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During the past decade, researchers working in a variety of subdisciplines within anthropology, psychology, and biology have made substantial progress in their study of imitative and nonimitative forms of social learning in animals. Nonimitative social learning is now known to play an important role in reproduction, food acquisition, and predator avoidance in a range of vertebrate species. Evidence is also available that not only great apes but also some birds and nonprimate mammals can learn by imitation.

Social Learning and Imitation

Why Study Social Learning?

Most scientists who study animal social learning are interested in one of two quite different issues. Primatologists and psychologists frequently want to know whether nonhuman animals are able to imitate behaviors that they have seen others perform. For these researchers, situations in which one animal can learn to do an act simply by watching another animal perform that act provide exciting opportunities to explore the cognitive abilities of species other than our own. Other researchers, those whose work on social learning in animals reflects a general interest in behavioral ecology, usually study social learning to understand how information acquired from others contributes to the development of adaptive patterns of behavior in free-living ani-

mals. These researchers are interested in social interactions that direct behavior in profitable directions regardless of whether imitation or some nonimitative social learning process that is less cognitively demanding than imitation is believed to support transmission of behavior from one animal to another. Both approaches to the study of social learning are useful, and both have venerable histories in the life sciences.

Since the end of the nineteenth century, there have been many attempts to define different types of social learning and to categorize instances of social learning in terms of the learning process on which each depends. Sometimes social learning seems to involve true imitation (learning to do a particular motor act from seeing it done), whereas other times it appears to rest on emulation (learning what is re-

quired for success in a task by watching a model perform, but not learning about the model's behavior per se; Tomasello, 1996), local enhancement ("apparent imitation resulting from directing the animal's attention to a particular object or part of the environment"; Thorpe, 1963, p. 134), or some other carefully defined behavioral process (Galef, 1988b; Whiten and Ham, 1992). Different types of social learning are believed to require different degrees of cognitive sophistication, so the question of what type of social learning is involved in the transmission of behavior from one individual to another has potentially important implications for our understanding of the cognitive abilities of animals.

Historically, the most important distinction, and the only one I make in this article, involves determining whether, in any particular case, an observer learns directly about the behavior of its model. In the various kinds of nonimitative social learning, an animal that watches another animal behave and sees the outcome of the behavior in which the actor engages learns something useful about either which parts of the environment are potentially important or what changes in the environment are caused by the actor's behavior (Heyes, 1996; Tomasello, 1996). Therefore, for example, if one chimpanzee were to watch another hunting grubs by turning over logs using its left hand to flip the logs end over end, the observing chimp might learn (i) that logs are interesting objects (learning about the environment), (ii) that food is revealed when the undersides of logs are exposed (learning about changes in the environment that the behavior causes), or (iii) that putting one's left hand under the end of a log and moving that hand rapidly upward is rewarded with food (learning about the actor's behavior). Only the last kind of learning, in which the observing chimpanzee learns directly about the behavior of the acting chimpanzee, would involve true imitation as imitation is currently defined (Heyes, 1996; Tomasello, 1996). Such "true" imitative learning seems to require that an animal or human first store a visual representation of the pattern of movement exhibited by another. Then, because the imitator rarely sees its own movements in a way that would allow it to match the sight of its limbs moving to the stored visual representation of the act to be imitated, the imitator must use its proprioceptive or kinesthetic senses to match its own movements to the stored visual representation. Such cross-modality matching is believed to be a cognitively demanding task that distinguishes true imitative learning from other possibly less complex, nonimitative forms of social learning.

Nonimitative Social Learning

Perhaps the simplest way to introduce outsiders to recent advances in the study of nonimitative social learning is to

briefly describe a selection of recent analyses of socially learned behaviors with potential to contribute to survival or reproductive success. I chose the examples discussed here to indicate both the range of behaviors affected by non-imitative forms of social learning and the very different ways in which information acquired from others can facilitate acquisition of adaptive patterns of behavior.

Learning What to Eat: Food Selection and Poison Avoidance by Norway Rats

Decades ago, an applied ecologist trying to increase the efficiency with which rodent pests could be controlled discovered that when he repeatedly offered a single poison bait to any population of rats (*Rattus norvegicus*), his efforts at control failed dismally. Although there was a decline in rat numbers immediately after he introduced a poison bait into an area, target populations repeatedly exposed to the same bait soon recovered their original size. The reasons for failure when using a single bait repeatedly in the same area were fairly straightforward.

First, although most rats ate a lethal dose of a toxic bait shortly after it was first introduced into their colony's territory, a few members of most colonies ate only a small amount of bait the first time they tasted it, became ill, but did not perish. These surviving rats learned in a single trial to associate the taste of the bait with its ill effects, and they would eat no more of it.

Second, and even more discouraging for efforts to improve the economics of pest control, young rats that came of age in colonies whose members were survivors of a first encounter with a poison bait also totally rejected the bait that the members of their colony had learned to avoid. They would eat only foods that survivors were eating. Somehow, the poison avoidance learned by survivors was being transmitted to the young of their colony.

Such socially learned avoidance of poison bait by weaning rats is a robust phenomenon and is easy to capture in the laboratory (Galef, 1988a). Consequently, it has proven possible to explore in-depth the social learning processes that result in transmission of food choices from adult rats to juveniles of their species.

Potential Prenatal Influences on Flavor Preference

Even before birth, a young rat can acquire information from its female parent about at least some of the foods that she is eating. Hepper (1988) fed garlic to pregnant rats late in gestation. An hour or less after litters were delivered by these garlic-fed mothers, Hepper gave the young to foster mothers that had never eaten garlic to rear. When the foster-reared pups were 12 days old and still ingesting only mother's milk, Hepper offered them a choice between two dishes, one containing garlic and the other onion. He found that pups that had been gestated by mothers that ate garlic while pregnant stayed near the dish containing garlic, whereas pups gestated by mothers that had not eaten any garlic during pregnancy did not prefer garlic to onion.

Flavor Cues in Mothers' Milk Flavors of foods that a rat eats while lactating can affect the flavor of her milk, and exposure to flavored milk affects the food preferences of rat pups as they wean. For example, weaning rat pups preferred the food eaten by a lactating female from whom they had suckled for several hours but did not prefer the same food after they interacted for the same length of time with a female that ate the same food and acted maternally toward the pups but did not give milk (Galef, 1977).

Effects during Weaning Galef and Clark used closed-circuit television and time-lapse video recordings to observe nine wild rat pups from three litters take their very first meals of solid food. All nine pups were observed to eat for the first time in exactly the same circumstances: Each ate at a site at which an adult was eating, and none ate at a nearby site at which no adult was present. Apparently, the physical presence of an adult rat at a feeding site made that site attractive to young rats and markedly increased the probability that they would wean to whatever food was to be found there (Galef, 1977). Indeed, simply anesthetizing an adult rat and placing it, while unconscious, near a feeding site made that site significantly more attractive to weaning rats than alternative locations that had no rat near them.

However, adult rats need not be physically present at a feeding site to guide their young to it. While eating, adult rats deposit residual olfactory cues in the vicinity of a food source, on any food they eat, and on the path they take when leaving a feeding site and returning home. All these odorants are attractive to young rats and cause them to approach and prefer feeding sites that adults have been using (Galef, 1977).

Effects after Weaning Galef and his students also found that after a young rat (an observer rat) interacts for a few minutes with a recently fed conspecific (a demonstrator rat), the observer exhibits a substantial increase in its preference for whatever food its demonstrator ate (Galef, 1988a, 1996). Exploration of the processes responsible for development of this socially induced preference in observer rats began with the finding that when observer rats were exposed to anesthetized demonstrator rats whose heads had been lightly dusted with particles of food (Fig. 1), the observer rats increased their preference for the food that they found on their respective demonstrators' heads. On the other hand, observer rats identically exposed to pieces of cotton wool dusted with food failed to develop a preference for that food (Galef, 1988a). Clearly, something about the presence of a demonstrator rat together with a food causes observer rats to alter their food preferences.

Experiments to discover the stimuli emitted by demonstrator rats that cause observer rats to increase their preference for foods associated with a demonstrator have shown that exposure to a constituent of rats' breath, carbon disulfide, and a food causes rats to increase their preference for the food, just as experience of a food together with a breathing rat increases preference for it (Galef, 1996).



FIGURE 1 An observer rat interacts with an anesthetized demonstrator rat whose head has been dusted with food (adapted from Galef and Stein, 1985).

Learning How to Eat: Exploitation of Pinecones by Roof Rats

The pine forests of Israel are inhabited by colonies of roof rats (*Rattus rattus*) that live on a diet consisting almost entirely of pine seeds and water (Terkel, 1995). Extraction of seeds from pinecones is a stable tradition in these rat colonies, permitting them to survive in areas in which pine seeds are the only food present in sufficient quantity to support a population of mammals.

Laboratory observations of the feeding behavior of rats taken from colonies living in pine forests have shown that the feeding method that allows rats to recover more energy from pine seeds than they spend in removing the tough, non-nutritious scales from pinecones requires that the rats take advantage of the structure of pinecones. The scales at the base of a cone must be removed first. Then the spiral of scales circling the cone's shaft to its apex must be removed in succession (Fig. 2).

Observation in captivity of rats taken from areas other than pine forests and offered pinecones to eat revealed that only 6 of 222 hungry, adult rats learned to use the spiral pattern of scale removal that permits a net energy gain from eating pine seeds. On the other hand, essentially all young rats reared by dams that efficiently stripped seeds from cones acquired the profitable technique. Apparently, some aspect of the interaction between mothers that strip seeds from pinecones and the young they rear is important in transmission of the efficient technique from one generation of rats to the next.

Further experiments demonstrated that experience of young rats in completing the stripping of scales from cones that had been started in the proper fashion by an adult rat (Fig. 3) allowed more than 70% of young rats to learn the efficient method of attacking cones (Terkel, 1995).

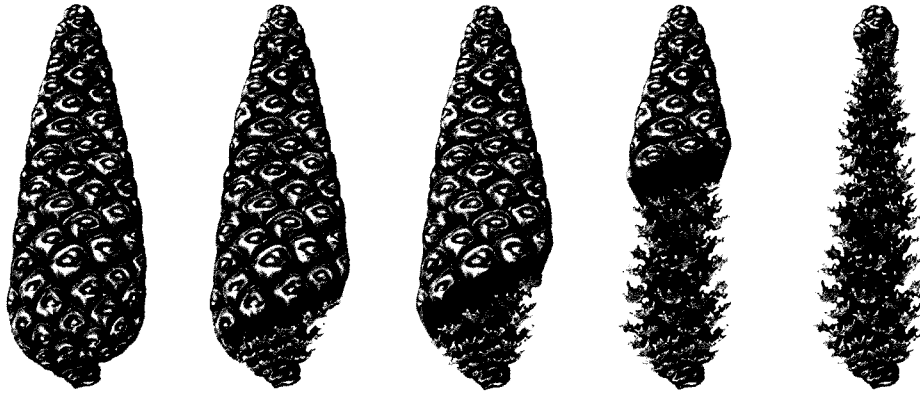


FIGURE 2 Sequence of the stripping of scales from a pinecone by a rat: from left to right, the scales are removed from the base to the top following their distribution on the cone (adapted from Heyes and Galef, 1996).

The tradition of pinecone exploitation seen in these forest-dwelling roof rats is of particular interest because it allows rats to thrive in a relatively sterile environment that would otherwise be closed to them. In this case, and perhaps in others as well, social learning has opened a new ecological niche to some members of a free-living species.

Learning What to Fear: Snake Avoidance by Rhesus Monkeys

How animals learn to avoid predators is difficult to understand because building an innate system to distinguish all harmless animals from all potentially dangerous animals seems almost impossible, given the wide range of predators to which many animals are vulnerable, and because learning to avoid predators by individual experience would not work very well either. Predators must be avoided the first time they are encountered. There is no time for trial-and-error learning.

It has been known for more than 40 years that although monkeys and apes that have been captured in the wild and brought into the laboratory will vigorously avoid contact

with snakes or snake-like objects, monkeys born and reared in captivity are relatively indifferent to the same objects that elicit strong fear responses in their wild-born brethren.

Mineka and Cook (1988) studied effects on the responses of laboratory-reared monkeys to snakes after these monkeys watching wild-born monkeys exhibit their fear of snakes. They found that laboratory-reared monkeys, which initially showed little or no response to snakes, responded vigorously to the sight of a snake after seeing a wild-reared monkey respond to a snake. This effect on the responses of laboratory-reared monkeys to snakes did not diminish over 3 months.

It is interesting to note that monkeys would not learn to respond emotionally to any object to which they watched a conspecific react. When Mineka and Cook (1988) showed laboratory-reared monkeys videotapes of wild-reared monkeys exhibiting fear responses elicited by snakes but edited the videotapes so that the monkeys appeared sometimes to be exhibiting fear of snakes and other times to be exhibiting fear of flowers, the laboratory-reared monkeys learned to fear the snakes but not the flowers. Apparently, the mon-



FIGURE 3 A rat pup feeding near its mother on a pinecone she has started to strip.

