
Interpretation and Explanation in the Study of Animal Behavior

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4. Tradition in Animals: Field Observations and Laboratory Analyses

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A field biologist, observing a troop of rhesus monkeys in an area where they have never before been studied, discovers many troop members behaving in a way that rhesus monkeys elsewhere do not. Suppose members of our hypothetical troop eat a type of plant other rhesus ignore or, even better, suppose they use a unique method to gather food or to process it.

Discovering a behavior, particularly a complex one, exhibited by only one of the many populations comprising a species would be a significant event in the career of any behavioral scientist. Surely, before very long, our field worker will want to tell colleagues about her observations. To do so, she is going to have to decide how she will refer to the unusual behavior she has seen.

The decision as to what to call a behavior found in only one of many populations of a species may seem trivial. However, dozens of such decisions, made over decades, have had cumulative, unintentionally detrimental effects on the study of behaviors unique to particular populations.

If our hypothetical field worker makes the conventional choice, there is little doubt that she will soon be referring to the unusual behavior she discovered as "traditional" in the troop she watched. Why contemporary field workers tend to label as "traditional" any behavior unique to a population is not obvious. Whatever the origins of the practice, it poses problems for students of animal behavior in general and of animal learning in particular.

In ordinary speech, description of a behavior as traditional is understood to mean that those performing the traditional behavior have both learned it in some way from others and can pass it on to naive individuals (Gove 1971); the English word "tradition" is derived from the Latin *traditio*, meaning the action of handing something over to another, or of delivering up a

possession (Lewis & Short 1969). Thus, calling a behavior traditional implies (or, at the least, may lead a listener to infer) that the user of the term believes that social learning of some sort played a role in acquisition of the "traditional" behavior.

Unfortunately for those who would call "traditional" all behaviors exhibited by the members of only one subpopulation of a species, development of behavioral differences between groups that appear to result from social transmission of behavior can sometimes be explained more parsimoniously in other ways. Consequently, by referring to all behaviors specific to local populations as traditional, important differences in their causes are obscured.

To avoid the semantic problem arising from use of the adjective "traditional" to refer to all behaviors that are unique to single populations, I shall refer to such behaviors as "locale-specific" unless I wish to indicate that social learning played some role in development of a behavior. I intend the term "locale-specific" to carry no implication as to the causes of a behavior being found in only some subpopulations of a species.

Referring to a socially learned behavior as traditional has had a second unfortunate consequence. Those with primary interest in functional analyses of behavior often assume that once it has been established that a behavior is, indeed, traditional in a population (i.e. that social learning played a role in its propagation), then the way in which the behavior spread is well understood.

Gaulin & Kurland (1976: 374) may have overstated the case in asserting that "Unless the spread of a behavioral trait is attributable to a particular diffusion mechanism, the concept of tradition is completely uninformative." They did, however, highlight an important issue. There are many different social learning processes that can result in transmission of behavior among individuals (Galef 1976, 1988). Consequently, from the perspective of those interested in understanding the development of behavior, calling a locale-specific behavior "traditional" answers few questions and raises many.

In sum, use of the term "traditional" in discussion of what I will call locale-specific behaviors has caused difficulties. Such use has led many to assume that locale-specific behaviors are socially transmitted, when no evidence of their social transmission is available. Calling behaviors traditional has also served to mask ignorance of the details of social-learning processes involved in the propagation of truly traditional, locale-

specific behaviors. Below, I consider, in turn each of these problems.

KNOWING IF LOCALE-SPECIFIC BEHAVIORS ARE TRADITIONAL

Three interacting types of information can influence the course of behavioral development in an individual: (1) genetically transmitted information received from parents, (2) socially transmitted information acquired from contemporaries, and (3) individually acquired information discovered as the result of transactions with non-social portions of the environment (Galef 1976). Consequently, systematic differences in the behavior of two populations of a species can be the result of any of three different processes or their interactions. Behavioral differences between populations can reflect: (1) differences in the frequencies of alleles that influence, either directly or indirectly, the course of behavioral development, (2) differences in the behavior of population members that influence behavioral development in new recruits to a group, or (3) differences in the environments in which local populations are living that produce systematic differences in the reinforcement population members receive for engaging in various behaviors. Consequently, although the most easily observed result of social learning might be behavioral differences among local populations of a species, discovery of differences in the behavior of two populations does not suffice to show that social transmission processes produced those differences (Galef 1976; Nishida 1987).

Less widely appreciated is the inverse proposition: Discovery of unique properties of the ecological situation or gene pool of a population exhibiting a locale-specific behavior does not exclude the possibility that the locale-specific behavior was socially learned. The relationship between findings in population genetics and ecology and the study of social learning is sufficiently poorly understood [see, for example, the exchange between Strum (1975, 1976) and Gaulin and Kurland (1976)] that consideration of a specific instance might prove useful.

The Vampire Finches of Wolf Island

The sharp-beaked ground finches (*Geospiza difficilis*) of Wolf (Wenman) and Darwin (Culpepper) Islands in the Galápagos Archipelago are classified as a distinct subspecies (*septentrionalis*) on the basis of measurements of the body parts

of adult males (Lack 1947, 1969; Schluter & Grant 1984). Members of the *septentrionalis* subspecies have, for example, longer wings and longer, more tapered beaks than do members of the other two subspecies of *G. difficilis* (Lack 1969; Schluter & Grant 1984). Presumably, such differences in morphology are heritable and reflect differences between the genotypes of members of the subspecies of *G. difficilis* found on relatively isolated Wolf and Darwin Islands (40 km apart and 100 km from the closest other island) and those subspecies of *G. difficilis* found elsewhere in the Galápagos.

The populations of *G. difficilis* on Wolf and Darwin Islands differ from those found elsewhere not only in presumably heritable, morphological characters, but also in the details of both the environment their members inhabit and the behaviors their members exhibit. For example, Wolf and Darwin Islands are not home to avian predators (owls and hawks) typically found elsewhere in the Galápagos. Possibly in consequence, *G. difficilis* on Wolf and Darwin Islands exhibit "a tameness..that is most striking" (Bowman & Billeb 1965: 41). *G. difficilis* on Wolf Island are also the only members of their species that inhabit an island both supporting a population of *Opuntia* cactus and lacking cactus-feeding-specialist bird species [*G. scandens* and *G. conirostris* (Grant 1986)]. Perhaps because of the absence of more efficient competitors on Wolf Island, *G. difficilis* there, but not *G. difficilis* found elsewhere, feed on *Opuntia* cactus and probe *Opuntia* flowers for nectar and pollen (Lack 1969).

More startling, *G. difficilis* on Darwin and Wolf Islands, but not others of their species, perch on the tails of masked and red-footed boobies (large, white-bodied seabirds of the genus *Sula*), draw blood by pecking at the base of feathers on the boobies' wings, and feed on the blood that flows from the wounds thus created. Also, on Wolf Island but not elsewhere, *G. difficilis* use their relatively long, tapered bills to pierce and eat the contents of seabirds' eggs (Bowman & Billeb 1965; Köster & Köster 1983; Schluter & Grant 1984). In sum, the *septentrionalis* subspecies of *G. difficilis* exhibits three locale-specific patterns of behavior--cactus feeding, egg feeding and blood feeding--the last of which is frequently referred to in the literature as a tradition of the finches of Wolf Island.

The case of blood feeding in *G. difficilis* is a particularly appropriate instance of locale-specific behavior to consider because there are available in the literature both detailed descriptions of the morphology, ecology, feeding habits and

biogeography of *G. difficilis* and suggestions as to the evolutionary forces responsible for the distribution of the morphological and behavioral phenotypes observed in the species [see Lack (1969) and Grant (1986) for examples]. The question before us is whether this wealth of information and theory relating to the ecology, taxonomy, natural history and evolution of sharp-beaked ground finches is of help in deciding whether the locale-specific behaviors of *G. difficilis* on Wolf Island are truly traditional. I think not.

To call a locale-specific behavior traditional is to propose an hypothesis about the factors leading to development of the locale-specific behavior in those individuals exhibiting it (Galef in press b). To test such an hypothesis, information is needed about social interactions that might increase the probability that an individual would exhibit the locale-specific behavior. Although hypotheses concerning the development of locale-specific behaviors may incorporate information about ecology or genetics, such developmental hypotheses must be at an individual, rather than an ecological or population-genetic level of analysis. For example, regarding the habit of blood feeding by *G. difficilis*, Bowman and Billeg (1965) have suggested that: (1) during the dry season, when free-living insects (the species-typical fare of *G. difficilis*) are hard to find, boobies often carry concentrations of black hippoboscid flies that are very conspicuous against the birds' white plumage and (2) finches might pursue flies onto the backs of boobies and develop the blood-feeding habit by accidentally puncturing the skin of boobies while in pursuit of flies. Although such an account fails to address the most interesting issue (why *G. difficilis* on Wolf and Darwin Islands feed on the blood of boobies, while those elsewhere do not), it is at a level of analysis appropriate for investigating that issue.

To test hypotheses about the origins of blood feeding, information is needed about the conditions associated with its development in individuals. Blood feeding by *G. difficilis* on Wolf and Darwin Islands might be the result of any of several factors: (1) heritable differences in tameness, (2) heritable differences in beak shape, (3) heritable differences in the tendency to attack seabirds, (4) differences in ecology that make blood feeding particularly energetically valuable on Wolf and Darwin Islands, (5) some sort of social transmission of the behavior of feeding on blood. Blood feeding might even develop in individuals in response to all five of these factors interacting in complex ways in the unique situation that is home to *G. difficilis septentrionalis*.

Of course field workers can often do much more than simply report the existence of locale-specific behaviors. Observation and description of social interactions during which naive individuals might acquire a traditional pattern of behavior can provide clues to the causes of the spread of a locale-specific behavior in a group of animals. Again a specific example may prove helpful in discussing general issues.

Development of Food Choices in Monkeys and Apes

Often by the time a young primate grows to adolescence, it has developed a locale-specific pattern of food selection similar to that of the adult members of its troop. How is this cross-generational convergence in acceptance and rejection of potential foods achieved? Is it, in fact, traditional?

Observations of social interactions provide useful clues. For example, as a result of study of the social situations prevailing when infant mantled howling monkeys (*Alouatta palliata*) fed for the first time on seasonally available leaves and fruits in the forests of Costa Rica, Whitehead (1986) concluded that some form of socially dependent learning governed ingestion of leaves, while a learning process independent of social influence governed feeding on fruits.

Whitehead reports that when feeding on leaves, infant howling monkeys: (1) looked at a parent before eating, (2) fed only when a parent fed, (3) ate only what parents ate, and (4) were subject to parental intervention when they chose incorrectly. On the other hand, when feeding on fruit, infants: (1) only occasionally looked at parents before feeding (2) sometimes fed independently and (3) ate or sampled fruits that adults did not. Thus, feeding on fruit by infant howler monkeys was generally less coordinated with adult feeding than was infant feeding on leaves.

Like howler monkeys eating leaves, 3- to 12-month-old vervet monkeys (*Cercopithecus ascanius*) tend to feed in synchrony with their mothers, to eat only the food items she does and, consequently, never even sample some foods that could be deleterious (Hauser 1988). Similarly, mother and infant chimpanzees share food (Silk 1978) as do mother and infant rhesus macaques (Kawamura 1959) and gorillas (Watts 1985).

While failure to observe infants feeding on the same food as their mothers may exclude certain modes of social learning as explanations of intergenerational congruence in food selection,

interpretation of observations of mothers and infants eating the same items is not so straightforward. Simple observation of feeding on the same foods by mothers and infants does not show that the feeding experiences of infant primates affect food selection by the young when they are grown. Common sense suggests that the food choices of adolescent primates should be affected by their feeding experiences as infants; there is even indirect evidence that infant feeding does affect adult food choice (Kawamura 1959: 45), but there is always the possibility of common sense misleading rather than enlightening. Again, an example might prove useful.

Development of Mouse Killing by Rats

Some years ago, I conducted a laboratory study of social influence on the development of predatory behavior in young Norway rats. I took pairs of mothers (both of whom reliably attacked mice), that had given birth on the same day, and cross-fostered half the litter of each mother to the other. I then placed each mother and her artificially constituted brood in a large enclosure. One mother in each pair, randomly assigned to the experimental condition, was given access to two mice a day, for 7 days, from the time that her pups were 16 days old. The other mother, assigned to the control condition, reared her young without seeing a mouse.

Once pups raised by mothers assigned to the experimental condition were old enough to wander about the enclosure, they exhibited tremendous interest in their mother's predatory behavior. Pups followed their dam to a mouse, chased the mouse, appeared to watch their mother kill it, pounced on the body of the mouse, and fed on it. When a beleaguered mother tried to carry her prey off to a secluded corner and eat in peace, her pups would often follow her, pulling vigorously at the dead mouse and acting very excited by their mother's predatory and carnivorous activities.

It seemed obvious that rat pups having such experiences, similar to those believed important in development of predatory skill by free-living domestic cats, tiger, cheetah, and meerkat (Ewer 1969), would exhibit facilitated development of their own predatory behavior. However, I could find no differences either in the probability that pups from control and experimental litters grew to be mouse predators or in the mean age at which pups from the two groups that did prey on mice made their first kills (Galef unpublished).

Common sense may suggest that early social feeding should influence development of later feeding behavior in rats or in primates. Unfortunately, observation plus common sense is not quite good enough.

Close observation of interactions between naive and knowledgeable individuals in appropriate contexts can increase the precision of hypotheses about how social transmission of behavior might occur [see Hauser (1988) for a particularly compelling example]. However, only controlled experiments can determine whether an observed, apparently relevant, social interaction actually plays a role in the development of a locale-specific behavior (whether, for example, the food eaten by an infant primate while in its mother's lap actually affects its food choices later in life). Further, as discussed more fully in Part 3, only experimentation under controlled conditions (see for examples, Galef 1980; Sherry & Galef 1984) can determine the particular social learning processes acting in a given instance (Galef in press a).

KNOWING HOW BEHAVIORS ARE TRANSMITTED

Those with relatively little interest in the development of behavior frequently attribute all traditions to learning by "observation" or by "imitation" (see, for examples, Strum 1976; Bonner 1980; Goodall 1986), although a century of laboratory research suggests that a variety of simpler kinds of social learning processes can be responsible for propagation of traditions. The possibility that traditional behaviors can rest on rather humble types of social learning was first discussed at length by Edward Thorndike (1898), one of the founders of experimental, animal psychology in North America. Unfortunately, Thorndike's approach to analysis of social learning processes has not yet everywhere replaced the view, prevalent earlier in the nineteenth century, that existence of animal traditions is indicative of an ability of animals to learn by imitation.

Pre-eminent among early advocates of interpretation of the development of behavior in animals as the result of learning by imitation was George Romanes, a protégé and disciple of Darwin's. The most influential, historically, of the many purported examples of imitation learning that Romanes described in his landmark monograph, *Animal Intelligence* (1882), concerned a cat that belonged to Romanes' own coachman. This animal had

learned, without formal tuition of any kind, to open a latched gate in Romanes' yard. The cat would jump up and hold the latch guard with one forepaw, depress the thumb piece with the other, and simultaneously push at the gatepost with her hind feet, thus opening the gate. Romanes argued that the cat must have observed humans grasp the latch guard, depress the thumb piece, and push open the gate. Then said Romanes (1882: 442), the cat must have reasoned, "If a hand can do it, why not a paw?" Motivated by this insight, the cat attempted to and succeeded in opening the latched gate.

Underlying Romanes' interpretation of the observation that the cat could open the gate are two implicit assumptions concerning the role of cognition in animal behavior: first, that the idea of a behavior can produce a behavior and, second, that the idea of a behavior can arise from observing others exhibit a behavior. While it would be foolish to get bogged down in the behaviorist-cognitivist debate, it is surely true that if animals can intentionally imitate motor patterns to achieve goals, as Romanes suggested, then animals are far more cognitive creatures than behaviorists have considered them to be.

Unfortunately, Romanes' observations of the behavior of his coachman's cat provide no compelling support for his interpretation. The cat could surely open the gate. However, observing an animal behave in an uncontrolled environment provides little useful information regarding the processes responsible for the development of the behavior the animal exhibits.

In the late 1890s, Thorndike brought the gate-opening behavior of cats into the laboratory and, under controlled conditions, examined the development of animals' solutions to a variety of mechanical problems. In Thorndike's best-known study, food-deprived cats were placed individually in a cage and observed on repeated trials as they learned to escape confinement and gain access to food by depressing a treadle located in the center of the cage floor (Thorndike 1898).

Considering the results of a number of conceptually similar experiments, Thorndike proposed that cats learned to solve all such mechanical problems, presumably including the opening of garden gates, by a gradual process of trial-and-error learning. Less generally appreciated is Thorndike's (1898) explicit rejection, on both empirical and theoretical grounds, of the possibility that animals would acquire such skills by imitation.

Thorndike had found that animals of several species, cats included, did not learn to escape from cages either by watching others do so or by observing humans demonstrate solutions. Indeed, Thorndike's data suggested that observation of a trained demonstrator by a naive individual would sometimes interfere with the trial-and-error learning in which a naive animal had to engage in learning to solve a problem.

Of course, Thorndike might not have been correct in asserting that animals do not imitate; there is, in fact, some more recent data than Thorndike's suggesting that animals do sometimes imitate (e.g. Dawson & Foss 1965). However, it is surely the case, given the large number of experiments performed during the last 90 years in which learning by imitation has not been found, that the burden of proving that learning by imitation underlies any particular traditional behavior surely rests on those who suggest the possibility.

Alternatives to Learning by Imitation for Social Transmission of Behavior

Just because simple observation of a performances does not often facilitate acquisition of behavior by naive animals does not mean that other sorts of social interaction are not important in development of behavior. Thorndike himself (1898) was careful to point out that a variety of social learning processes other than imitation could shape behavioral development in animals. This notion of a multiplicity of non-imitative, social-learning processes that influence behavioral development was an important contribution to understanding of animal traditions that was largely ignored for more than 50 years in a generally unsuccessful search for evidence of learning by imitation in animals.

Only during the last two decades have students of animal, social learning begun to examine systematically in the laboratory locale-specific behaviors observed in the field to discover how social learning might shape the development of patterns of behavior exhibited by free-living animals. One of the more extensively analyzed, locale-specific behaviors involves patterns of food selection first reported in free-living Norway rats (*Rattus norvegicus*). Below, I briefly describe this program of research on social influences on diet selection in rats as an example of the level of understanding of a traditional behavior that can be achieved within the framework Thorndike first proposed.

Traditions of Food Preference in Norway Rats

Fritz Steiniger, an applied ecologist, who worked for many years on control of rodent pests, observed in 1950 that, if a single type of poison bait were used in the same place for a long time, despite great initial success, with rats eating large quantities of bait and dying in large numbers, later acceptance of the bait was surprisingly poor. Steiniger observed that young rats, born to animals that had survived their initial encounters with a bait, never even tasted the bait that their parents had learned to avoid. Steiniger (1950) hypothesized that after learning not to eat a poisoned bait, adult rats marked the bait with their urine and feces and thus dissuaded their young from eating it.

My students and I have spent the past 20 years trying to understand the behavioral processes responsible for such locale-specific avoidance of poison baits by young rats. The first thing we learned from our experiments was that simple observation of a socially learned behavior, in this case avoidance of an adult-avoided food by juveniles, tells the observer little about the causes of that socially learned behavior.

Despite repeated attempts to demonstrate, as Steiniger had suggested, that adult rats that had learned not to eat a food would mark the food and thus cause naive others to avoid eating it, we have not been able to find any evidence consistent with that view (Galef & Clark 1971; Galef & Beck 1985). To the contrary, our results over 20 years have repeatedly suggested that, although naive young rats may appear to have learned not to eat a poison their parents are avoiding, young rats do not learn from adults to avoid a food (Galef 1985). In the laboratory, young wild rats learn through social interaction only to eat those foods that adults of their colony are eating; the young avoid a poisoned food in large part because they avoid eating any food they have not been socially induced to eat (Barnett 1958; Galef & Clark 1971).

The reason why we have been studying social transmission of food choice in Norway rats for so many years is that there is no simple answer to the question "How do young rats come to prefer foods that adults of their colony are eating?" In fact, we have uncovered four different behavioral proclivities in young rats each of which would suffice, in appropriate circumstances, to produce the phenomenon first reported by Steiniger (1950), a tendency for young rats to eat the same foods that adults of their colony are eating: (1) The milk of a mother rat contains cues reflecting the flavor of the foods she has been eating, and weaning

rats select solid foods to eat that have the flavors they were exposed to in their mother's milk (Galef & Henderson 1972; Galef & Sherry 1973). (2) Young rats prefer to eat together with adult rats; consequently, if foods are distributed in patches, weanlings tend to eat the same foods that adults of their colony are eating (Galef & Clark 1971; Galef 1977). (3) Adult rats deposit attractive odors both in areas where they eat and in foods they have eaten. The odors deposited by adults bias young rats to feed both in the areas and on the foods adults have marked (Galef & Heiber 1976; Galef & Beck 1985). (4) For some hours after eating a food, a rat emits olfactory cues that allow other rats to identify and induce them to prefer the food the recently fed individual has eaten (Galef & Wigmore 1983; Galef 1989).

The Status of Laboratory Studies of Locale-Specific Food Preferences in Norway Rats.

Unfortunately, just because we have found four, socially mediated, behavioral processes, each sufficient to explain Steiniger's (1950) observations of locale-specific food preference in rats, that does not mean that there are not four more waiting to be discovered. Further, data indicating that in simplified laboratory situations rats can exploit others as sources of information about where and what to eat do not show that those abilities are used (or usable) by free-living rats occupying more complex, natural habitat (Galef 1984).

Both the analysis described briefly in the preceding section (reviewed in greater detail in Galef 1977, 1986), and other laboratory analyses of traditional behaviors demonstrate that traditional patterns of behavior can be based on very simple social learning processes (see for example, Curio et al. 1978; Cook et al. 1985). Further, multiple determination of single, traditional behaviors makes it unlikely that occurrence of learning by imitation can ever be established by unobtrusive observation outside the laboratory (Galef 1984).

Unfortunately, experiments based on field observations of social interactions that might contribute to the propagation of traditional behaviors are few in number (see Marler & Tamura 1964; West et al. 1981; Curio et al. 1987 for examples). In the absence of a multitude of such experimental analyses, field reports of tradition and of learning by imitation have been accepted at face value and become part both of the textbooks and of the *Zeitgeist* of animal behavior. Below, I discuss the most widely

cited example of a locale-specific behavior assumed to be traditional and to spread by imitation learning, sweet potato washing by Japanese macaques (*Macaca fasciata*) living on Koshima Islet. In analyzing sweet potato washing, I consider two questions: Is sweet potato washing traditional? Is it based on imitation learning?

SWEET POTATO WASHING BY JAPANESE MACAQUES AT KOSHIMA

In 1953, an 18 month old, female macaque (Imo) began to take pieces of sweet potato covered with sand to a stream and to wash the sand from the potato pieces before eating them. Most Japanese macaques brush sand from pieces of sweet potato with their hands, but Imo started to wash sandy pieces of potato in water and, during the next 9 years, sweet potato washing became common in her troop.

Sweet potato washing did not spread randomly through the Koshima Islet macaques; spread of the behavior followed lines of social affiliation. First, potato washing was exhibited by Imo's playmate Semushi, who began to wash potatoes a month after Imo did. Sweet potato washing was then performed by Imo's mother (Eba) and by a second playmate of Imo's (Uni), both of whom began to potato wash three months after Semushi. During the following two years (1955-1956), seven more youngsters learned to wash potatoes, and by 1958, 14 of 15 juveniles and 2 of 11 adults in the Koshima troop had started to do so (Kawamura 1959; Kawai 1965; Itani & Nishimura 1973; Nishida 1987). According to the secondary literature, the spread of sweet potato washing behavior occurred because naive monkeys observed Imo and other sweet potato washers wash potatoes and then imitated them.

It will, of course, never be known with certainty what caused sweet potato washing to spread through the Koshima Islet troop 35 years ago. Possibly, some or all of the monkeys did learn to wash potatoes by imitating Imo or others. However, as discussed below, interpretation of the spreading of washing behavior through the Koshima troop of macaques as either traditional or due to imitation is open to challenge.

One property of sweet potato washing that makes it seem a likely candidate for social propagation is the bizarreness of the behavior and the intuitive improbability of many monkeys learning independently to wash potatoes. It is, therefore, surprising to find that sweet potato washing has been observed in

four other provisioned troops of Japanese macaques in addition to the troop at Koshima (Kawai 1965). Imo was not so creative a "genius" as the secondary literature suggests and potato washing is not so unlikely a behavior for monkeys to develop independently as one might imagine. Recently, Visalberghi (unpublished) reported very rapid learning of food washing by both crab-eating macaques (*Macaca fascicularis*) and tufted capuchin monkeys (*Cebus apella*) in captivity. Apparently food-washing behaviors can be learned relatively easily by monkeys and could become common in a troop through processes other than imitation of a rare "creative genius." However, even if monkeys find it easy to learn to food wash in appropriate circumstances, it is not obvious why sweet potato washing became widespread among the macaques at Koshima, but not among other troops of macaques provisioned with sweet potatoes.

It has been suggested (Green 1975) that maintenance of sweet potato washing in the Koshima troop might not be the result of natural processes. For many years the Koshima troop has been provisioned by caretakers, local people employed to supplement the natural diet of the monkeys with sweet potatoes, wheat, and peanuts. When Green visited Koshima in the 1970s, he observed that the woman who was provisioning the macaques there, and who had been a caretaker for many years, gave sweet potatoes only to those monkeys that washed them. She thus reinforced monkeys for engaging in sweet potato washing. Green suggested that such human intervention may have maintained potato washing in the Koshima troop while it died out in other groups in which individuals initiated it. If social learning of any kind played a role in the spread of sweet potato washing at Koshima, human maintenance of washing behavior by monkeys that began to wash spontaneously could have promoted spread of the behavior. Why should caretakers at Koshima have bothered to maintain potato washing by their charges? Perhaps because some of the local income derived from visiting scientists and tourists who came to see the monkeys perform, stayed in the local inn, and gave tips to the caretakers (Green personal communication).

Green (1975) also pointed out that, while foraging, a macaque troop is spatially organized in such a way that the likelihood of individuals being close to or distant from a human reinforcing agent would vary with their age class and matriline. Hence, human intervention could produce a pattern of spread of washing behavior that would make the behavior appear traditional to an unsuspecting observer.

Of course, even if potato washing were maintained in the 1970s by caretakers, it might originally have spread by imitation learning. There are, however, a few things that make me question this conclusion. First is the fact that so many of the locale-specific behaviors observed in the Koshima troop, [e.g., sweet potato washing, wheat placer mining, caramel eating, and give-me-some behavior (Kawai 1965)], involved food provided by humans. None involved an indigenous food.

Second, some locale-specific behaviors seen in the Koshima troop, clearly not the result of social transmission, spread in a fashion strikingly similar to sweet potato washing. Consider bathing behavior. Before the summer of 1959 none of the members of the Koshima troop would do more than dip their hands and feet in the sea. That summer one of the caretakers, Mrs. Mito, induced a 2 year old male (Ego) to walk into the water of Otamari Bay by throwing peanuts (one of Ego's favorite foods) into the sea. Over a period of 3 years, Mrs. Mito induced 63 percent of the Koshima monkeys to enter the water. Japanese scientists observed and described the spread of bathing behavior. Like sweet potato washing, bathing behavior was originated by a juvenile (Ego), spread through the originator's peer group, on to their mothers, and then from those mothers to their young (Kawai 1965). Orderly spread of a behavior along social lines may not be evidence of tradition. It is surely not evidence of imitation learning.

Third, there are two parameters of the spread of sweet potato washing, generally unmentioned in published descriptions of the spread of the behavior, that lead me to suspect that social learning may have had little to do with the prevalence of sweet potato washing at Koshima. In all discussions of learning by social transmission with which I am familiar, it is assumed that an advantage of social learning over trial-and-error learning is that social learning is more rapid than trial-and-error learning. One sign of social learning should, therefore, be a relatively rapid spread of a behavior through a population.

Imo invented sweet potato washing in September of 1953, when 18 months old. At that time, there were eight members of the Koshima troop that were Imo's age or older who eventually came to wash potatoes. One of the eight, Semushi, began to wash potatoes in October of 1953. Two other troop members, Uni and Imo's mother Eba, started to do so in January of 1954. The remaining five of the eight monkeys acquiring the behavior began to wash potatoes in 1955 ($\bar{n} = 1$), 1956 ($\bar{n} = 2$), and 1957 ($\bar{n} = 2$). Both the mean and median times to acquisition of sweet

potato washing (for those who ever developed the behavior) were roughly 2 years after Imo started to demonstrate it. Such painfully slow propagation of behavior fails to provide support for the hypothesis that the behavior was learned either by imitation or by simpler forms of social learning. Wheat placer mining, a second often-cited, locale-specific behavior of the Koshima troop, spread even more slowly than did sweet potato washing (Kawai 1965; Nishida 1987)

Further, most models of social learning assume that the rate of spread of a socially transmitted behavior should increase with an increase in the number of its practitioners. In other words, the rate of recruitment to a behavior should be positively correlated with its frequency of occurrence in a population, until saturation occurs. Figure 1 shows, for each year from 1953 to 1958: (1) the number of monkeys in the Koshima troop old enough to sweet potato wash (i.e. > 1.5 years of age), (2) the number of monkeys demonstrating sweet potato washing, and (3) the number of monkeys that learned the behavior during that year.

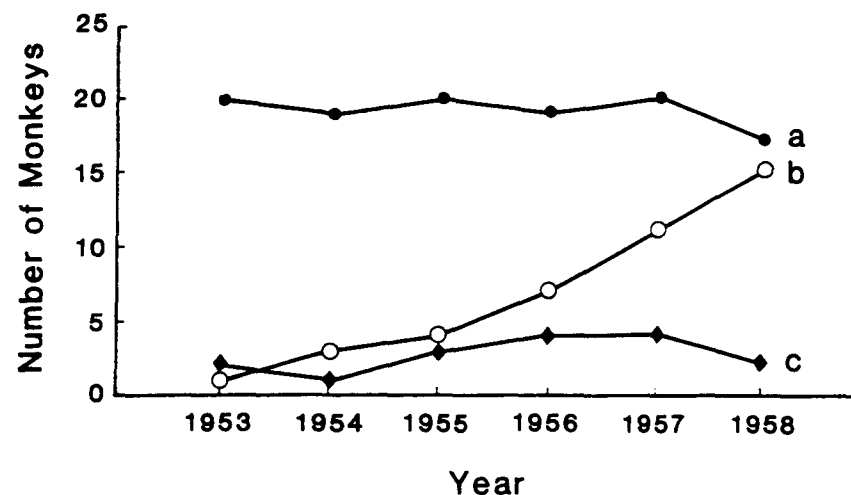


Figure 1. The number of monkeys at Koshima in each year from 1953 to 1958: (a) both greater than 1.5 years of age and not sweet potato washing, (b) sweet potato washing and (c) that began to wash sweet potatoes during the year. Figure prepared from data in Kawai (1965).

As can be seen in the figure constructed from data published by Kawai (1965): (1) the potential learners remained essentially constant over time, (2) the number of demonstrators rose dramatically (3) the rate of recruitment to the behavior did not increase. These data do not suggest that social learning was possible for the development of potato washing in the individual. It came to exhibit it.

Last, it is, perhaps, considering Kawai's own statement (1965: 8) of the reasons that led him to suggest that social interactions were possible for the acquisition of sweet potato washing behavior in macaques.

Sweet potato washers eat potatoes at the edge of water. So that potato skin is scattered around at the bottom of the water. Babies, who have the experience of eating potato water at the beginning of the development of feeding behavior, are conscious of the association of potato water. In the process of learning, eating potato by getting it up out of water is to them equally on a level as eating natural food.

Being always with their mothers, babies stare at their mothers' behavior while they are doing sweet potato washing behavior. In this manner, infants acquire sweet potato washing behavior through their mothers' behavior.

The question is whether, all, or only one of the interactions among demonstrators, mothers, and infants mentioned by Kawai in the preceding quotation were either necessary or sufficient for the spread of sweet potato washing through the Koshima troop. Observation does not suffice to answer the question. Surely, observation is not sufficient to show that imitation of one by another was responsible for propagation of potato-washing behavior, as so many secondary sources have suggested.

The point of all this pe nit-picking is not that the monkeys at Koshima did not to sweet potato wash either socially or by imitation. They well have. Because the learning occurred more than 30 years ago, under conditions where the processes responsible for the spread of the behavior could not, in principle, be determined, we never know what role social learning or learning by imitation played in the spread of potato washing at Koshima. There are, however, alternatives to social

learning and imitation learning that can explain the spread of sweet potato washing through the Koshima troop: (1) each monkey acquired the behavior independently (as have monkeys elsewhere), taking an average of more than 2 years each to do so; (2) the monkeys at Koshima were individually shaped by their caretakers to wash sweet potatoes; and (3) early experience of feeding on potato scraps taken from water in some way increased the likelihood that monkeys would later bring pieces of potato to the water and wash them. Without compelling evidence that sweet potato washing was either traditional or learned by imitation, and I know of none, there is no reason to treat the behavior as a paradigmatic case both of tradition and of imitation learning, as is often done.

CONCLUSION

Careful observation of the behavior of many different populations of a species in the field is the only way to discover locale-specific patterns of behavior. Investigations of the ecological setting in which populations do and do not demonstrate a locale-specific behavior, physical measurements that reveal the distribution of genotypes across environments, and descriptions of social interactions that might result in propagation of a behavior are frequently the best sources of hypothesis about the causes of differences in behavior among populations. Experimentation in controlled conditions is often needed to determine whether a locale-specific behavior observed in the field can be acquired by social learning and should be considered traditional. Experimentation in the laboratory is needed to determine the types of social interaction that might permit social transmission of a traditional behavior (Galef in press a).

It is important to keep in mind that simple acquisition processes can be responsible for rather complex behavioral outcomes. Until the processes underlying the development in individuals of particular locale-specific behaviors are examined carefully, observations of locale-specific behaviors in a species, though thought-provoking, do not provide persuasive evidence either of tradition or of imitation learning. A healthy skepticism, attention to ecological detail, and a commitment to empiricism are necessary precursors to understanding of the processes leading to development of local-specific behaviors in animals.

