

SOCIAL LEARNING IN NON-PRIMATE MAMMALS

Bennett G. Galef

Department of Psychology, Neuroscience & Behavior

McMaster University

Hamilton, Ontario, Canada

Phone: (905) 525-9140, ext. 23017

Fax: (905) 529-6225

Email: galef@mcmaster.ca

Keywords: alarm calls, Beldings ground squirrels, deer mice, dolphins, elephants, food choice, hamsters, mate choice, meekats, poison avoidance, predator avoidance, rats, wallabies, whales

Synopsis:

Social learning plays an important role not only in mammals' learning of arbitrary responses in the laboratory, but also in their acquisition of behaviors critical for survival and reproduction in natural habitats. Development of adaptive patterns of food selection, mate choice and predator avoidance are all facilitated by interaction with successful conspecifics. Consequences of such social learning are profound, allowing mammals to flourish in portions of the environment otherwise closed to them by, for example, learning socially to select valuable foods that would otherwise be ignored or to overcome defenses of potential prey that would otherwise prove impossible to exploit.

Introduction

Preceding articles in this section demonstrate that social interactions of various kinds facilitate the acquisition of adaptive patterns of behavior by insects, fishes and birds, and articles to follow will provide similar evidence of social learning in monkeys and apes. The non-primate mammals (hereafter mammals), with which this article is concerned, are similar to animals with nervous systems both more and less complex in that interaction of the naïve with the knowledgeable often guides the behavior of the naïve in adaptive directions.

Arbitrary Behaviors

Early work on social learning by mammals was concerned with the rapidity with which they learned arbitrary responses (such as pressing a lever to acquire food or stepping on a treadle to open a door) that were unrelated to their natural behavior. Results of such experiments were often discussed as demonstrating imitation, although today the same data would almost certainly be interpreted as demonstrating simpler types of social learning such as local or stimulus enhancement (see Zentall, this volume). For example, in a classic study conducted 40 years ago, kittens (*Felis catus*) were found to learn to press a lever to obtain food far more rapidly after watching their mother press the lever and get food than after watching a strange female cat do so. The more rapid learning by kittens that watched their mother was interpreted as showing that kittens imitated her behavior, although it can be explained more parsimoniously as showing only that kittens attend more closely to objects that their mother manipulates than to objects with which other adult female cats interact (i.e. as an instance of local enhancement).

More recently, Norway rats (*Rattus norvegicus*) that observed a rat pushing a joy stick either to left or right were reported to learn to press a joy stick in the same direction (left or right) as had their respective demonstrators, and it was suggested that the observer rats imitated their demonstrator's behavior. However, subsequent work showed that demonstrator rats left olfactory cues on the side of the joy stick that they had touched and that these cues influenced the behavior of other rats when they encountered it.

Perhaps the most striking instance of social learning of an arbitrary action by a mammal concerns golden hamsters (*Mesocricetus auratus*) that learned to use their teeth and forepaws to retrieve a piece of food dangling at the end of a short chain attached to a shelf. Three quarters of young hamsters whose mothers demonstrated retrieval behavior for them learned to pull in the chain to obtain the food, while only a fifth of pups reared by a mother that did not exhibit retrieval learned the trick. Unfortunately, nothing is known of the behavioral mechanisms supporting this instance of social learning.

Natural Behaviors

Whereas the early history of laboratory studies of social learning in mammals was largely concerned with social learning of arbitrary responses, more recent work has focused almost entirely on social influences on behaviors similar to those observed in free-living animals. Below, I briefly describe representative experimental studies based on observations of the behavior of mammals living in natural circumstances in which subjects: (1) chose appropriate substances to ingest, (2) overcame defenses of potential foods, (3) avoided predators, and (4) selected a mate.

Choosing Food

Much work on social learning in mammals has been concerned with learning how to forage successfully. Here I consider three examples of such social learning each of which depends upon quite different social learning processes.

Rats avoiding poisons

In the 1950s, rodent control operatives evaluated a method of rodent control that appeared to have considerable potential to reduce the cost of exterminating rodent pests. By placing permanent poison-bait stations in rat-infested areas, the rodent control experts hoped to substantially avoid the expense involved in constantly replacing temporary baits.

The permanent bait stations had great initial success, with rats eating ample amounts of poison and dying in large numbers. However, later bait acceptance was very poor, and targeted rat colonies soon returned to their original sizes. The failure of permanent stations resulted from a few adult colony members surviving their first ingestion of bait and, as a result of suffering the ill effects associated with ingesting the poison, learning to avoid eating the bait. These knowledgeable survivors somehow dissuaded their young from even tasting the poisoned bait that the adults had learned not to eat.

Laboratory analyses of the transmission of food choices from adult rats to their young revealed that adults do not directly dissuade their young from eating poisonous substances. Rather, young rats are both strongly inclined to eat whatever foods adults of their colony are eating and extraordinarily reluctant to eat foods that they have not eaten before. Consequently, young eat foods that adults of their colony are eating, not foods that those adults are avoiding. The poison avoidance is a byproduct of tendencies to avoid ingesting novel foods and learn from others what foods to eat.

Starting before birth and extending throughout life, many different socially mediated experiences are involved in such social induction of young rats' food choices. For example, if a gestating female rat is fed garlic, garlic is subsequently detectable in her amniotic fluid, and following parturition, her young show an enhanced preference for the scent of garlic. When young begin to nurse, flavours incorporated into maternal milk reflect the flavors of foods that a lactating female is eating, and experience of these flavours in mother's milk causes weaning young to prefer foods their mother ate during the weeks that she was suckling them. Also, lactating rats are great hoarders of food, returning to the burrows where their young shelter with large quantities of food. When an adult rat picks up a piece of food from such a hoard, any young in its vicinity become intensely interested in the particular piece of food that the adult is holding. The young rats often try to steal the piece of food that the adult is eating, and adults are surprisingly willing to give up food to juveniles. After a juvenile eats food taken from an adult,

the juvenile shows an increased preference for that food that it does not show after taking the same food directly from the floor and eating it.

As young rats grow older and leave the nest site their dam provides to feed in the larger world, they use visual cues to locate an adult rat at a distance from the nest entrance and approach and feed with that adult. Because approaching young tend to crawl up under an adult's belly and to begin to feed with their heads right under an adult's chin, adults can rather precisely direct young to foods that they are eating. And when an adult rat leaves a feeding site to return to its burrow, the adult deposits a scent trail that leads young rats seeking food to the same location where the adult has fed. Also, while feeding, adult rats deposit, both on and near foods, olfactory cues that are highly attractive to pups and cause them to prefer feeding sites and foods that adults have previously exploited.

In a number of mammalian species in addition to Norway rats (mice, voles, European rabbits, Mongolian gerbils, golden and dwarf hamsters, bats and dogs) a naïve animal (an observer) that interacts with another of its species that has recently eaten a food (a demonstrator) subsequently shows a substantial increase in its preference for whatever food its demonstrator ate.

Exposure to a demonstrator rat can markedly increase the survival of rats in environments where ingesting the most palatable foods present does not lead to selection of a nutritionally adequate diet. For example, young rats placed in enclosures where they had continuous access to four different foods, three relatively palatable, but low in protein and one relatively unpalatable but protein rich lost weight, and would surely have died of protein deficiency. By contrast, pups that shared their enclosures with adult rats previously trained to eat the relatively unpalatable, protein-rich food grew at almost the same rate as pups offered just the protein-rich diet.

The relatively simple social learning mechanisms available to rats are also sufficient to support the sort of behavioral traditions that are common in our own species and present in other primates as well (See Whiten, this volume). All four members of each of several colonies of rats assigned to one condition were trained not to eat a pepper-flavored food and to eat a horseradish-flavored food, whereas all four members of each colony assigned to a second condition were taught the reverse. Following this training, each colony was offered a choice between pepper-flavored food and horseradish-flavored foods for 3 hr/day, and each day immediately after a colony had been fed, one of its members was removed and replaced with a naïve rat. After 4 days, all members of original colonies had been replaced, and for 10 days thereafter, the individual in each colony that had been there longest was replaced with a naïve rat. Even after replacement of replacements of replacements of original colony members, large effects of the food preferences learned by original colony members were still evident (Figure 1). Similar transmission chains have also been found among colonies of rats trained to dig in sawdust for food.

<Insert Figure 1 about here>

Overcoming the defenses of prey

Pinecone stripping by roof rat

Roof rats (*Rattus rattus*) living in the pine forests of Israel and of Cyprus (places where no squirrels are present to compete for pine seeds), but not roof rats living elsewhere, subsist on a diet of pine seeds that they secure by stripping the scales from pinecones and eating the seeds that the scales protect. Laboratory studies of pinecone stripping by wild-caught rats revealed that

to recover more energy from eating pine seeds than is expended in removing scales from pinecones, rats must take advantage of the architecture of pinecones, first stripping the scales from the base of a cone, and then removing the remaining scales in succession as they spiral around the cone to its apex (see figure 2).

<Insert Figure 2 about here>

Less than 6 percent of rats captured outside pine forests and given pinecones to eat learn to open them efficiently. However, more than 90 percent of rats born to mothers that could not remove the scales from pine cones efficiently but reared by foster mothers that did so in the presence of their foster young, learned the efficient method of stripping scales from cones. Similarly, juvenile red squirrels (*Tamiasciurus hudsonicus*) that have watched an experienced adult squirrel open hickory nuts, open similar nuts at a substantially younger age and with greater efficiency than siblings lacking such experience.

When a roof-rat mother removes the scales from a cone, her young gather around her and attempt to snatch the pine seeds as she uncovers them. As the young mature, they snatch entire partially opened pinecones from their mother and then continue the stripping process that their mother started. Indeed, just providing young rats with pinecones started properly by an adult rat or even by a human experimenter using a pair of pliers to start a pinecone properly by removing scales from its base, results in 70 percent of the young rats learning the efficient method of removing scales. Thus, a very simple sort of social learning enables young rats to learn a skill that enables them to survive in pine forests, a habitat that would otherwise be closed to them.

Meerkats learning to eat scorpions

Meerkats (*Suricata suricatta*) are highly social animals that live in arid regions of southern Africa where they feed on a range of vertebrate and invertebrate prey, some of which, like scorpions, are potentially dangerous. Young meerkat pups are initially incapable of foraging for themselves, and when from 30 to 90 days of age, are provisioned by adult group members that respond to begging calls pups emit when hungry. These begging calls change with the pups' age and determine the type of prey that adults present to calling young. Adults typically kill or remove the sting of scorpions before they give them to very young meerkats. However, as the pups grow older and better able to handle intact, live scorpions, adults provide an increasing proportion of intact prey to pups. When human experimenters provisioned young meerkats in the field with live, scorpions with their stings removed, the pups' subsequent ability to handle such 'dangerous' prey without being either pseudo-stung by them or letting them escape increased markedly. Thus, adult meerkats' provisioning of their young facilitates their acquisition of an important skill.

Learning to avoiding predators

Predator recognition and avoidance pose a challenge both to the young of many mammals and to scientists trying to understand how animals learn to avoid predators without personal experience of the potentially disastrous consequences of direct contact with them. Although there have been far fewer studies of the role of social learning in development of anti-predator than of foraging behaviors, work on predator avoidance learning in birds, fish and primates, together with that conducted in non-primate mammals, suggests a potential solution to the problem. Such work is of some practical importance in that attempts to reintroduce captive-reared endangered species into natural habitat often fail because captive-reared animals released into the wild often respond inadequately to the approach of a predator.

Predator recognition in wallabies

Captive-reared Tamar wallabies (*Macropus eugenii*) were given the opportunity to observe either a demonstrator wallaby that had been previously trained to avoid a stuffed fox or a naïve demonstrator wallaby that was indifferent to foxes. Observer wallabies that had seen a fearful demonstrator interact with the stuffed fox showed significantly longer periods of vigilance in response to presentation of the fox than observer wallabies that had seen an indifferent demonstrator interact with the fox, and the response was specific to foxes and not shown to other stuffed animals..

In a conceptually similar study, juvenile captive-reared black-tailed prairie dogs (*Cynomys ludovicianus*) were exposed to various animals restrained behind a screen barrier: a ferret, a rattlesnake, a hawk and a harmless rabbit. The prairie dogs were then given additional exposure to each stimulus animal either with or without an experienced adult demonstrator present. During this training, the alarm vocalizations and vigilance behavior of the juveniles closely matched that of their demonstrators, and following training, juveniles trained with an experienced adult were more wary of the three predatory animals than were juveniles that had experienced the predators without a demonstrator.. Perhaps most interesting, when the prairie dogs were released back into the wild, those that had been exposed to predators in the presence of an experienced demonstrator had a significantly greater probability of surviving for 1 year than did those lacking such training.

Learning to avoid biting flies

Blood-feeding biting flies are amongst the most common of mammalian predators, and their attacks elicit avoidance responses ranging from elephants manufacturing tools from branches for fly switching to self burying in mice. Deer mice (*Peromyscus maniculatus*) experiencing a single 30-min session of attack by biting flies and then exposed to flies whose ability to bite had been surgically removed, buried themselves in the substrate, whereas mice without prior experience of biting flies did not. However, mice that had no personal experience of biting flies but had witnessed another mouse under attack by biting flies, engaged in self burying when subsequently exposed to flies that were unable to bite.

Development of response to alarm calls

Adult Belding's ground squirrels (*Spermophilus beldingi*) that detect an avian predator such as a hawk or eagle whistle, and other adults respond to their whistles by running to the nearest burrow entrance. When adults detect a relatively slow-moving ground predator, they emit a trill to which other adults respond by standing on their hind legs and looking about.

Newly emerged young ground squirrels do not behave differently either to the two alarm calls of adults or to alarm calls and other sounds. Development of appropriate responses to alarm calls of juvenile squirrels maintained in captivity without their dams was slower than that of captive young squirrels maintained with their dams, suggesting that interaction with dams exhibiting appropriate responses to alarm calls sped juvenile's learning of the appropriate responses.

Choosing a mate

Rats and mice

Although most experiments on social influences on sexual behavior have been carried out in birds and fishes a few studies suggest that in mammals as well, social interactions of various kinds can influence both choice of a mate and sexual performance. Female Norway rats prefer as sex partners males that have recently copulated with other females, and female mice spend more time investigating urine collected from males exposed overnight to an estrous female than to urine from unstimulated males, although as yet, there is no evidence that this change in the attraction of female mice to male urine causes females to change their preferences for a partner.

Farm animals

Although strictly speaking a case of social influence that only suggests possible social learning, many species of farm animal (e.g. goats, cattle, horses and pigs) exhibit enhanced sexual performance after viewing conspecifics copulating. For example, sexual performance of male sheep (*Ovis aries*) is enhanced following interaction with another male that has recently interacted with a ewe. It is hypothesized that olfactory cues transferred from females to males during their period of interaction have a stimulating effect on other males

Animals Inconvenient for Controlled Studies

There is an expectation that animals with large brains are more likely to engage in complex sorts of learning, including social learning, than animals with small brains, and many large-brained mammals from elephants to whales have large bodies that make them inconvenient subjects for controlled, experimental studies. However, despite the difficulty of providing conclusive

evidence of social learning in such creatures, there is a growing body of evidence suggesting that many such animals may be sophisticated social learners.

Bottlenose dolphins

In the wild, young dolphins (*Tursiops sp.*) and their mothers forage together for several years giving the young ample opportunity to learn complex foraging behaviors from their mothers. For example, while foraging in deep-water channels, some adult female dolphins carry marine sponges that are believed to be used to protect their noses while probing the sea floor to locate small, bottom-dwelling fish. At Shark Bay in Western Australia, the only study site where sponge carrying has been observed, the behavior occurs almost exclusively within a single maternal line, with most daughters (and a few sons) of sponge-carrying females adopting the habit. Although a genetic explanation of the pattern of sponge use at Shark Bay seems plausible, examination of several possible modes of genetic inheritance make it unlikely that a genetic propensity is responsible for the observed distribution of the behavior. Further, because only some of the many female dolphins that forage in deep-water channels use sponges while foraging there, it is unlikely that exposure to deep channels in itself results in sponge use.

Whales

There are numerous reports of behavior consistent with the view that many cetaceans (i.e. whales and dolphins) engage in social learning. For example, the rate of spread among humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine of a novel foraging behavior, “lobtail feeding” (in which the whales slam their tail flukes in the water before diving for prey), is consistent with social transmission of the behavior, although explanation in terms individual learning in response to a change in prey availability is also possible. Similarly, although scattered reports of mother killer whales (*Orcinus orca*) “teaching” their young to beach themselves to capture seals are consistent with the view that such behavior is socially learned, the reports do not offer strong support for that interpretation.

Elephants

The social knowledge possessed by the matriarch in a family of elephants (*Loxodonta africana*) influences the social behavior of other family members, reducing the probability that they will engage in unnecessary defensive behaviors when encountering familiar families that pose no threat. The older the family matriarch, the better are family members at discriminating vocalizations of familiar and unfamiliar individuals and responding appropriately to them. Age of a family matriarch predicts more than 30 percent of the variation among families in the number of young that they produce suggesting that the social knowledge of older females has adaptive consequences for her kin. Although it has not been shown that other family members learn from the matriarch which female’s vocalizations to respond to and which to ignore and continue to respond appropriately in her absence, it seems probable that such social transmission of social knowledge would occur.

Conclusion

Although the study of social learning in mammals is still in its infancy, many biologically important activities in which mammals engage have already been found to be modifiable by socially acquired information. In future, we can expect to see both more examples of behavior in free-living mammals that are likely to be a product of social learning and ever more convincing experiments leading to deeper understanding of the ways in which social interactions improve the acquisition of adaptive patterns of behavior.

Additional readings: [xxxx Can Add six]

Bilko A, Altbacker, V and Hudson R (1994) Transmission of food preference in the rabbit: the means of information transfer. *Physiology & Behavior* **56**: 907-912.

Box HO and Gibson KR (eds.) (1999) *Symposia of the Zoological Society of London, Vol. 72: Mammalian Social Learning: Comparative and Ecological Perspectives*. Cambridge: Cambridge University Press.

Galef, BG Jr (2003) Traditional behaviors of brown and black rats (*R. norvegicus* and *R. rattus*). In: Perry S and Frigaszy D (eds.). *The Biology of Traditions: Models and Evidence*, pp. 159-186. Chicago: University of Chicago Press.

Galef, BG Jr (2007) Social learning by rodents. In: Wolff JO and Sherman PW (eds.). *Rodent Societies: An Ecological & Evolutionary Perspective*, pp. 207-215. Chicago: University of Chicago Press.

Griffin AS (2004) Social learning about predators: a review & prospectus. *Learning & Behavior* **32**: 131-140.

Heyes CM and Galef BG Jr (2004) Special Issue: Social Learning and Imitation. *Learning & Behavior*, **32** issue 1.

Janik VM and Slater PJB (2003) Traditions in mammalian and avian vocal communication. In: Frigaszy DM. and Perry S (eds.). *The Biology of Traditions: Models and Evidence*, pp. 213-236. Cambridge: Cambridge University Press.

Mann J and Sargeant B (2003) Like mother like calf: the ontogeny of foraging traditions in the wild Indian Ocean bottlenose dolphin. In: Frigaszy DM and Perry S (eds.) *The Biology of Traditions: Models and Evidence*, pp. 236-266. Cambridge: Cambridge University Press.

Rendell L and Whitehead H (2001) Culture in whales and dolphins. *Behavioral & Brain*

Sciences **24**: 309-382.

Zentall TR (1988) Experimentally manipulated behavior in rats and pigeons. In: Zentall TR and Galef BG Jr (eds.) *Social Learning: Psychological and Biological Perspectives*, pp.191-206. Hillsdale: Lawrence Erlbaum Associates.

Figure Captions.

Figure 1. Amount of pepper-flavored diet (diet cp) eaten by members of colonies offered a choice between diet cp and horseradish-flavored diet (diet hr) and initially trained to eat either diet cp or diet hp.

Figure 2. Drawing of a pinecone being stripped of its scales in the efficient manner by taking advantage of the architecture of the pinecone.

Author Biography

After receiving my Ph.D. from the University of Pennsylvania in 1968, I moved as an Assistant Professor to McMaster University in Hamilton, Ontario where, for 38 years, my research focused on understanding social influences on the feeding behavior of Norway rats and the mate choices of Japanese quail. Empirical work in my laboratory on social learning in animals has resulted in publication of more than 100 scientific articles (www.sociallearning.info) and my scholarly pursuits have produced three co-edited volumes [*Social Learning: Psychological and Biological Perspectives* (with TR Zentall), *Social Learning and Imitation: the Roots of Culture* (with CM Heyes) and *The Question of Animal Culture* (with KN Laland)] as well as a special issue of the journal *Learning & Behavior* [2004, 32, No. 1 (with CM Heyes)]. I was honored in 2005 with the Lifetime Contribution Award of the Social Learning Group, St. Andrews University, Scotland.

XXXX Colour photograph