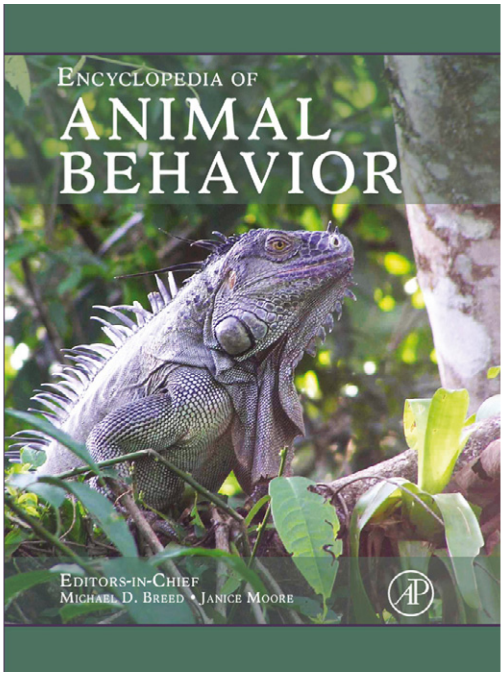

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Avian Social Learning

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Introduction

In 1921, birds described as tits (Paridae) were first seen to open milk bottles in the small, southern English town of Swaythling. Over the next 25 years, observations of birds opening milk bottles were reported from hundreds of other sites all over Great Britain, Ireland, and continental Europe. The first scientific article on the phenomenon was published in 1949. A short discussion of bottle opening by birds is a good introduction to the topic of avian social learning because the questions asked about milk-bottle opening are indicative of those that have governed almost all subsequent research on avian social learning: How did this behavior originate? Did its appearance in blue tits (*Parus caeruleus*) have anything to do with the cleverness or boldness of this species? Was the rapid spread of bottle-opening over many areas of Great Britain and Ireland due to cultural transmission? If so, were the birds imitating one another or was something simpler going on? Given that eleven species of birds were found to open bottles, did we see transmission between as well as within species? (**Figure 1**).

Cultural Transmission of Foraging Behavior

First of all, why did the new behavior appear in tits? In England, home delivery of bottled milk, which had started in the years before the First World War, was interrupted during that conflict, to be resumed shortly after its conclusion. The fact that the instances of milk bottle opening by birds were first recorded after the resumption of home delivery of milk bottles suggests that the innovation might be less surprising than often thought. Tits, and in particular, the species thought to have originated the new behavior, blue tits, are relatively tame, urbanized, and inquisitive birds, easily attracted to winter feeders and other sources of food provided by humans. One of the blue tits' normal food searching behaviors is to peck and peel bark from trees to look for insects, a technique very similar to the one they use to open bottle caps.

At the taxonomic level of the family, tits are also large-brained, ranking above all others in the parvorder Passerida (3500 species) in terms of the brain size corrected for body size. Several tit species, especially the great tit (*P. major*) and the blue tit, are known for other novel or unusual feeding behaviors, such as piercing the base of flowers to drink nectar, eating the brain of a pied flycatcher, or folding paper to store food in it.

Was the increase in bottle opening observed over the years due to cultural transmission? Culturally transmitted behaviors are sometimes said to 'spread like wildfire.' This description implies three things: rapid spread, a vast spatial scale, and a temporal pattern that starts off slowly and then spreads rapidly, until the spread eventually ceases for lack of new material to spread to. In mathematical terms, such a pattern of increase is called a logistic function and is characterized by an S shape. Milk bottle opening shows all the three features of 'wildfire': In 25 years, it spread from a single site to nearly 400 locations, with the number of milk bottle-opening birds presumably increasing from one to several hundred thousand; the spatial scale went from a single doorstep in one small town to several countries; the mathematical function that describes the spread of bottle opening shows two of the phases of a logistic, S-shaped curve, the slow start (1921–1936) followed by a sharp acceleration (1937–1947). The absence of the final slowdown phase of the logistic is probably due to the fact that, in 1947, the last year surveyed, there were still many places to which the new behavior could spread. However, the spread of bottle opening does not show one feature of mathematical models of cultural transmission. If an innovation originates in a particular place and spreads elsewhere through a kind of 'wave of advance,' then sites close to Swaythling should show early dates of bottle opening and sites progressively farther and farther away should show progressively later dates. This is not what we see. There is no clear relationship between distance from Swaythling and the time that has elapsed since the presumed origin of bottle opening in 1921.

This exception might lead us to think that something besides cultural transmission was behind the increase seen in bottle opening over time. What could that something be? Could many different birds all over the British Isles have discovered how to open milk bottles independently? Tits are very inquisitive. Consequently, it is quite possible that many of them could have invented the new behavior on their own. This possibility suggests a crucial control test that needs to be incorporated in any study of social learning. One or several observers placed in front of a knowledgeable demonstrator might very well adopt the new behavior, but they could be doing so on their own by trial-and-error learning, without actually needing demonstrations. In other words, tits might just be so exploratory that they easily discover by themselves that

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Figure 1 Blue tit opening a milk bottle. Photo courtesy of BBC Devon.

a bottle top can be pierced. Back in Britain, they might also have stumbled upon a bottle that had already been opened by another bird and drunk some leftover cream (it is the fat from the cream that the tits can digest, not the carbohydrates from the milk), without witnessing the bottle being opened by another tit. Even if naïve observers profited from watching demonstrators, the social information they acquired might have been vague and served only as a basis for individual perfection of the complete technique of milk-bottle opening. Researchers in Canada and Austria have set up laboratory analogs of bottle opening with captive tits and chickadees. Independent spontaneous discoveries, learning by feeding on an open bottle, and social learning, all occurred in these experiments, supporting the view that bottle opening probably spread in the wild via independent innovations as well as several learning processes, both social and nonsocial.

Imitation of Foraging Behavior

Our discussion of the spread of milk-bottle opening in birds suggests that individuals can obtain many types of information from each other. Social learning is a very general term used to describe *any* process through which one individual (the 'demonstrator') influences the behavior of another individual (the 'observer') in a way that makes the observer more likely to learn the behavior in which the demonstrator engages. Imitation has always been the most popular social learning process to study. Milk-bottle opening would be an instance of imitation if an observer bird learned to copy the precise technique used by its demonstrator. Birds that invented milk-bottle opening on their own, without a demonstrator, or birds that obtained only vague social information about what to fiddle around with might use any technique such as piercing the bottle cap with sharp downward pecks, or ripping it with a sideways motion. In contrast, an imitator would copy the precise technique that it saw demonstrated.

To understand how you could demonstrate imitation in birds experimentally, we can examine in some detail a study Fawcett and colleagues conducted with starlings (*Sturnus vulgaris*). The study has two important features, a 'two-action method' and a 'ghost control.' The two-action method ensures that we can separate the effects on an observer of seeing the behavior of its demonstrator from the effects of seeing a demonstrator act on a particular object. The 'ghost control' ensures that the information an observer obtains is truly social, that is, that the information comes from observing the behavior of the demonstrator itself and not from observing the effects of its demonstrator's behavior on the objects with which the demonstrator interacts.

In the 'two-action' method, each observer sees a demonstrator use one of two actions directed toward exactly the same portion of the environment. In the case of the study with starlings, the demonstrators were trained to remove a plug from a box to gain access to food either by pushing the plug downwards into the box (Figure 2(a)) or by pulling it upwards out of the box (Figure 2(b)). In the 'ghost control' condition, the plug was pushed or pulled via a fishing line controlled by the researchers, independent of the actions of the bird in the demonstrator compartment.

As is usual in such social learning experiments, the demonstrator and the observer were in adjacent but separate cages during training, so that the observer could watch the demonstrations but not interact with the demonstrator or the box during the experiment. In addition, the observer did not have access to a box of its own during the demonstration, so it needed to memorize the information it saw for later use.

After numerous demonstrations, the demonstrator was removed and the apparatus was presented to the observer. In Fawcett's experiment, observers that had seen a 'Pull demonstrator' were more likely to open the box by pulling the plug; those that had seen a 'Push demonstrator' were more likely to open the box by pushing the plug. Observers that had seen ghost control pushes and pulls were equally likely to push or pull. The fact that the observer starlings moved the plug *in the same way* as the demonstrator cannot be explained by any social learning process other than imitation. For example, observers were not simply attracted to the plug (stimulus enhancement) or to the same location as the demonstrator (local enhancement).

Learning from Other Species

As we mentioned before, several bird species learned to open milk bottles in Great Britain, Ireland, and continental Europe. Did they learn by watching blue tits, the first and most frequent openers? One of the usual assumptions of social learning is that copying members of one's own species should be more likely than copying members of

Figure 2 Typical response topographies of (a) a Push demonstrator and (b) a Pull demonstrator. Note the widely gaping beak of the Push demonstrator. Reprinted from Fawcett TW, Skinner AMJ, and Goldsmith AR (2002) A test of imitative learning in starlings using a two-action method with an enhanced ghost control. *Animal Behaviour* 64: 547–556, Copyright (2002), with permission from Elsevier Ltd.

other species. Why? Because the goals of other members of one's own species (food, mates, nesting sites, and predator avoidance), as well as the sensory equipment and the motor capabilities available to reach those goals, are more similar within than between species. If both a tit and a starling see a tit ripping open a milk-bottle top, the adequacy of the beak as a ripping instrument, the propensity to approach bottles or other man-made objects, and the motivational value of cream are all greater for an observing tit than for an observing starling. Despite all these reasons favoring social learning within species, we see a surprising amount of social learning between species.

On the tropical island of Barbados in the West Indies, Carib grackles (*Quiscalus lugubris*) and Zenaida doves (*Zenaida aurita*) often form mixed foraging flocks with bullfinches (*Loxigilla noctis*), Shiny cowbirds (*Molothrus bonariensis*), and Ground doves (*Columbina passerina*). Amid the many hotels, restaurants, and parks along the Barbados coast, members of all the five species readily join with others and feed together on food remnants left by humans.

Although these five bird species are all opportunistic feeders, they belong to two distinct avian orders that differ greatly in cognitive ability. Zenaida and Ground doves are Columbiformes that show less innovative behavior, perform worse on learning tasks in captivity, and have smaller brains than do Passeriformes, the order to which the grackles, bullfinches, and cowbirds belong. The Carib grackle is particularly innovative, belonging to the genus with the second highest number of reported innovations of all passerines in North America.

Carib grackles forage in small mobile flocks and are usually among the first birds to arrive when food becomes available. Although they boldly exploit feeding opportunities, grackles remain constantly vigilant for predators. As soon as one grackle in a flock detects danger, such as an approaching mongoose, monkey, dog, or threatening human, it gives alarm calls that induce flight and even more alarm calls in nearby grackles. Zenaida doves, in contrast, are rarely the first to discover a food source, feed alone or with their mates, and have no alarm calls of their own. They are territorial over most of Barbados and vigorously chase away other Zenaida doves that represent a threat to both mate and territory. However, Zenaida doves are rarely aggressive toward grackles.

The assumption that learning from members of your own species is easier than learning from members of other species implies that doves will learn from doves. However, the feeding ecology of doves and grackles suggests otherwise. Grackles are useful informers about food and danger, whereas doves are territorial competitors that fight with one another when they meet. In accordance with this ecological and social scenario, only one of eleven Zenaida dove observers learned the solution of a feeding task from a dove demonstrator, whereas the majority of doves learned the solution when it was demonstrated by a grackle.

Grackles, on the other hand, do not defend foraging territories against other grackles, and learned as readily from grackle as from dove demonstrators, copying the precise technique that each of their demonstrator species used: closed beak pecking by doves, and open beak probing by grackles. Grackles also learned to treat a previously innocuous stimulus (a painted pigeon decoy) as a potential predator (a dog decoy) when grackle alarm calls were paired with it.

Social Learning About Predators

Although most research on avian social learning concerns song and feeding, some of the most elegant work on avian social learning both within and between species has been done on habitat choice (see section 'Social Learning About Habitats and Nest Sites') and predator recognition. Curio and colleagues conducted the pioneering experiments on social transmission of predator recognition with European blackbirds (*Turdus merula*). In the presence of a predator, these birds emit mobbing calls that summon nearby individuals to cooperate in attacking the predator.

As a result of co-evolution between predator and prey, predator avoidance behaviors may become heritable, making individual trial-and-error learning about coevolved predators by their natural prey unnecessary. However, species change their ranges over time, predators' diets change with changes in predator and prey abundance, and humans introduce nonnative species. Thus, birds may be preyed upon by evolutionarily unfamiliar species that they do not innately recognize as predators. Because a bird might not get a second chance after an encounter with a predator, social learning to recognize predators could be very valuable.

For their experiments, Curio and colleagues devised an ingenious apparatus containing observer and demonstrator blackbirds in opposite compartments, separated by a hallway containing a presentation box (Figure 3). The compartment of the presentation box facing the observer contained an object that the blackbirds had never seen before, while the compartment facing the demonstrator contained a little owl (*Athene noctua*), a familiar predator that triggered vigorous mobbing in demonstrators. Because the demonstrator and observer could not see the compartment of the apparatus that the other was able to see the observer was tricked into perceiving the demonstrator as mobbing the novel object.

Curio used two novel objects similar in size to the little owl to test for cultural transmission of predator recognition: a dummy of an Australian honeyeater (*Philemon corniculatus*), a bird unfamiliar to wild blackbirds, and a multicolored plastic bottle. Observation of the demonstrator mobbing the owl led the observers to mob whichever novel object was presented in their compartment of the presentation box. Furthermore, the observers also mobbed that novel object when it was presented 2 h later in the absence of the demonstrator, showing that the observers had learned to treat that novel object as a predator. However, observers showed a stronger mobbing response toward the honeyeater than toward the bottle. This last result suggests that learning about danger is influenced by characteristics of the 'dangerous' stimulus.

After the original blackbird demonstrator, who mobbed the owl, trained a first blackbird observer to mob the honeyeater, that observer was used as a demonstrator for a second observer. This second observer learned to mob the honeyeater and then became the next demonstrator for a naïve blackbird, and so on. Information about the honeyeater passed along a chain of six blackbirds without any noticeable decrease in response strength.

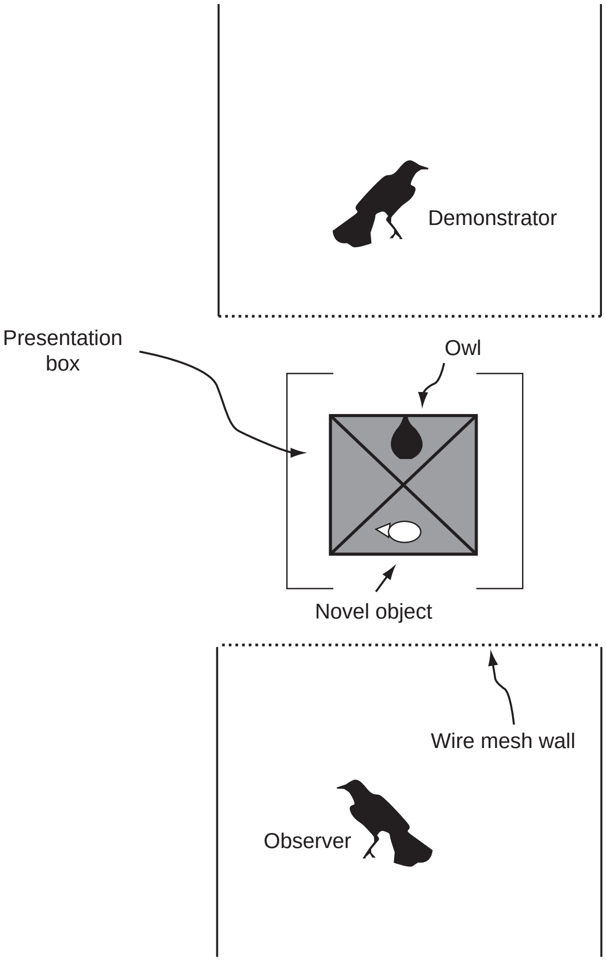

Figure 3 Experimental apparatus to test for social learning of predator recognition in blackbirds. The owl and novel object are positioned to elicit mobbing behavior in the observer towards the novel object through the demonstrator's mobbing of the owl. Reproduced from Vieth W, Curio E, and Ernst U (1980) The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: Cross-species tutoring and properties of learning. *Animal Behaviour* 28(4): 1217–1229, Copyright (1980), with permission from Elsevier Ltd.

Social Learning About Mates

The fitness of an animal depends not only on finding food and avoiding predators, but also on choosing a mate likely to maximize its reproductive success. If sampling candidate mates and comparing their quality are costly in terms of energy and time, then learning from the mate choice of others might provide the most efficient way to obtain a good match.

In some polygynous species such as black grouse (*Tetrao tetrix*), sage grouse (*Centrocercus urophasianus*), and white-bearded manikins (*Manacus trinitatis*), males gather at a 'lek,' an area where each male has his own tiny territory to display to the female audience. Often, only a very small number of the many males displaying on a lek acquire the great majority of matings.

Researchers studying black grouse in the field could not find any physical or behavioral traits that were consistently associated with the few successful males, while the pattern of female visits to leks suggested that females may simply copy the choices of females that mated before they did. If so, a male that was able to mate with a female that came to a lek early might well become overwhelmingly popular. In the field, however, it is difficult to separate social and individual factors governing mate choice, something that can be accomplished much more easily in laboratory experiments.

In the laboratory, female Japanese quail (*Coturnix japonica*), given a choice between an unmated male and one that they had seen courting and mating with another female, preferred the previously successful male. Furthermore, females that had watched a nonpreferred male mate with another female laid more fertilized eggs after mating with him than did females that did not see a nonpreferred male mate with another female.

While domesticated Japanese quail will court and mate whenever the opportunity arises, zebra finches (*Taeniopygia guttata*) form pair bonds that often last for life. One might expect mate choice copying to be rare in this and other monogamous species as compared to the polygynous quail and grouse species. However, in the dry areas of Australia where zebra finches abound, the time available for mate choice and reproduction is constrained; zebra finches have to be ready to reproduce whenever the unpredictable rainfalls provide necessary resources for rearing young. It might therefore benefit inexperienced females to copy the mate choices of others rather than spend time appraising mates for themselves. Indeed, laboratory experiments show that female zebra finches, like female Japanese quail, tend to copy the mate choices of other females of their species. More importantly for a monogamous bird, female zebra finches transfer their socially acquired preference to males similar to the one they had seen with a female. If a male seen mating wore a white leg band, virgin females presented with a pair of unfamiliar males preferred the one with a white leg band over the one with an orange leg band.

Social Learning About Habitats and Nest Sites

Imagine a young migratory bird, for instance, a collared flycatcher (*Ficedula albicollis*), arriving later than most of its fellows at a breeding area. Young birds have little prior breeding experience and need to find a nest site and start laying eggs as soon as possible. They do not have time to explore an area for a couple of weeks to pick the best site for a nest. In these conditions, a young bird might rely on the information provided by birds that have already settled in an area. These settled birds might be individuals of its own species or they might be birds of a resident species that stays in the area all year round. Researchers from both France and Finland have shown that flycatchers use cues both from resident birds of other species and by monitoring the breeding success of birds of their own species that have settled in an area before them to choose their nesting sites.

Doligez, Danchin, and colleagues manipulated the apparent breeding success of flycatchers by adding or removing chicks from a set of nests. Areas with added chicks were settled by a greater number of incoming flycatchers, while the opposite was true of areas where chicks were removed; control areas where chicks were simply taken from and put back in their original nest showed no change in the number of incoming flycatchers choosing to settle in them.

In a conceptually similar experiment, Seppänen and Forsman put nest boxes in four 5–12 ha. forest patches, two in the Swedish island province of Gotland and two in the Finnish city of Oulu. Once resident great and blue tit species had started building nests in these boxes, the researchers painted white circles around the nest box entrances in one forest patch in Gotland and Oulu, and white triangles in the other forest patch. They placed an empty nest box with the opposite symbol on the nearest tree similar to that containing the occupied nest box, to create the impression that the nesting tits in the patch had all chosen nest boxes with a particular geometric symbol.

The first males from the two migratory flycatcher species under study (Gotland: collared flycatchers *F. albicollis*; Oulu: pied flycatchers *F. hypoleuca*) arrived in the forest patches after the resident tits had started to nest. The researchers placed additional pairs of empty boxes, one box with a triangle, the other with a circle, 25 m from the nearest tit nest (**Figure 4**). Female flycatchers arriving and laying their eggs early did not have a preference for either symbol. However, as the breeding season progressed, female flycatchers started to match the nest box 'preference' shown by the tits, and more than 75% of the last third of females arriving at the breeding area chose a nest box with the same symbol as that on the tits' nest boxes.

Nest site choice used to be considered an innate and inflexible behavior. This field study shows, however, that migratory birds can copy the nest site choice of resident birds when the date of arrival at the breeding area imposes time constraints on individual learning.

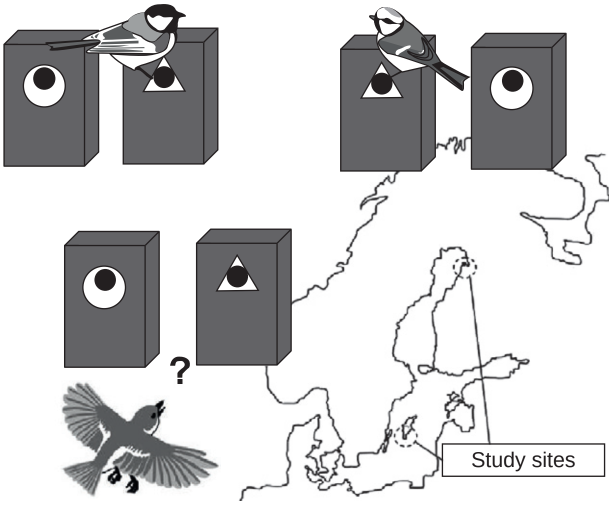

Figure 4 Experimental design to test for nest site copying between species. Once the resident great and blue tits had initiated nests, either a circle or a triangle was painted at the nest box entrance of all nests in a given forest patch. An empty box with the opposite symbol was placed 2–6 m away. Arriving migrant flycatchers were forced to choose between an empty nest box with the symbol 'preferred' by the resident tits and an empty nest box with the other symbol. Reprinted from Seppänen J-T and Forsman JT (2007) Interspecific social learning: Novel preference can be acquired from a competing species. *Current Biology* 17: 1248–1252, Copyright (2007), with permission from Elsevier Ltd.

Is Avian Social Learning Rare and Limited to Large-Brained, Social Species?

Blue tits are as good at individual learning as they are at social learning. They are far faster at both types of learning than are, for instance, Marsh tits (*P. palustris*, who are best at spatial learning). Across all species and individuals that have been studied in captivity, social and individual learning show positive correlations. Such positive correlations led most researchers to view social and individual learning as the same process, rather than treating them as separate cognitive modules that are adaptively specialized to different lifestyles.

Do social and individual learning in birds also correlate with brain size? Social learning does correlate with brain size in primates: the species that show the most social learning are also the ones that have the largest cortex. In birds, the trends are not as clear. In the field, the great majority of purported cases of avian social learning occur in a single suborder, the Oscines (songbirds). This bias precludes a fair analysis of overall trends throughout the class Aves.

Birds also differ from mammals in that a species' ability to imitate does not seem to vary with its brain size. Apes, for example, are far better imitators than are monkeys, and apes also have a larger cortex than any monkey species; similarly, large-brained dolphins are thought to be capable of imitation, whereas small-brained horses seem to be incapable of even the simplest form of social learning. In birds, even small-brained species such as Japanese quail and pigeons (*Columba livia*) seem to be able to pass the two-action test. At the other extreme of brain size, social learning in the kea (*Nestor notabilis*), an opportunistic, omnivorous, and large-brained parrot, has proved remarkably limited in two field studies, and keas also showed little evidence for imitation in laboratory experiments.

Inhibitors of Avian Social Learning

Researchers have identified several behavioral mechanisms that block or slow down social learning in birds: scrounging, bystanding, and territoriality. In many species, the discovery of a new food source, whether by social or individual learning, attracts the attention of others that often join the discoverer and feed with it. Joining can lead to theft or to simple scrounging. In scrounging, joiners unaggressively consume part of the food that the producer discovered rather than taking food away from its discoverer. In many cases, joining allows close observation of a producer's food finding behavior and seems to favor social learning by a scrounger. In other cases, however, scrounging can actually prevent social learning. In pigeons, competing with other scroungers, as well as identifying and following a given producer to its food discoveries, seems to interfere with observation of the producer's food-finding technique. Scrounger pigeons that have followed a producer to hundreds of its food discoveries will not perform the food-finding technique themselves after the producer is removed.

Like scrounging, the presence of bystanders seems to interfere with social learning in pigeons. If a caged demonstrator showing a food-finding technique is surrounded by several caged birds doing nothing but pacing in their cages, the observers' social learning is worse than in situations where only a single observer watches a demonstrator.

A final situation in which social learning appears to be impeded involves territorial boundaries. You may recall that in experiments on wild-caught birds, territorial Zenaida doves did not learn well from other doves. In the field, this implies that an innovation that occurs on one territory would not spread to adjacent territories. Unless grackles spread a new behavior, an innovation occurring on a dove territory would stay there. There are two examples where feeding innovations are known to have remained localized in a territorial species. As we have seen, winter flocks of tits learn socially to feed on milk bottles. However, flower piercing, an innovation performed in the spring when tits defend territories, has not spread. A similar localized pattern characterizes the opening of sugar packets by bullfinches in Barbados. Rather than observing and learning from an intruder opening sugar packets on its territory, a naïve territory holder aggressively attacks the intruder, preventing the innovative sugar-packet opening behavior from spreading beyond a restricted area. Packets offered to bullfinches foraging only a few hundred meters from the site where other bullfinches routinely open sugar packets are ignored.

Conclusion

Research on avian social learning has come a long way since the publication, 60 years ago, of the pioneering article on milk-bottle opening by tits. Many questions remain, however, concerning (1) the rarity of social learning in birds compared to primates and (2) the fact that all birds tested so far seem to pass the two-action test for imitation, regardless of their brain size. Among the most promising directions today are field experiments on breeding sites and predator recognition.

In tests of social learning about food in the wild, often, as we have seen in the case of bottle opening, it is impossible to separate individual and social learning processes. Only in controlled experiments can the effects of social and environmental cues about food be distinguished. In contrast, social and individual information can be manipulated separately when avian social learning tests involve alarm calls, mobbing calls, and the presence or success of others at breeding sites. In the coming years, field experiments in well-studied ecological settings on behaviors other than feeding should lead to rapid advances in research on avian social learning.

See also: Apes: Social Learning; Imitation: Cognitive Implications; Vocal Learning.

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