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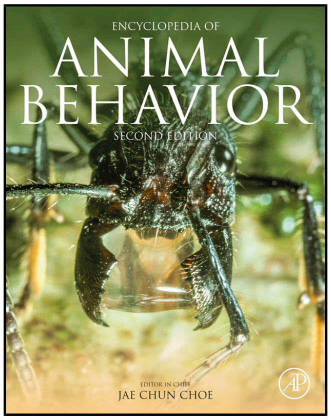

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Mammalian Social Learning: Non-Primates☆

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Abstract

Social learning can be a major factor in mammals learning either arbitrary responses in the laboratory or behaviors critical to their survival and reproduction in natural habitat. Development of adaptive patterns of food selection, mate choice, predator avoidance, and communication are all facilitated by interaction with 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 the defense of potential prey that would otherwise prove impossible to ingest.

Keywords

Alarm calls; Bats; Communication; Dolphins; Elephants; Food choice; Mate choice; Meerkats; Poison avoidance; Prairie dogs; Predator avoidance; Rats; Vocal learning; Whales

Introduction

Other articles in this encyclopedia demonstrate that social interactions of various kinds can facilitate insects', fishes' and birds' acquisition of adaptive patterns of behavior, facilitating foraging, mate selection, communication, navigation and numerous other activities important in survival and reproduction. Articles to follow will provide similar evidence of social learning in monkeys and apes. Like other animals, mammals from bats to whales engage in many different types of social learning (see Zentall this volume; Whiten and Ham, 1992) ranging from local enhancement to imitation, each acting to induce individuals to behave similarly to one another. And as in other animals, such interaction of naïve mammals with more experienced conspecifics most often serves to facilitate naïve individuals' acquisition of adaptive behaviors (Laland, 2004).

Arbitrary Behaviors

Early work on mammalian social learning focused on the role of social interactions in the acquisition of arbitrary responses (e.g. pressing a lever to acquire food or stepping on a treadle to open a door) that were unrelated to the natural behavior of the subject species. Results of such experiments were often discussed as demonstrating imitation, although today the same data would almost certainly be interpreted as demonstrating cognitively less demanding types of social learning such as local enhancement or stimulus enhancement. 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 (Chesler *et al.*, 1968). The more rapid learning by kittens that watched their respective mothers was interpreted as showing that kittens imitated her behavior, although such facilitation of behavior acquisition 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).

Similarly, naïve Norway rats (*Rattus norvegicus*) that observed a trained rat pushing a joy stick either to left or right learned to press a joy stick in the same direction (left or right) as had their respective demonstrators. It was suggested that the observer rats imitated their demonstrator's behavior (Heyes and Dawson, 1990). 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 the joy stick (Mitchell *et al.*, 1999).

A 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 food-retrieval behavior for them learned to pull the chain to obtain the food, while only a fifth of pups reared by a mother that did not exhibit retrieval learned the trick (Previde and Poli, 1999). Unfortunately, nothing is known of the behavioral mechanisms supporting this instance of social learning.

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Natural Behaviors

Although the early history of laboratory studies of social learning in mammals was largely concerned with understanding the acquisition of arbitrary responses, more recent work has focused almost entirely on social influences on behaviors similar to those observed in free-living members of a species. Such studies have been concerned with understanding both the mechanisms of such social learning and the contributions of social learning to individual fitness. In the following sections we 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 the defenses of potential foods, (3) avoided predators, (4) selected a mate, and (5) learned to communicate with others of their species.

Choosing Food

Much work on social learning in mammals has been concerned with the contribution of social information to success in foraging. Below, we consider three examples of such social learning, each dependent on 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 for reducing the cost of exterminating rodent pests. By placing permanent poison-bait stations in rat-infested areas, the rodent-control experts hoped to substantially decrease the expense of 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 even a small quantity of the bait, learning to avoid eating it. These knowledgeable survivors somehow dissuaded their young from even tasting the poisoned food 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 wild rats are: (1) strongly inclined to eat whatever foods adults of their colony are eating, and (2) extraordinarily reluctant to eat foods that they have not previously eaten. Young, naïve rats' avoidance of poisons that adults of their colony have eaten is thus best understood as a byproduct of their tendencies to both learn from others what foods to eat and avoid ingesting other foods.

Starting before birth and extending throughout life, many different socially mediated experiences are involved in such social induction of young rats' food preferences. 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 rats begin to nurse, flavors incorporated into maternal milk reflect the flavors of foods that a lactating female is eating, and experience of these flavors in mother's milk causes weaning young to subsequently prefer foods their mother ate during the weeks that she was suckling them. Also, lactating rats are great hoarders of food, returning large quantities of food to the burrows where their young shelter. When an adult rat takes 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 that piece of food, and adults are surprisingly willing to surrender it 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 eating the same food taken directly from the floor.

As young rats grow older and leave the nest site 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. Further, 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 shortly after that other has 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 clear implication of such data is that once a single rat has learned to forage successfully in a novel environment, it can lead others of its species to feed successfully there (Galef, 2005).

The relatively simple social learning mechanisms available to rats are also sufficient to support the sort of behavioral traditions that are common in not only in our own species but also in other primates.

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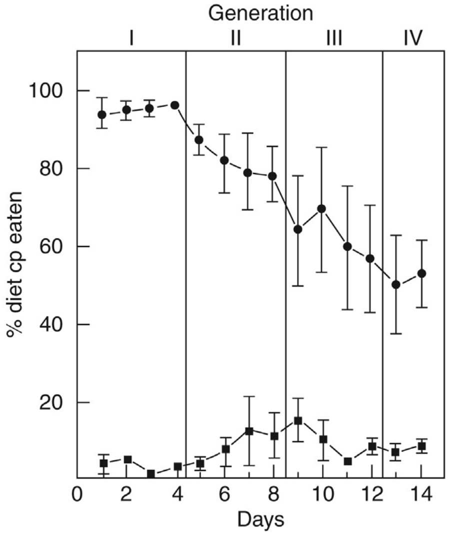

Fig. 1 Amount of pepper-flavored diet (diet cp) eaten by members of colonies offered a choice between diet cp and horseradish-flavored diet (diet hr) and initially trained to eat either diet cp or diet hr. Reproduced from Galef, B.G., Jr., Allen, C., 1995. A new model system for studying animal tradition. Animal Behaviour 50, 705–717. (Figure 5).

All four members of each of several colonies of rats were trained not to eat a pepper-flavored food and to eat a horseradish-flavored food, while 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- and horseradish-flavored foods for 3 h day^{-1}, 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 original colony members, large effects of the food preferences learned by original colony members were still evident (**Fig. 1**; Galef and Allen, 1995).

Overcoming the Defenses of Prey

Pinecone Stripping by Black Rats

Black 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 black 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 **Fig. 2**).

Less than 6% of rats captured outside pine forests and given pinecones to eat learn to open them efficiently. However, more than 90% of rats born to mothers that could not remove the scales from pine cones efficiently but reared by foster mothers that stripped pinecones in the presence of their foster young, learned the efficient method of removing scales from cones.

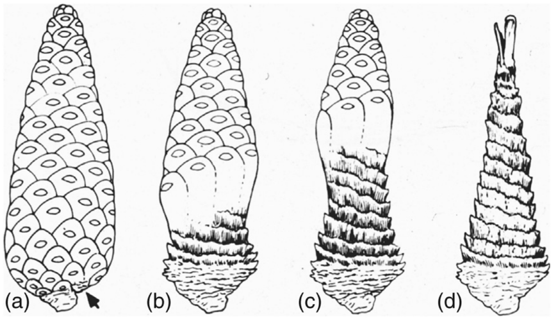

Fig. 2 Schematic diagram of pinecones being efficiently stripped of their scales in the efficient manner taking advantage of the architecture of the pinecone. Reproduced from Terkel, J., 1996. Cultural transmission of feeding behavior in the black rat (Rattus rattus). In: Heyes, C.M., Galef, B.G., Jr. (Eds.) Social learning in animals the roots of culture. San Diego: Academic Press, pp. 17–48. (Figure 5).

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When a black rat mother removes the scales from a cone, her young gather around her and attempt to snatch 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 remove scales from its base results in 70% of the young rats learning the efficient method of removing scales. Thus, a very simple sort of social learning allows young rats to learn a skill that enables them to survive in pine forests, a habitat that would otherwise be closed to them (Terkel, 1996). 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 (Weigl and Hanson, 1980).

Bottlenose Dolphins Using Tools to Forage

Bottlenose dolphins (*Tursiops sp.*) like rats and red squirrels can learn socially to exploit a new feeding niche, though the way in which they do so is quite different from that seen in rodents. In the wild, young dolphins and their mothers forage together for several years giving the young ample opportunity to learn complex foraging behaviors from their mothers. While foraging in deep-water channels, some adult female dolphins carry marine sponges thus protecting 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 (Mann and Sargeant, 2003). Last, and most relevant to the dolphins, use of sponges opens a new feeding niche to those employing sponges as tools; the diet of sponge-carrying dolphins varies markedly from that of dolphins living in the same area that have not learned to use sponges (Krützen *et al.*, 2014), another instance of social learning opening a new feeding niche to social learners.

Lobtail Feeding in Humpback Whales

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 of individual learning in response to a change in prey availability is also possible (Allen *et al.*, 2013; Rendell and Whitehead, 2001). 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.

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. Young meerkat pups are initially incapable of foraging for themselves, and when from 30 to 90 days of age, are brought prey by adult group members in response to begging calls that the pups emit when hungry. Some of these prey, for example scorpions, are potentially dangerous. However, adults typically kill or remove the sting of scorpions before they give them to very young meerkats, so the scorpions are safe to eat. 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 pseudostung by the scorpions or allowing the scorpions to escape increased markedly. Thus, adult meerkats' provisioning of their young with disabled scorpions facilitates the young meerkats' acquisition of an important skill (Thornton and McAuliffe, 2006). Meerkats provide the clearest example of teaching (Caro and Hauser, 1992) yet reported in a mammal either primate or non-primate.

Learning to Avoid 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 any 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 the development of antipredator 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

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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 watched 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 (Griffin and Evans, 2003).

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 juvenile prairie dogs 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. 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 those prairie dogs lacking such training (Shier and Owings, 2006).

Belding's Ground Squirrels' Response to Alarm Calls

Adult Belding's ground squirrels (*Spermophilus beldingi*) whistle when they detect an avian predator such as a hawk or eagle, and other adults respond to such 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 to the two alarm calls of adults or respond to alarm calls in generally. 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 juveniles' learning of the appropriate responses (Mateo and Holmes, 1999).

Deer Mice Learning to Avoid Biting Flies

Blood-feeding biting flies are among 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 that had been surgically deprived of the ability to bite buried themselves in the substrate, whereas mice without prior experience of biting flies did not. Most interesting 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 (Kaveliers *et al.*, 2005). Essentially nothing is known of how this social learning proceeds.

Choosing a Mate

Norway Rats

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 the choice of a mate and sexual performance. Female Norway rats prefer as sex partners males that have recently copulated with other females (Galef *et al.*, 2008), and female mice spend more time investigating urine collected from males exposed overnight to an estrous female than to urine from males exposed to a female not in estrous, 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

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 has been hypothesized that olfactory cues transferred from females to males during their period

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of interaction have a stimulating effect on other males (Maina and Katz, 1999). Such observations suggest the possibility that social interactions might affect mate choice in such species, though there is, as yet, no evidence that such is the case.

Learning to Communicate Within and Between Groups

Social learning also functions to allow individuals to communicate with and thus integrate into their social group. One means by which mammals can maintain group cohesion is by learning and using group-specific vocal repertoires. While this type of social learning is most commonly studied in humans and songbirds, vocal learning has been documented in some mammalian species, from bats to elephants.

Vocal Repertoires of Bats

Greater spear-nosed bats (*Phyllostomus hastatus*) live in long-term social units comprising many unrelated individuals. Females use contact 'screech' calls to coordinate flights from the roost for group foraging forays and to facilitate social recognition amongst group mates. The acoustic properties of these screech calls vary across groups but are very similar within groups, suggesting that social learning is responsible for the different vocal dialects.

Studies that experimentally switched bats between captive groups revealed that the bats began changing their calls within a month of the switch. Interestingly, it was not just the transferred bats that changed their calls; the changes were reciprocal, with the resident bats also changing their calls to conform to their newly created group. Five months after the switch, the frequency and temporal characteristics of the screech calls of the residents and transfers were almost indistinguishable. (Boughman, 1998).

Greater sac-winged bats (*Saccopteryx bilineata*) have a complex vocal repertoire with context-specific vocalizations. Males are territorial and defend groups of females as well as young. Territorial males vocalize to identify and defend their territories using vocalizations that have been referred to as 'songs' because of their functional and developmental similarities to the songs of birds. Young bats learn the songs of male territory holders through a process of vocal imitation very similar to the way songbirds learn their songs. Recordings taken from young pups living in groups in the wild show patterns of vocal development that, like those of song birds, begin as plastic babbling and develop into the mature territorial song (Knörnschild *et al.*, 2010).

The Egyptian fruit bat (*Rousettus aegyptiacus*) is a highly social species that engages in extensive vocal communication. Pups in this species also learn group-specific vocal dialects though social learning. Playback experiments have broadcast recordings of thousands of vocalizations of colonies of fruit bats from three different vocal dialects to groups of captive young bats. Results of these experiments revealed that the pups learn their group-specific vocalizations as a result of listening to the ambient sounds produced by the 'crowd' in the roost and not necessarily from individuals who directly interact with them (Prat *et al.*, 2017).

Communication Between Families of African Elephant

A rather different way in which social learning contributes to communication has been found in African elephants (*Loxodonta africana*) The social knowledge possessed by the oldest female (the matriarch) in a family of elephants 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 is, the better the family members are at discriminating vocalizations of familiar and unfamiliar individuals and responding appropriately to them. Further, the age of a family matriarch predicts more than 30% 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 a social transmission of social knowledge occurs (McComb *et al.*, 2011).

Conclusion

Although the study of social learning in mammals is still in its infancy, many of the biologically important activities in which mammals engage have already been found to be modifiable by socially acquired information. The mechanisms underlying such social learning are highly variable, ranging from very simple influences on behavior to cognitively demanding feats of information acquisition and use. Examples provided above reveal that even simple social learning mechanisms can have important effects both on individual fitness and on the creation and maintenance of behavioral traditions within groups. In future, we can expect to see both many more examples of behavior in free-living mammals that are products of social learning and ever more convincing experiments leading to a deeper understanding of the ways in which social interactions improve acquisition of adaptive patterns of behavior.

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See also: **Learning and Teaching:** Social Information Use; Social Learning: Theory

References

Allen, J., Weinrich, M., Hoppitt, W., Rendell, L., 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science 340, 485–488.

Boughman, J.W., 1998. Vocal learning by greater spear-nosed bats. Proceedings of the Royal Society of London, B 265, 227–233.

Caro, T.M., Hauser, M.D., 1992. Is there teaching in nonhuman animals? Quarterly Review of Biology 67, 151–174.

Chesler, E.R.J., Bartlett, F., Victor, I., 1968. Observation learning in cats. Science 159, 1451–1489.

Galef Jr., B.G., 2005. Social learning. In: Wishaw, I.Q., Kolb, B. (Eds.), The Behavior of the Laboratory Rat: A Handbook With Tests. Oxford University Press, Oxford, pp. 363–370.

Galef Jr., B.G., Allen, C.A., 1995. A new model system for studying animal traditions. Animal Behaviour 50, 705–717.

Galef Jr., B.G., Lim, T.C.W., Gilbert, G.S., 2008. Evidence of mate-choice copying in Norway rats, Rattus Norvegicus. Animal Behaviour 75, 1117–1123.

Griffin, A.S., Evans, C.S., 2003. Social learning of antipredator behavior in a marsupial. Animal Behaviour 66, 485–492.

Heyes, C.M., Dawson, G.R., 1990. A demonstration of observational learning in rats using a bidirectional control procedure. Quarterly Journal of Experimental Psychology, B 42, 59–71.

Kaveliers, M., Colwell, D.D., Choleris, E., 2005. Kinship, familiarity, and social status modulate social learning about “micropredators” (biting flies) in deer mice. Behavioral Ecology and Sociobiology 58, 60–71.

Knörnschild, M., Nagy, M., Metz, M., Mayer, F., von Helversen, O., 2010. Complex vocal imitation during ontogeny in a bat. Biology Letters 6, 156–159.

Krützen, M., Kreicker, S., Macleod, C.D., et al., 2014. Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (*Tursiops sp.*) provides access to a novel foraging niche. Proceedings of the Royal Society, B 281, 20140374.

Laland, K.N., 2004. Social learning strategies. Learning & Behavior 32, 4–14.

Maina, D., Katz, L.S., 1999. Scent of a ewe: Transmission of a social cue by conspecifics affects sexual performance in male sheep. Biology of Reproduction 60, 1373–1377.

Mann, J., Sargeant, B., 2003. Like mother like calf: The ontogeny of foraging traditions in the wild Indian Ocean bottlenose dolphins (*Tursiops sp.*). In: Fragaszy, D.M., Perry, S. (Eds.), Thebiology of Traditions: Models and Evidence. Cambridge University Press, Cambridge, UK, pp. 233–266.

Mateo, J.M., Holmes, W.G., 1999. How rearing history affects alarm-call responses of Belding’s ground squirrels (*Spermophilus beldingi, Scuridae*). Ethology 105, 207–222.

McComb, K., Shannon, G., Durant, S.M., et al., 2011. Leadership in elephants: The adaptive value of age. Proceedings of the Royal Society, B 278, 3720–3726.

Mitchell, C.J., Heyes, C.M., Gardner, M.R., Dawson, G.R., 1999. Limitations of a bidirectional control procedure for the investigation of imitation in rats: Odor cues on the manipulandum. Quarterly Journal of Experimental Psychology, B 52, 193–202.

Prat, Y., Azoulay, L., Dor, R., Yovel, Y., 2017. Crowd vocal learning induces vocal dialects in bats: Playback of conspecifics shapes fundamental frequency usage by pups. PLOS Biology 15 (10), e2002556.

Previde, E.P., Poli, M.D., 1999. Social learning in the golden hamster (*Mesocricetus auratus*). Journal of Comparative Psychology 110, 203–208.

Rendell, L., Whitehead, H., 2001. Culture in whales and dolphins. Behavioral and Brain Sciences 24, 309–382.

Shier, D.M., Owings, D.H., 2006. Effects of predator training on behavior and post-release survival of captive prairie dogs. Biological Conservation 132, 126–135.

Terkel, J., 1996. Cultural transmission of feeding behavior in the black rat (Rattus rattus). In: Heyes, C.M., Galef Jr., B.G., et al. (Eds.), Social Learning in Animals: The Roots of Culture. Academic Press, San Diego, pp. 17–48.

Thornton, A., McAuliffe, K., 2006. Teaching in wild meerkats. Science 313, 227–229.

Whiten, A., Ham, R., 1992. On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. Advances in the Study of Behavior 21, 239–283.

Weigl, P.D., Hanson, E.V., 1980. Observational learning and the feeding behavior of the red squirrel *Tamiasciurus Hudsonicus*: The ontogeny of optimization. Ecology 61, 213–218.

Further Reading

Bilko, A., Altbacker, V., Hudson, R., 1994. Transmission of food preference in the rabbit: The means of information transfer. Physiology and Behavior 56, 907–912.

Box, H.O., Gibson, K.R., 1999. Symposia of the Zoological Society of London, Vol. 72: Mammalian Social Learning: Comparative and Ecological Perspectives. Cambridge University Press, Cambridge.

Galef Jr., B.G., 2003. In: Perry, S., D. Fragaszy, D. (Eds.), The Biology of Traditions: Models and Evidence. University of Chicago Press, Chicago, pp. 159–186.

Galef, B.G., 2007. Social learning by rodents. In: Wolff, J.O., Sherman, P.W. (Eds.), Rodent Societies: An Ecological and Evolutionary Perspective. University of Chicago Press, Chicago, pp. 207–215.

Griffin, A.S., 2004. Social learning about predators: A review and prospectus. Learning & Behavior 32, 131–140.

Heyes, C.M., Galef Jr., B.G., 2004. Special issue: Social learning and imitation. Learning & Behavior 32, 1–140.

Janik, V.M., Slater, P.J.B., 2003. Traditions in mammalian and avian vocal communication. In: Fragaszy, D.M., Perry, S. (Eds.), The Biology of Traditions: Models and Evidence. Cambridge University Press, Cambridge, pp. 213–236.

Sargeant, B.L., Mann, J., 2009. From social learning to culture: Intrapopulation variation in bottlenose dolphins. In: Laland, K.N., Galef, B.G. (Eds.), The Question of Animal Culture. Harvard University Press, Cambridge, pp. 152–173.

Whitehead, H., 2009. How might we study culture? A perspective from the ocean. In: Laland, K.N., Galef, B.G. (Eds.), The Question of Animal Culture. Harvard University Press, Cambridge, pp. 125–151.

Zentall, T.R., 1988. Experimentally manipulated behavior in rats and pigeons. In: Zentall, T.R., Galef Jr., B.G. (Eds.), Social Learning: Psychological and Biological Perspectives. Lawrence Erlbaum Associates, Hillsdale, NJ, pp. 191–206.