Rapid Communication

Social influences on food choices of Norway rats and mate choices of Japanese quail

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(Published electronically 30 July 2002)

My interest in social learning derives from the observation that much of what an animal living outside the laboratory needs to learn, it needs to learn rapidly. A fledgling bird or weanling mammal venturing from the site where it has been sustained by conspecific adults has to learn to avoid predators before being eaten by one. It has to learn to select a nutritionally balanced diet before it exhausts its internal reserves of any critical nutrients and without ingesting harmful amounts of toxins.

A young animal faced with such challenges would be well advised to take advantage of interactions with conspecific adults. To have survived, an adult must have learned to respond adequately to each of the challenges posed by its environment, and adults with whom a juvenile interacts will have overcome challenges in the same environment where the juvenile is struggling to achieve independence. To the extent that juveniles can use the behavior of adults to guide their own behavioral development, juveniles should be able to reduce the costs of independent learning by trial and error (Galef, 1995).

My students and I have studied social influences on food choice in Norway rats (*Rattus norvegicus*) as a model system to investigate the complexities of social biasing of behavioral development. Norway rats are colonial animals that, in natural environments, inhabit burrows from which they emerge to forage and to which they return between foraging bouts. Theoretical treatments suggest that members of social species that forage from a central place, as do Norway rats, should profit from exchange of information about availability of foods in the larger environment (Ward & Zahavi, 1973). For example, when one member of a rat colony discovers a new food, eats it, and then returns to its burrow, other colony members could extract information from the returning forager facilitating their own subsequent identification and location of the new food.

My students and I discovered some years ago that when we fed a "demonstrator" rat a distinctive food, and then let it interact with a naive "observer" rat, the observer subsequently exhibited an enhanced preference for whatever food its demonstrator had eaten (Galef & Wigmore, 1983). We have repeated this basic experiment many times using as subjects, wild and domesticated rats, old rats and young, male rats and female, rats familiar with or related to one another and rats both unfamiliar and unrelated. In every case, we have seen the profound effects of foods fed to demonstrators on observers' later food preferences (Galef et al., 1984). In fact, we have not discovered any circumstance where observer rats might reasonably be expected to acquire information from demonstrators as to foods that the demonstrators have eaten where observers have not exhibited enhanced preferences for their demonstrators' foods. Such socially induced changes in food preference are long lasting and powerful, able to reverse both learned flavor aversions and food preferences based on inherent palatability (Galef, 1989).

Our analyses of how information is communicated from demonstrators to observers indicate that olfactory cues emitted by demonstrators as a result of processes involved in normal ingestion and digestion carry the message from demonstrators to observers (Galef & Wigmore, 1983). Observers can identify foods from smelling either food particles on the fur of recently fed demonstrators or food-related odors escaping from their gastrointestinal tracts (Galef & Stein, 1985). When these food-related odors are experienced in the context provided by a living demonstrator rat, an observer rat exhibits enhanced preferences for foods its demonstrator ate.

Using mass spectrometry, we identified the compounds on rat breath. We found that after rats experienced the smell of a food together with carbon disulfide, a compound found in rat breath, they increased their preference for a food, just as they did after simultaneous exposure to a food odor and demonstrator rat (Galef *et al.*, 1988).

Based on a presentation to the Columbia University Seminar on Appetitive Behavior, March 14, 2002, Harry R. Kissileff, Chairman, supported in part by Merck Research Laboratories, GlaxcSmithKlink and The New York Obesity Research Center, St. Luke's/Roosevelt Hospital. E-mail: galef@mcmaster.ca

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Such socially induced food preferences can have important consequences. For example, when we offered weaning rats a choice, 24-h/day, among four different foods only one of which had sufficient protein for normal growth, the weanlings did not eat sufficient protein-rich diet to survive. However, when we offered weanlings the same choice together with adult rats trained to eat the protein-rich food, the young thrived (Beck & Galef, 1989). Thus, social learning about food allowed animals to survive in an environment otherwise closed to them.

It is not only feeding behaviors of animals that are open to important social influences. Other critical aspects of survival and reproduction, from predator avoidance (Cook *et al.*, 1987) to sexual behavior (Dugatkin, 1992), can be shaped by social interactions.

For several years, my laboratory has explored effects of observation of mating behavior of others on mate preferences of male and female Japanese quail. We have found that "focal" female Japanese quail are more likely to affiliate with a "target" male conspecific after seeing him court and mate with a "model" female (Galef & White, 1998). On the other hand, focal male Japanese quail avoid target females seen courting and mating with a model male (White & Galef, 1999b).

These changes in attractiveness of members of the other sex that a focal animal has seen mating do not result from changes in appearance of animals that have mated. Rather, focal animals must actually see potential partners mate to show a change in tendency to affiliate with individuals that have mated (Galef & White, 1998; White & Galef, 1999b). Members of both sexes prefer to mate with those with whom they prefer to affiliate, so changes in affiliative preference are of biological importance (White & Galef, 1999a).

Males should avoid mating with a recently mated female because she is temporarily infertile (Birkhead & Moller, 1998). Females should copy mate choices of other females, because mate-choice copying reduces the cost of mate selection (Gibson & Hooglund, 1992). If such assertions are correct, as theoreticians assure us they are, then aversions of focal male quail to target females seen mating should be transitory, whereas the preferences focal female quails show for target males seen mating should be long lasting. After less than 24 h, a mated female is as fertilizable as she ever was, whereas a male who was a good choice one day should be again, unless a superior potential partner is available.

In fact, 48 h after a focal male quail sees a target female mate, he shows enhanced preference for, not aversion, to her, whereas socially learned preferences of focal female quail for target males seen mating persist over days (White & Galef, 2000b). Such differences in direction and duration of response of male and female quail to seeing a member of the other sex mate may reflect adaptive, domain-specific information processing systems (Cosmides & Tooby, 1995).

Social effects on female mate choice can affect evolution of male secondary sexual characteristics only if females that have seen a male mate are subsequently more likely to mate not only with a male seen mating, but also with other males sharing his characteristics (Brooks, 1998). In fact, female quail that see a visually distinct male mate prefer to affiliate with other males sharing his distinctive characteristics (White & Galef, 2000a), suggesting that gene–culture interactions may play a role in evolution of sexually dimorphic features.

The take-home messages from such research are quite simple. First, whether you are interested in feeding, sex, predator avoidance or, I suspect, any other behavior that is important for survival and reproduction, information acquired from conspecifics is potentially useful. Second, these social influences on behavioral development are open to empirical analysis in laboratory settings.

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