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Tradition and Imitation in Animals

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The Past

Charles Darwin spent a summer morning in the 1850s watching bumble bees as they cut small holes in the calyces of flowers and fed on nectar through the openings thus created. The next day Darwin observed large numbers of honeybees feeding at the holes that had been made by the bumble bees. He wrote in his journal, "I must think that the hive bees [honeybees] either saw the humble bees [bumble bees] cutting the holes and understood what they were doing and immediately profited by their labour; or that they . . . imitated the humble bees after they cut the holes and when sucking at them." (Darwin, in Romanes, 1884, p. 221). The question, implicitly raised here by Darwin, was whether animals could imitate one another's behavior, and it was destined to play a central role in the controversy between Alfred Russell Wallace and Darwin over whether human mind had evolved from animal mind by purely natural processes (Galef, 1988; Romanes, 1884).

Naturalists working in the decades after publication of the *Origin of Species* considered learning by imitation to be a faculty of mind that had its highest level of expression not in rational, adult Western man but in young children, savages and the feeble-minded. Consequently many 19th-century naturalists, among them George Romanes (Darwin's protégé and intellectual heir in matters behavioral), thought that the Darwinian view of a continuity of human and animal mind required that extant higher animals—similar in mental development to savages, children, and the feeble minded—should be able both to learn by imitation and to exhibit at least rudimentary traditions, homologous to those found in "primitive" human cultures.

Seeking evidence of imitation learning and tradition in animals, Romanes was quick to find both in the romantic anecdotal descriptions of animal behaviour that were the raw data of the comparative psychology of his day. Romanes's two classic texts in comparative psychology (1882, 1884) provide numerous examples which, if they are accepted at face value, provide incontrovertible evidence of both imitation learning and tradition in animals. For example, mice in Iceland had been reported by two observers of irreproachable reputation (an upper-class lady and a clergyman) to load supplies of berries onto mushrooms, to place these rations on dried cow patties, to launch their improvised, provisioned vessels into streams, and to then steer them from one stream bank to the other using their tails as rudders in the rush of water.

It was assumed by Romanes that Icelandic mice had originally learned such tricks by observing and then imitating humans provisioning and launching boats and that an ability to store provisions and to construct and steer rafts had become traditional in some mouse populations (Romanes, 1882). Perhaps as a consequence of Romanes's extraordinary zeal in seeking to persuade his contemporaries that animals can learn by imitation, even today, more than 100 years later, those who haven't thought much about the issue are often willing to accept rather unconvincing evidence of imitation learning by animals.

Of course, not all of Romanes's examples of imitation learning by animals were quite so improbable as his recounting of his correspondents' observations of yachting mice. Indeed, some seem very likely indeed. For example, a cat that happened to belong to Romanes's own

coachman had learned, without formal tuition of any kind, to escape from the garden in which it was customarily confined by leaping up, grabbing hold of the latch guard with one forepaw, and depressing the thumb piece with the other, while pushing at the gatepost with her hind legs. Romanes (1882, p. 422) proposed that the cat had first observed humans grasping the latch guard and moving the latch in order to open the gate and had then reasoned, "If a hand can do it, why not a paw? Then, strongly moved by this idea she made the first trial."

Of course, the problem with Romanes's interpretation is that the simple observation of an animal of unknown history performing a complex behavior in an uncontrolled environment provides very little information as to how that performance developed. Possibly Romanes's coachman's cat did learn to open the garden gate in the manner Romanes proposed. More probably, given what we know today about the ways in which cats and other animals learn to solve mechanical problems like that posed by a latched garden gate (Thorndike, 1898), the cat learned to open the gate by trial and error.

The Present

Although contemporary comparative psychologists often begin their studies of imitation and tradition in animals with observations made outside the laboratory, as did Romanes, the quality of contemporary observations is often quite different from that in Victorian times. Furthermore, today's observations in uncontrolled environments often serve as a starting point for behavioral analyses that permit conclusions to be drawn concerning processes supporting social learning. Modern techniques for experimental analysis of social learning processes are at a level far beyond those available during the last century.

In the remainder of this essay, I review a selection of contemporary research programs on imitation and tradition in animals; these programs were chosen to convey the flavor of modern work in the area.

Roof Rats in Israel

Aisner discovered some years ago that the pine forests of Israel were inhabited by roof rats (*Rattus rattus*) that subsisted on a diet consisting solely of pine seeds and water (Aisner &

Terkel, 1992). The extraction of pine seeds has been a stable tradition in these forest-dwelling rodents for many generations, and there is every reason to expect the persistence of extraction techniques that enable rats to survive in a relatively sterile habitat, where pinecones contain the only food sufficient to support a population of mammals.

Laboratory studies have revealed that the only efficient way for rats to remove the tough scales from a pinecone and gain access to the energy-rich seeds that they conceal is to take advantage of the architecture of pinecones, starting by chewing through the scales at the base of a cone and then removing, one after another, the spiral of scales running around a cone's shaft to its apex. Investigations of the development of the efficient spiral pattern of scale removal (which is necessary if rats are to realize a net energy gain while feeding from pinecones) have shown that only 6 of 222 adult rats, which were maintained in the presence of pinecones for several weeks while maintained at 85% of normal body weight and given a supply of fresh pinecones, were able to learn the efficient pattern of pinecone opening by individual trial-and-error learning. The remaining 216 subjects either ignored the pinecones or gnawed at them randomly in a way that did not permit the extraction of more energy from the pine seeds than was expended in their extraction and ingestion. On the other hand, essentially all young rats developed the efficient method of opening pinecones if they were reared by an adult rat that, in their presence, stripped scales from pinecones in the efficient manner.

Rats born to mothers that did not strip pinecones efficiently, but that were reared by a dam that exhibited the efficient means of stripping cones for her foster young, grew to be efficient strippers of pinecones. Rats born to mothers that stripped pinecones but foster-reared by dams that did not exhibit cone-stripping behavior failed to learn to strip cones efficiently. Clearly some aspect of the postnatal interaction between mothers that strip pinecones and the young they rear is important in the transmission of the behavior from one generation to the next (Aisner & Terkel, 1992; Zohar & Terkel, 1991).

Further experiments demonstrated that 70% of the young rats that completed the pinecone stripping that had been started appropriately by an experienced adult rat (or by an experimenter using a pair of pliers to imitate the pattern of scale removal used by experienced cone-stripping rats to start stripping a pinecone)

developed the efficient method of opening cones (Aisner & Terkel, 1992).

The tradition of pinecone stripping transmitted from generation to generation by roof rats living in the forests of Israel does not appear to be transmitted or maintained either by imitation or by any other complex social learning process. Rather, practitioners of the tradition of cone stripping alter the environment in which the young of their species develop by giving them access to partially stripped pinecones. The adults thus markedly increase the probability that young rats will acquire the traditional pattern of behavior.

Food Preference and Poison Avoidance by Norway Rats

Some years ago, an applied ecologist, Fritz Steiniger (1950), working to control the pest populations of Norway rats (*Rattus norvegicus*), discovered that when he used the same poison bait in an area for many months, he had great success at first, exterminating most members of a target population, but his later success rate was quite poor. Rats born to the few individuals that survived their initial intake of poison bait and that learned to avoid eating the toxic food rejected the poison bait without even sampling it for themselves. These young fed exclusively on safe foods available in their colony's territory and totally avoided contact with the poison bait that their elders had learned to avoid. This socially induced avoidance of poison baits, like the efficient stripping of pinecones, is a robust phenomenon that is easily captured in the laboratory. Consequently it has proven possible to analyze the social learning processes responsible for such traditions of food preference in rat populations, and five different ways in which Norway rats can bias their young to feed on one food rather than another have been identified.

Physical Presence of Adults at a Feeding Site. Galef and Clark (1971b) used a closed-circuit television system and a time-lapse video recorder to observe nine wild rat pups from three different litters taking their very first meals of solid food. All nine took their first meal under exactly the same circumstances: each pup ate while an adult was eating; each ate at the site where the adult was feeding and not at nearby vacant sites. Indeed, anesthetizing a rat and placing it near a feeding site made that site far more attractive to weaning rat pups than alter-

native sites with no anesthetized rat near them (Galef, 1981). Apparently, the simple physical presence of an adult rat at a feeding site makes that site attractive to young rats and markedly increases the probability that they will wean to whatever food is to be found there (Galef & Clark, 1971b).

Because young, wild Norway rats are exceedingly hesitant to eat any foods that they haven't eaten before, biasing a young wild rat to wean to any one food effectively prevents that rat from eating other foods (Galef & Clark, 1971a). A young wild rat may wait for as long as five days before it samples a novel food that has been made available to it, even if it does not have access to any familiar foods and the hesitancy to eat unfamiliar foods results in successive days of self-starvation (Barnett, 1958; Galef, 1970). Consequently, any behavioral processes that direct weaning young to a safe food results in the young avoiding any poison baits in their vicinity (Galef, 1985).

Olfactory Cues at a Feeding Site. Adult rats need not be present at a feeding site to guide the juveniles in their colony to that site. While eating, adult rats deposit residual olfactory cues both in the vicinity of a food source (Galef & Heiber, 1976; Laland & Plotkin, 1991, 1993) and on any food that they are eating (Galef & Beck, 1985). These odorants are attractive to rat pups and cause them to start feeding at marked sites in preference to unmarked ones. Work recently completed (Galef & Buckley, 1996) indicates that when returning to their nest sites after successful foraging expeditions, adult rats deposit olfactory trails that guide the subsequent movement of conspecifics. There is every reason to suspect (though there is as yet no evidence) that such odor trails can direct young rats to food sources that knowledgeable adults are exploiting.

Learning About Foods Prepartum. In addition to being able to influence a rat pup's choice of feeding site, and thus to influence indirectly its food preference, the mother of a litter of pups can provide information to her young that permits them to identify foods that she has been eating and thus, at least potentially, directly influences the choice of foods that her young will make.

Some food tastes or odors are experienced by rat fetuses while they are still in their mother's womb, and such an experience of fla-

vors *in utero* can effect a young rat's responses to foods after birth. Hepper (1988) fed pregnant rats garlic on days 15 to 21 of gestation and, within one hour of delivery one or two days later, gave the young born to his garlic-fed mothers to foster mothers (that had never been exposed to garlic) to rear. When the pups were 12 days old, they were offered a choice between two dishes, one containing garlic and the other containing onion. Young born to mothers that had eaten garlic during pregnancy showed a significant tendency to stay near the dish containing garlic, while pups assigned to control litters (delivered by mothers that had not eaten garlic during pregnancy) failed to exhibit a preference for either garlic or onion odor.

Although direct evidence of the effect of a mother's diet during gestation on the food preferences of rat pups at weaning is not yet available, it seems likely that pups that exhibited an enhanced preference for the odor of garlic on day 12 postpartum would also exhibit an enhanced intake of either garlic or garlic-flavored food when they wean on day 17 or 18 postpartum.

Learning About Foods While Suckling. Direct evidence is available of an effect of the diet eaten by a rat dam during lactation on the food preferences of her pups at weaning. By manually expressing milk from lactating rat dams that were fed different foods, feeding the milk thus obtained to rat pups, and then testing the pups for their food preferences at weaning, Galef and Sherry (1973) were able to show that the milk of a lactating rat contains flavor cues reflecting the taste of foods she has been eating. At weaning, pups prefer foods having flavors found in their mother's milk to foods containing other flavors (Galef & Henderson, 1972; Martin & Alberts, 1979).

Flavor Cues on the Breath of Rats. Both olfactory cues escaping from the digestive tract of adult rats and the smell of bits of food clinging to their fur allow young rats to identify the foods that adults with whom they interact have been eating (Galef, Kennett & Stein, 1985). Galef and his coworkers exposed young rats either to pieces of cotton batting dusted with a novel food or to anesthetized adult rats dusted with the same food, and then examined the food preferences of the pups. They found that although simple exposure to the smell of a food is not, in itself, sufficient to enhance a young rat's preference for the food it smelled, exposure

to the same food smell together with rat-produced odors markedly increased young rats' preferences for that food (Galef, Kennett & Stein, 1985; Galef & Stein, 1985). House mice showed a similar (and probably homologous) ability to influence one another's food preferences (Valsecchi & Galef, 1989).

Investigations of the nature of the rat-produced odor that increases the preference for foods experienced in contiguity with it have revealed that the relevant chemical is carried on the breath of rats (Galef & Stein, 1985). Both chemical analysis and behavioral studies suggest that carbon disulfide is the active agent in rat breath: mass-spectrographic analyses of rat breath reveal the presence of carbon disulfide in the air taken from the noses, but not from the mouths, of rats (rats breathe only through their noses, not through their mouths). Rats exposed to pieces of cotton batting both dusted with a novel food and moistened with a dilute carbon disulfide solution subsequently exhibit an enhanced preference for that food, while rats exposed to pieces of cotton batting dusted with the same food and moistened with water do not (Galef, Mason, Preti & Bean, 1988).

Summary

To the unsophisticated Victorian observer, the two previously discussed examples of traditional behavior in rodents might have appeared to provide evidence that rats can learn by imitation. However, in both cases modern analyses of the behavioral processes supporting the diffusion and maintenance of these feeding traditions in animals demonstrate unequivocally that the traditional feeding habits result from processes quite different from the humanlike imitative learning that Romanes and his contemporaries inferred from their observations of traditional behavior in animals. Indeed, it can be and has been argued (Galef, 1990, 1992) that all of the many traditions that have been described in free-living animals (from the milk-bottle opening exhibited by British birds (Fisher & Hinde, 1949) to the sweet-potato washing displayed by the troop of Japanese macaques living on Koshima Island in Japan [Kawai, 1965; Kawamura, 1959]) result from processes other than imitation learning.

Milk-Bottle Opening. In a laboratory study of the processes responsible for the spread of milk-bottle opening in populations of wild

birds, which was first described by Fisher and Hinde (1949), Sherry and Galef (1984) took into account the fact that the presence in an area of a bird that opened milk bottles and fed from them not only provided naive birds with demonstrations of opening behavior to imitate, but also provided open milk bottles from which naive birds could feed. In the laboratory, naive black-capped chickadees (*Parus atricapillus*) that were given experience in feeding from milk bottles that had been opened by a human experimenter while he was out of sight of the subjects were highly likely to learn to open closed milk bottles, as were chickadees that had the opportunity to observe other chickadees opening milk bottles (Sherry & Galef, 1984, 1990). However, a chickadee that watched a conspecific opening milk bottles was no more likely to open a closed milk bottle in its own cage than was a chickadee that had a closed milk bottle in its cage and a view of a conspecific without a milk bottle in its cage.

Although the evidence that small birds in Great Britain have established a tradition of opening milk bottles and feeding from them is convincing, it does not seem appropriate to attribute the spread of milk-bottle-opening behavior to learning by imitation.

Sweet-Potato Washing. Questions similar to those asked about the processes supporting the spread of milk-bottle opening can be asked about the spread and maintenance of the tradition of sweet-potato washing exhibited by Japanese macaques (*Macaca fasciata*) living on Koshima Island in Japan. Analyses both of the rate of the spread of sweet-potato washing and of changes over time in the probability of young animals learning the behavior cast some doubt on the interpretation that the behavior has resulted from learning by imitation (Galef, 1990, 1992). The average time taken by a naive monkey that eventually learned to wash sweet potatoes to begin to exhibit the behavior was more than two years after Imo, the behavior's originator, first exhibited it. A period of two years between first seeing a behavior performed and starting to exhibit that behavior seems much too long for learning by imitation to be involved in its propagation. Also, if monkeys learn to wash sweet potatoes by first watching others perform the behavior and then imitating them, one would expect increasing numbers of naive young animals to learn to wash sweet potatoes as, over the years, more and more models be-

came available to observe and imitate. Yet an analysis of Kawai's (1965) data has shown that the rate per year at which naive individuals learned to wash sweet potatoes remained essentially constant, since the number of models exhibiting the behavior increased from 1 to 4 over a five-year period (Galef, 1990). Furthermore, the relatively constant rate of recruitment to washing behavior was not caused by a steadily shrinking pool of the naive individuals available to learn the behavior. In each of the five years of Kawai's study, there were approximately 20 individuals in the population that had not yet learned to wash potatoes. Yet, each year, only one to four of them acquired the behavior (Galef, 1990; Kawai, 1965).

Other Traditional Behaviors

Other traditional behaviors that have been described in the last few years may, of course, prove to be the result of imitation learning. Boesch and Boesch (1984) have described the use by chimpanzees in Tai National Park in the Ivory Coast of hammers and anvils to crack nuts, and Goodall (1970, 1973, 1986) has provided detailed descriptions of the tradition of termite fishing, which is exhibited by chimpanzees at Gombe National Park in Tanzania. Behaviors like nut cracking and termite fishing are not seen in all wild populations of chimpanzees (McGrew, 1992). Consequently it seems reasonable to suppose, at least as a working hypothesis, that such behaviors are traditional in the populations that exhibit them in the sense that they are passed from one individual to another within a population by social learning processes of some sort (Galef, 1990). However, it is impossible to know how naive animals learn traditional behaviors until their acquisition has been analyzed under controlled conditions. Such analyses present a formidable methodological challenge to those interested in understanding both the genesis of animal traditions and the mental abilities of our closest relatives.

Imitation

It is tempting to dismiss as unconvincing anecdotes all reports of apparent imitation learning by animals of unknown history that have been observed in uncontrolled environments. However, one has to be cautious in cavalierly discarding evidence that contradicts the current *zeitgeist*, especially when that evidence has been

collected in a systematic way by experienced observers. For example, Russon and Galdikas (1993, 1995) have observed a large number of orangutan behaviors that appear to involve the imitation of the actions of humans. Orangutans free to move in and out of a rehabilitation center at Tanjung Puting National Park, Indonesia, have been seen engaging in literally dozens of complex activities (painting walls with a paintbrush and paint; attempting, unsuccessfully, to use a length of hose to siphon gasoline from a container; etc.) that resembled human actions that the animals either had observed or were observing when they appeared to imitate.

The need to entertain the possibility that animals can imitate and that, consequently, some of the traditional patterns of behavior observed in animal populations are the result of imitation has become increasingly apparent in the last few years with development of demonstrations, under controlled conditions, of what appear to be instances of imitation learning by members of several vertebrate species.

Norway Rats. Hungry rats that observed a conspecific demonstrator pushing a joy stick to the left for a food reward made significantly more left-pushing responses during the acquisition of the behavior of pushing the joy stick than did rats that had observed a demonstrator pushing a joy stick to the right (Heyes & Dawson, 1990). Further, when the axis of movement of the joy stick was rotated through 90 degrees between a subject's observation of a demonstrator and testing of the observer, the observers showed a significant tendency to push the joy stick in the same direction, relative to their own bodies, as had their respective demonstrators (Heyes, Dawson & Nokes, 1992). These results are consistent with the hypothesis that rats are capable of learning either responses or response-reinforcer relationships by observing the behavior of others.

An African Grey Parrot. Moore (1992) has studied the imitative behavior of an African grey parrot (*Psittacus erithacus*) in a unique and compelling paradigm. The parrot was housed alone in a room, which Moore visited several times each day. Whenever he left the room, Moore waved good-bye and repeated the word "ciao." Although the parrot was silent during Moore's daily visits, a microphone and video camera in the room permitted the observation of the bird's behavior after its visitor had left.

Such observations eventually proved highly informative.

About a year after Moore initiated his visits, his parrot began to say the word "ciao" and, at the same time, to wave one of its feet (or its wing) while alone on its perch. Subsequently Moore paired the phrase "Look at my tongue" with tongue protrusions, and the bird, while in isolation, started sticking out its tongue after speaking the appropriate phrase. Over a period of years, the parrot learned to emit several other gestures at the same time that it emitted the vocalizations that Moore had paired with them.

Chimpanzees. Custance, Whiten, and Bard (1995) used molding, shaping, and reinforcement to train two chimpanzees to reproduce familiar gestures after hearing the command "Do this!" They then modeled for the chimps 48 arbitrary actions (e.g. touching the nose, touching the shoulder, smacking lips, and chattering teeth) of varying degrees of novelty. Independent observers scored videotapes of the chimpanzees' behavior in the experiment and attempted to determine which action a chimp had been instructed to imitate. The observers were able to identify an experimenter's behavior correctly by watching videotape of a chimp's behavior far more frequently than one would expect by chance.

Tomasello, Savage-Rumbaugh, and Kruger (1993) systematically compared the imitative ability of human children 18 to 30 months of age with that of two groups of chimpanzees. The first group of chimps, those that had been "enculturated," had been raised in a humanlike cultural environment that included "language" (Wallman, 1992) instruction; the second group of chimps ("non-enculturated") had been raised mostly with others of their species. After being trained (in response to the command "Do as I do!") to copy experimenters' behaviors directed toward familiar objects, all subjects were tested with novel behaviors directed toward unfamiliar objects. Enculturated chimpanzees were, if anything, even more proficient at imitation than 30-month-old human children. Non-enculturated chimpanzees fared poorly at the imitation tasks.

Conclusion: The Future

A significant number of recent experiments provide data that are consistent with the hypoth-

esis that birds, rats, and chimpanzees may be capable of learning by imitation. Indeed, more purportedly successful controlled studies of imitation learning have been reported in the last five years than in the preceding 100. Of course, there will be controversy whether all (or any) of these demonstrations represent true imitation in the sense of learning a novel act from seeing it done (Thorndike, 1898; Thorpe, 1963). However, if the progress of the past few years continues unabated, it is clearly only a question of time before irrefutable evidence of imitation learning in animals is reported, assuming that such evidence is not already to hand.

Controversy concerning the interpretation of the presently available examples of imitation learning in animals is likely to center on the question of just how "novel" a novel act exhibited by a purported imitator need be in order to qualify as imitation learning. If learning (by observation) the appropriate context in which to perform a motor pattern already in one's repertoire is considered a legitimate instance of imitation learning, then we probably already have evidence of imitation in a variety of animals. If, on the other hand, the motor act performed in imitation learning must be truly novel to the performer, then one can question the adequacy of most if not all evidence of imitation available today.

A second issue that needs to be addressed concerns the relationship between demonstrations of an ability of some animals to learn by imitation in highly contrived laboratory situations and the role of imitation in the development of traditions in free-living populations of animals. As indicated in preceding discussions of traditions in Norway rats, roof rats, and chickadees, traditional patterns of behavior observed in the wild and brought into the laboratory for analysis have, to date, invariably proven to rest on learning processes other than imitation. Behavioral ecologists interested in the contributions of behavior to the survival and reproduction of animals rather than in the cognitive structures supporting behavior need to know whether an ability to learn by imitation, demonstrated in laboratory situations, is actually used by members of any natural population to acquire elements of their adaptive behavioral repertoires. An ability to imitate meaningless gestures or movements in the laboratory is one thing. An ability to use the capacity to imitate to acquire adaptive patterns of behavior in problem-solving situations is quite another.

Investigators both of animal traditions and of animal imitation have made impressive progress during the last decade. However, much useful work remains to be done before the questions raised by Darwin and Romanes about the role of imitation and tradition in the ordinary lives of animals are finally answered in a convincing fashion.

We appear to be on the verge of demonstrating that animals can truly learn by imitation, but we still have far to go to determine both the conditions under which that ability is expressed and whether an ability to imitate is used by animals in acquiring those traditions that promote their survival and reproduction in natural conditions.

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