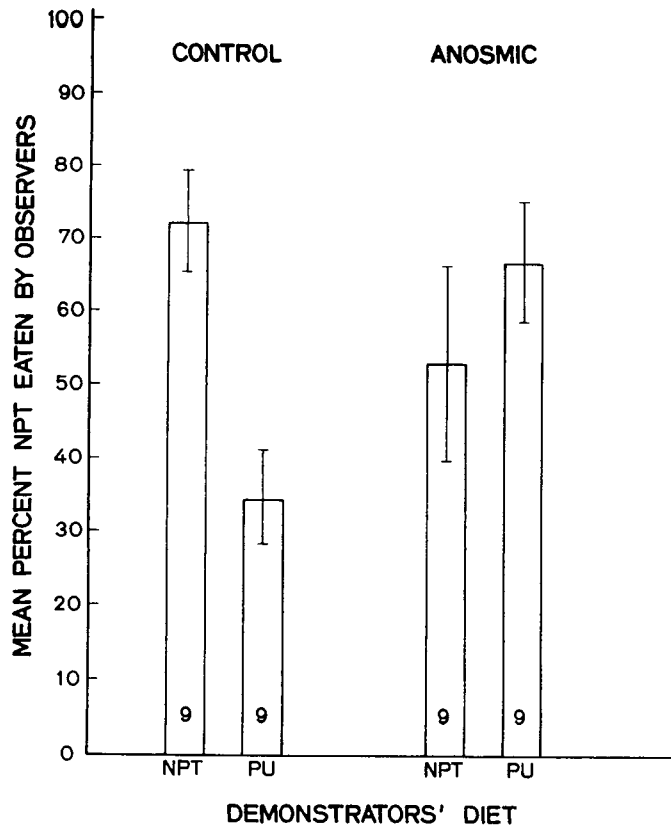


Figure 5. Mean ( $\pm$  SEM) amount of cocoa-flavored diet (Diet Co) eaten by observer rats that interacted with demonstrator rats fed either cinnamon- or cocoa-flavored diet as a percentage of total intake over 23 hr. Control = subjects whose nasal passages had been rinsed with saline solution. Anosmic = 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.

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