

THE QUESTION OF ANIMAL CULTURE

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In this paper I consider whether traditional behaviors of animals, like traditions of humans, are transmitted by imitation learning. Review of the literature on problem solving by captive primates, and detailed consideration of two widely cited instances of purported learning by imitation and of culture in free-living primates (sweet-potato washing by Japanese macaques and termite fishing by chimpanzees), suggests that nonhuman primates do not learn to solve problems by imitation. It may, therefore, be misleading to treat animal traditions and human culture as homologous (rather than analogous) and to refer to animal traditions as cultural.

KEY WORDS: Animal tradition; Animal culture; Imitation and learning; Koshima Island (Japan); Gombe National Park (Tanzania); Nonhuman primates

"Imitation is natural to man from childhood, one of his advantages over the lower animals being this, that he is the most imitative creature in the world, and learns at first by imitation." (Aristotle 1941:4486)

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It has become increasingly fashionable during the past decade for scientists to see evidence of humanlike mental processes in animals as diverse as chickens and chimpanzees. The possibility that animals may be conscious, deceitful, self-aware, Machiavellian, etc., is under serious consideration. Consequently, use by scientists of vocabulary traditionally used to describe human activities to describe the behavior of animals is probably more frequent today than at any time since the latter part of the nineteenth century, when George Romanes, Darwin's protégé and intellectual heir in matters behavioral, wrote at length of similarities in the psychological processes underlying the behavior of animals and humankind (Romanes 1882, 1884).

Is it reasonable, in light of current knowledge, to discuss the politics of chimpanzees (de Waal 1982), the deceptions of chickens (Gyger and Marler 1988) or the feigning of injury and death by piping plovers and hog-nose snakes (Burghardt 1991; Ristau 1991)? Quite honestly, I don't know. Neither, I think, does anyone else.

Some feel (and I confess that this is my own bias) that it is probably best for scientists to be conservative, to adopt the simplest descriptions and explanations of behavioral phenomena consistent with available evidence (Morgan 1894; Williams 1966). Others have argued cogently that the goal of behavioral studies is to describe and explain behavior as correctly, not as simply, as possible. We should, in Wilson's (1975:30) words, "enumerate all possible explanations, improbable as well as likely, and then devise tests to eliminate some of them."

For the behavioral scientist, the problem posed by Wilson's program of hypothesis generation and subsequent testing (consistent though it may be with the views of Hempel, Popper, and Platt) is that eliminating explanations, even the more unlikely among them, takes more time than might be anticipated. During the decades when testing and elimination of alternative hypotheses is underway, a question remains as to whether it is useful to describe or explain behavior in terms of hypothesized processes for which little or no evidence has yet been developed. Perhaps, as the more conservative insist, explanation and description should be restricted to processes that have passed rigorous tests, that have been repeatedly demonstrated.

On the other hand, during the past half century, the traditional, conservative approach to analysis of animal behavior led research in experimental animal psychology down paths of steadily decreasing interest to the rest of the community of life scientists. Clearly, it is not always the case that the conservative approach to description of animal behavior is the most heuristic one (much as I might like it to be).

The question of whether animals exhibit culture is part of this wider debate regarding the relationship between human and animal behavior and the appropriate way to discuss the complex behaviors of animals.

PROBLEMS OF DEFINITION

Lumpers and Splitters

Disagreement concerning use of the term *culture* to describe the products of social learning by animals is as great as is disagreement concerning the proper labels to use to describe other humanlike behavioral phenomena in animals. Sahlins (1976:13), for example, views culture as an emergent property of only the most complex brains. He suggests that "Culture . . . developed in the hominid line about three million years ago." On the other hand, Bonner (1980) entitled a chapter concerned with motility in bacteria "The Early Origins of Cultural Evolution," and Wilson (1975:168) has suggested that "culture, aside from its involvement with language, which is truly unique, differs from animal tradition only in degree."

Clearly, in attempts to categorize social influences on behavior, as in other taxonomic enterprises, there are both "lumpers," like Bonner and Wilson (who regard all traditions as resting on similar fundamental processes), and "splitters," such as Sahlins (who would draw sharp distinctions among types of traditions to be found in different branches of the phylogenetic tree).

Like Sahlins, I am of the splitter persuasion. Unlike Sahlins, I would draw distinctions among types of traditions (of which culture is an instance) based not on differences in the supposed complexity of vertebrate brains, but on differences in the behavioral processes that support particular traditions (Galef 1988).

Tradition and Culture

In ordinary speech, a behavior described as "traditional" is one that has both been learned in some way from others and can be passed on to naive individuals (Gove 1971); the English word *tradition* derives from the Latin *traditio* (Lewis and Short 1969), meaning the action of handing something over to another or of delivering up a possession. Consequently, labeling a behavior "traditional" implies that social learning of some sort played a role in the acquisition of the behavior by those exhibiting it (Galef 1976, 1990; Nishida 1987).

Some animal behaviorists have proposed that the words *culture* and *tradition* should be considered synonyms. For example, "[an] individual's behavior can also be modified by its mother or by the group in which it is raised. If such social modification spreads and perpetuates a particular variant over many generations, then we have 'culture' in the broad sense in which a student of animals can use the term. . . . The definition

states nothing about the precise mechanism of social modification (because it is unknown in most cases)" (Kummer 1971:13).

Kummer's definition of culture, and others like it, rests on analogy rather than on homology. The definition explicitly accepts as cultural all traditions, i.e., all socially transmitted modifications of behavior, regardless of the processes that resulted in their propagation. For example, a scent trail that resulted in many generations of a population of ants following the same path each day from nest entrance to feeding ground would be defined as an agent for the propagation of culture. This usage seems to me to violate the usual meaning of the term *culture*.

On the other hand, Goodall (1973:144–145) has suggested that whether behaviors may be considered to have been influenced by culture "depends on the manner in which they were acquired by the individual, i.e., the kind of learning process involved." As a psychologist, I might wish to make finer distinctions than would Goodall regarding "the kinds of learning processes involved" in development of a tradition to decide whether a given traditional pattern of behavior was cultural. Nonetheless, Goodall and I clearly wish to approach the problem of defining culture in the same way (and in contradiction to that proposed by Kummer) in terms of the social learning processes supporting propagation of behavior.

Culture in human populations is believed to be largely a result either of teaching (see Premack 1991 or Mead 1970 for discussion of the contribution of pedagogy to human culture) or of learning by imitation (see Boyd and Richerson 1985 for discussion). There is little question that humans are able to teach and that, even as infants, they can learn to do acts simply by watching others perform those acts. Indeed, I know of no one who has questioned either assumption. Further, there is every reason to believe that humans use their ability to imitate to acquire patterns of behavior that form a part of human culture (see, for example, Vygotsky 1962; Bandura 1977; Speidel and Nelson 1989). The relative importance of pedagogy and of learning by observation and imitation in human acquisition of culture is an open question, but one that lies beyond the scope of this paper.

On the other hand, a century of laboratory analysis of the learning processes supporting traditions in animals (see Galef 1976, 1988, 1990 for reviews) indicates that animal traditions are generally a result of such processes as "local enhancement" ("apparent imitation resulting from directing the animal's attention to a particular object or to a particular part of the environment"; Thorpe 1963:134) or "social facilitation," the energizing of responses as the result of the simple presence of conspecifics (Clayton 1978; Zajonc 1965), which are quite different from the behavioral mechanisms that underlie propagation of culture in humans (see Galef 1988 for a review). Consistency in usage would require that

animal culture be defined as animal tradition that rests either on tuition of one animal by another or on imitation by one animal of acts performed by another.

There are, of course, differences between animal tradition and human culture in addition to differences in the learning process that support them. For example, human culture accumulates over generations and can lead to invention and transmission of increasingly complex behaviors. No one has claimed that any animal learns any behavior from conspecifics that it could not learn independently through interaction with its physical environment. With respect to the present definition, these differences between the traditions of animals and those of humans are seen as consequences of differences in acquisition processes rather than as defining features.

Teaching and Imitation

Barnett (1968:748) proposes that to identify teaching we need establish two things: "first, the behaviour of the putative teacher must induce a specific change in the behaviour of another. . . , second, the teacher's behaviour must be persisted in, and perhaps adapted, until the pupil achieves a certain standard of performance." Thorpe (1963:135) defines true imitation as "the copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency."

As far as is known, no nonhuman animal teaches, in Barnett's (1968) sense of the term. Even adult chimpanzees rarely handle objects in such a way as to engage the attention of infants (Bard and Vauclair 1984; but see Boesch 1991 for interesting observations). Purported examples in the literature of tuition in animals are restricted to a few observations (mostly of primates) either preventing infants or juveniles from contacting potentially dangerous objects (Goodall 1973; Kawamura 1959; Menzel 1966; Nishida et al. 1983) or "encouraging" an infant to walk by moving a short distance from it and then pausing (Altmann 1980; Milton 1988). In the former cases, neither the frequency with which the naive are prevented from contacting desirable objects by adults nor changes in the behavior of the naive as a result of purported teaching episodes have ever been assessed. In the latter, there is no evidence that the adults are teaching. Adults motivated both to locomote and to remain close to their young might be expected to exhibit hesitant locomotory patterns, and there is no reason to invoke tuition to explain their behavior. Consequently, I find myself in agreement with those (Ewer 1969; Hinde 1971; Premack 1991) who reject such observations as evidence of pedagogy in nonhuman animals (but see Barnett 1968; Caro and Hauser 1991).

More contentious is the question of whether nonhuman animals are

able to imitate the behavior of conspecifics, and more specifically, whether any traditional patterns of behavior exhibited by members of some groups of animals living in natural habitats are, in fact, the result of learning by imitation. In terms of the approach to definition of culture proposed above, the empirical issue is whether traditional behaviors observed in some groups of animals are the result of imitation of one animal by another and, therefore, cultural in the sense that term is defined above.

PURPORTED EVIDENCE OF CULTURE IN ANIMALS

The terms *culture* and *imitation* appear in the indices of most contemporary introductory texts in animal behavior. On the relevant pages, one usually finds an account of one or more locale-specific behaviors: of chimpanzees in Gombe National Park using twigs as tools to "fish" for termites (Goodall 1986), of Japanese macaques on Koshima Island washing sweet potatoes (Kawai 1965; Galef 1990), or of various species of small birds in England opening milk bottles and drinking cream from the surface (Fisher and Hinde 1949; Sherry and Galef 1984, 1990). Textbook accounts of the development and spread of these behaviors often lead the reader directly to the conclusion that the only explanation for the existence of idiosyncratic behaviors in some primate troop or bird flock is their spread from one individual to another by imitation learning. For example, regarding the Gombe chimps, Bonner (1980:172) reports that successful fishing for termites "requires a number of skills and especially knowledge about where to poke and what kind of stick is best and how to twiddle the stick. These accomplishments are clearly learned by imitation and are passed down as cultural traditions." There are, however, alternatives to this selective recounting of observations of differences in the behavior of members of different animal populations (Galef 1976, 1990; Nishida 1987).

Below, I discuss two of the most frequently cited instances of animal culture, sweet-potato washing and termite fishing. It is my intention to question the validity of the usual textbook interpretation of these behaviors as instances of learning by imitation and, consequently, as instances of animal culture.

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 population of macaques; rather, 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 wash potatoes three months after Semushi began. 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 washing potatoes (Itani and Nishimura 1973; Kawai 1965; Kawamura 1959; Nishida 1987). According to the secondary literature, the spread of this behavior occurred because naive monkeys observed Imo and others wash sweet potatoes and then imitated them; sweet-potato washing was cultural.

It will, of course, never be known with certainty what caused sweet-potato washing to spread through the Koshima troop of macaques 40 years ago. Possibly, some or all of the monkeys did learn to wash potatoes by imitating either Imo, the initiator of the behavior, or others. Interpretation of the spread of washing behavior through the Koshima troop of macaques as the result of imitation learning, however, can be questioned.

One property of sweet-potato washing that makes it seem a likely candidate for propagation by imitation 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 as creative a "genius" as the secondary literature suggests, and potato washing is not as unlikely a behavior for monkeys to develop independently as one might imagine.

Recently, Visalberghi and Fragaszy (1990b) have reported very rapid learning of food washing by both captive crab-eating macaques (*Macaca fascicularis*) and captive tufted capuchin monkeys (*Cebus appella*). Apparently, food-washing behaviors are learned relatively easily by monkeys and can become common in a troop through processes other than imitation of a rare "creative genius." Even if monkeys find it easy to learn to wash food in appropriate circumstances, however, it is not obvious why sweet-potato washing became widespread among macaques at Koshima and not among those found elsewhere.

Greene (1975) suggests that maintenance of sweet-potato washing in

the Koshima troop might not be a 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 agricultural products: sweet potatoes, wheat, peanuts, etc. When Green visited Koshima in the 1970s, he observed that the woman provisioning the macaques, who had been a caretaker for many years, gave sweet potatoes only to those monkeys that washed them. She thus rewarded monkeys for washing sweet potatoes. Green suggests that human intervention may have maintained potato washing in the Koshima troop, whereas it died out in other troops because the individuals that washed potatoes were not rewarded.

Green (1975) also points out that, while foraging, a macaque troop is spatially organized in a way that increases or decreases the likelihood of individuals being close to or distant from a human provisioner according to the macaque's age class and matriline. Hence, human intervention could produce a pattern of spread of washing behavior that would make the behavior appear to an unsuspecting observer to be a result of imitation learning. Of course, even if potato washing was maintained in the 1970s by caretakers, it might originally have spread by imitation learning. A few things, however, make me question this proposition.

First, some locale-specific behaviors seen in the Koshima troop, clearly not the result of imitation learning, 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 Otomari Bay by throwing peanuts (one of Ego's favorite foods) into the sea. Over a period of 3 years, Mrs. Mito induced 63% 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) and spread through the originator's peer group to their mothers and then from those mothers to their young (Kawai 1965). Orderly spread of a behavior along matriline is not necessarily evidence either of imitation or of culture.

Second, two parameters of the spread of sweet-potato washing, usually unmentioned in published descriptions of the behavior, lead me to suspect that social learning may have had little to do with the prevalence of sweet-potato washing at Koshima. One probable 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 relatively rapid spread of a behavior through a population.

Imo invented sweet-potato washing in September 1953, when she was

18 months old. Within several years, eight members of the Koshima troop Imo's age or older eventually began to wash potatoes. One of the eight, Semushi, began to wash potatoes in October 1953. Two other troop members, Uni and Imo's mother Eba, started in January 1954. The remaining five of the eight monkeys that acquired the behavior began to wash potatoes in 1955 ($n = 1$), 1956 ($n = 2$), and 1957 ($n = 2$). Both the mean and median times for acquisition of sweet-potato washing (for those who ever developed the behavior) were roughly 2 years after Imo started to demonstrate it. I consider this painfully slow propagation of behavior to be inconsistent with the hypothesis that the behavior was learned by imitation. Wheat placer mining, a second often-cited, locale-specific behavior of the Koshima troop, spread even more slowly than sweet-potato washing (Kawai 1965; Nishida 1987).

Third, most models of social learning assume that the probability of acquiring a socially transmitted behavior should increase with an increase in the number of models engaged in that behavior (Boyd and Richerson 1985). In other words, other things being equal, the rate of recruitment to a behavior should be positively correlated with its frequency of occurrence in a population, until saturation occurs.

In fact, Kawai's (1965) data reveal that (a) the pool of potential learners remained essentially constant over the years, (b) the number of demonstrators rose dramatically, yet (c) the rate of recruitment to the behavior did not increase (see Galef 1990 for further detail). These data do not suggest that imitation learning was responsible for the development of potato washing in the individuals that came to exhibit it.

Last, consider Kawai's own statement (1965:8) of the observations that led him to suggest that social interactions were responsible for the acquisition of the behavior by juvenile macaques.

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

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

The question is whether any, all, or only one of the interactions mentioned by Kawai were necessary for the slow spread of sweet-potato washing through the Koshima troop. The question cannot be answered by unobtrusive observation of the monkeys. Surely, unobtrusive obser-

vation does not demonstrate that imitation of one animal by another was responsible for propagation of the behavior, as so many secondary sources have suggested.

Termite "Fishing" by Chimpanzees at Gombe National Park

Field Observations. Chimpanzees in Gombe National Park in Tanzania capture termites using twigs or blades of grass as tools to probe the passageways of the termites' earthen mounds. When the insects react defensively to an intruding probe, biting and clinging to it, the chimpanzees carefully extract the probe and eat any termites that they find clinging to it.

Nearly all members of the Gombe study population that are more than 5 years old fish for termites for 1 to 5 hours per day during October and November. Similar methods of probing for insects with twigs, vines, or grasses have been observed in all chimpanzee communities studies in East Africa, as well as in some, but not all, chimpanzee groups observed in West Africa (McGrew and Rogers 1983; McGrew et al. 1979). There is also variation among chimpanzee populations in the species of ant or termite for which they fish, in the materials used as probes, and in the ways in which probes are prepared for fishing.

Goodall (1986:561) has suggested that "Young chimpanzees learn the tool using patterns of the community during infancy, through a mixture of social facilitation, observation, imitation, and practice—with a good deal of trial and error learning thrown in." Secondary sources often considerably truncate Goodall's analysis and suggest that learning by imitation and "culture" are responsible either for development of termite fishing generally or for development of the variations in termite fishing technique to be found in different communities of chimpanzees (Bonner 1980; McFarland 1985).

There is little question that some observed differences in insect-fishing behavior are readily explained either as responses to differences in the behavior of various species of insect prey (McGrew et al. 1979; Nishida and Uehara 1980) or as differences in the availability of materials used as probes (McBeath and McGrew 1982). For instance, the genus of termite for which the Gombe chimpanzees fish is absent from the main study area at Mahale, and the termites present at Mahale produce a distasteful defensive secretion that protects them from chimpanzee predation (Collins and McGrew 1987; Nishida and Uehara 1980). It is therefore not necessary to invoke "tradition" to explain the fact that Gombe chimpanzees fish for termites and Mahale chimpanzees do not.

On the other hand, no ecological explanation is currently available for

the fact that chimpanzees at Gombe are more likely to use both ends of a probe before discarding it than are chimpanzees at Assirik in Senegal (West Africa) or that the bark is usually peeled from twigs used as probes by chimpanzees at Assirik, whereas those found in Gombe are not peeled (McGrew et al. 1979). Of course, the present lack of an ecological explanation for locale-specific behaviors cannot be used to infer that they are the result of imitation learning (Tomasello 1990). Subtle ecological factors may explain all such differences in behavior. Indeed, as discussed in the next section, it is difficult to imagine how a locale-specific behavior, such as peeling bark from a probe, could be sustained in a population in the absence of rewards for that behavior in the particular area in which it occurred.

A Field Experiment. Although the skills used by chimpanzees to fish for insects appear at first glance to be relatively unsophisticated, Teleki (1974:585–588) reports that when, after months of careful observation of Gombe chimpanzees fishing for termites, he tried to fish for termites himself, he was unable to locate tunnel entrances of termite mounds consistently, to select twigs or grasses of the proper rigidity to use as probes ("Despite months of observing and aping adult chimpanzees as they selected probes with enviable ease, speed and accuracy, I was unable to achieve their level of competence"), and to catch termites efficiently by probing their tunnels. Teleki concludes (1974:587) that "each stage of a particular complex [of insect fishing] may well have to be learned via a cultural tradition that is passed from individual to individual within a population." Teleki's own failed attempts to learn to fish for termites efficiently by observing the behavior of accomplished adult chimpanzees seem to contradict his interpretation. Unless chimpanzees are more proficient than doctors of philosophy at learning termite-fishing techniques by imitation, observation of probe selection and probe manipulation by adults cannot in itself lead to development of efficient termite fishing by young chimpanzees at Gombe or elsewhere.

Imitation by Chimpanzees in Captivity. If it had been shown in the laboratory that chimpanzees could learn to solve problems by observing and then imitating the behavior of successful conspecifics, then it might be a bit pig-headed to insist that free-living chimpanzees do not use their ability to imitate to learn to fish for insects. Evidence of an ability of chimpanzees (or of other primates) to learn novel behaviors by observing and then imitating their fellows (reviewed recently and thoughtfully in both Tomasello 1990 and Visalberghi and Fragaszy 1990a), however, is surprisingly limited, almost entirely anecdotal, and as discussed below, probably irrelevant to understanding the spread of goal-directed behaviors like fishing for insects.

Typical of descriptive reports of imitation by chimpanzees are those of Köhler (1959:84, 280) and, more recently, those of de Waal (1982, in press) of imitation of locomotory patterns by chimpanzees in other than goal-directed situations. For example, de Waal (1982:80) reports: "Krom means 'crooked.' Her body is distorted and she has a hunched-up way of walking. . . . The young apes . . . Once had an 'ape Krom' craze. For days on end they would walk behind her, single file, all with the same pathetic carriage as Krom. . . ."

In goal-directed circumstances, imitation is not as easily seen in chimpanzees. Concerning chimpanzees' imitation of novel, meaningful acts (of which fishing for termites would surely be an example), Köhler (1959:18) reports, "Unfortunately, this is a very rare occurrence, even among chimpanzees, and when it does occur, the situation, as well as its solution, must lie just about within the bounds set for spontaneous solution."

Köhler (1959) emphasizes two limits on imitation learning of meaningful acts by chimpanzees: first, the chimpanzees have to be able to perceive the crucial relationships leading to solution of a problem, and second, naive animals cannot simply copy movements made by a skilled animal. That is, chimpanzees in problem-solving situations imitate only what Köhler called the *substance* of an action (the purpose of the sequence of movements), not its *form* (the movements themselves). It is difficult to imagine a situation in which observation is less likely to lead to "perception of crucial relationships" or in which the "substance" of an action would be more obscure than it is in termite fishing.

Consistent with Köhler's interpretation, Tomasello et al. (1987) found that naive chimpanzees that observed a trained conspecific use a rake to reach food outside its cage were more likely to learn to use the rake for the same purpose than were naive chimpanzees that lacked this observational experience. The observers did not use the same motor patterns that their demonstrator had used, however. Acquisition of the motor patterns needed to obtain food efficiently was the result of individual trial-and-error learning (see also Sumita et al. 1985).

AN ALTERNATIVE VIEW

One might reasonably ask, given that I question the view that young chimpanzees learn to fish for termites by imitating adults of their troop, how would I explain the existence of the behavior and its variants? I would answer that I accept Goodall's (1986:561) explanation of the development of termite fishing (quoted above), except that I would leave imitation out of the analysis. The effects of social facilitation, local

enhancement, and trial-and-error learning on the development of behavior are well established. Evidence of a contribution of imitation to the acquisition, even by chimpanzees, of problem-solving behaviors (such as termite fishing) is weak (Tomasello 1990).

As is the case with sweet-potato washing, it seems intuitively improbable that each chimpanzee discovers for itself the effectiveness of using twigs or blades of grass to fish in termite mounds for food. It is, however, easy to underestimate the complexity of the motor patterns that infant chimpanzees develop in the course of their unrewarded (playful) interactions with the physical environment (Birch 1945; Menzel et al. 1970; Schiller 1952, 1957).

Development of Fishing Behavior

Unfortunately we know little of the development of behaviors used by chimpanzees when fishing for insects. At Gombe, young chimpanzees 2 to 5 years old typically accompany their mothers when they fish for insects, play with their mothers' discarded probes, and exhibit adultlike competence in termite fishing when they are only 5 to 6 years of age. Goodall (1986) reports that infant chimpanzees at Gombe frequently play with ants, often poking at them with tiny twigs. Infant chimpanzees also use sticks to investigate holes in trees. While still an infant, Flint, a Gombe chimp, "fished" as though for termites in the hairs of his mother's leg. . . [and] when he was four years old, used these fishing techniques when drinking water from a hollow tree" (Goodall 1986:563). Goodall suggests that in these cases Flint was exhibiting termite fishing in novel contexts. Because infants do not fish for termites (Teleki 1974), I consider Goodall's description of Flint's behavior ill-considered. Plucking blades of grass or twigs, sticking them in holes and then into one's mouth, chasing ants with them, etc., are behaviors that probably develop in all young chimpanzees during their spontaneous interactions with the physical environment.

If probing in holes with twigs or blades of grass emerges in the course of normal chimpanzee development, then interaction with adult chimpanzees fishing for termites might well bias infants or juveniles to use these motor patterns to probe in tunnel entrances that were a focus of adult activity. The presence of probing implements abandoned by adults near termite nests that adults were exploiting might increase the probability that young chimpanzees would employ those implements to explore adult-created openings in termite mounds. Any probing of termite tunnels by naive juveniles would be rewarded, and thus maintained, by the occasional capture of termites. Differential reward following use of

appropriate probes and appropriate fishing techniques could gradually shape performance (Galef 1980) until young chimpanzees were purposefully fishing for termites, rather than simply exploring tunnels opened by others with implements found nearby.

Interactions between Social Learning and Individual Learning

The preceding account of the development of termite fishing in chimpanzees, speculative though it may be, presents two departures from the descriptions one often finds in the literature. First, it suggests that complex skills like termite fishing are the result of interactions between social and individual learning processes (see also Tomasello 1990). Second, it suggests that socially learned behaviors are modifiable and will be shaped by their consequences.

These two propositions are, I believe, well established in the psychological literature but often ignored in discussions of animal tradition. For example, in a recent paper, Rogers (1988:822) proposes that "when all learning is social, no one is monitoring the environment, and the information acquired will eventually be worthless." This approach, implying that social and individual learning are independent entities, seems to me to be misleading.

Individual organisms behave. Their behavior is modified by experience of the consequences of their actions (reinforcements). Social influences can bias an individual to direct actions toward one object rather than another; social influence might even introduce novel behaviors into an individual's repertoire. Unless socially induced actions are reinforced with higher probability than other actions in an individual's repertoire, however, socially learned behaviors, like any other learned behavior, will extinguish in short order.

Some have suggested (see, for example, McFarland 1985:513) that differences in methods of insect capture exhibited by chimpanzees living in different parts of Africa may be "learned by imitation and passed through the population by cultural tradition." One example of culturally induced variation in tool use given by McFarland is McGrew et al.'s (1979) report mentioned above that chimps in East Africa do not often peel bark from the twigs they use in termite fishing whereas chimps in West Africa frequently do. McGrew et al. (1979:206-207) also see this behavioral variance as one of only two instances in which they believe "cultural preference predominates over environmental demands" in producing differences in the behavior of chimps living in different areas.

I must confess that I am not entirely convinced. Observations of differences in the behavior of chimpanzees in different locales tells us

nothing of the forces that either shaped the development of those behaviors or maintain them. The inference of culture influence rests entirely on the absence of information concerning the ontogeny of the behaviors in question. McGrew et al. (1979:207) are sensitive to this problem, indicating that "further data are needed." We are fortunate that, in the case of termite-fishing chimpanzees, there is opportunity to collect additional observations.

In my view, although imitation might introduce some novel behavior into the repertoires of members of a population, through time (probably counted in days) this behavioral novelty would be maintained, modified, or extinguished depending on its effectiveness (relative to available variants) in acquiring rewards. There is no reason to believe that inefficient behaviors introduced socially into animal populations are any more resistant to extinction or modification than are individually learned behaviors. For example, learning by imitation, if it were to exist, would not necessarily offer a compelling explanation of the stable differences in the ways tools are made for insect fishing by chimpanzees in different parts of Africa (McGrew et al. 1979). There may be differences in the environments occupied by different troops of chimpanzees that maintain diversity in tool construction over decades. The idea of a population of 20-year-old chimpanzees using an inefficient method to prepare probes for termite fishing because, as infants, they watched their mothers do so, is at variance with what is known of the ways in which the behavior of animals tracks environmental demands. The burden of proof rests on those proposing unlikely explanations.

Summary

Goodall (1970:161) once stated, "Undoubtedly, given the investigative and manipulative tendencies of the young chimpanzee and his ability to learn through trial and error, almost all of the feeding and tool using behaviors I have described could be invented anew by each individual, especially since the behavior of others in his group will serve to direct his attention to the relevant parts of the environment." I agree wholeheartedly. On the other hand, I see no reason to accept either the premise or the conclusion of Goodall's next sentence: "However, in a species which is so well known for its imitative abilities it seems sensible to suppose that most, if not all, of the behaviours outlined above . . . are passed down from one generation to the next through observational learning in a social context."

Like Visalberghi and Frigaszy (1990a) and Tomasello (1990), I find no convincing evidence in the literature that monkeys or apes in general, or chimpanzees in particular, can learn by imitation to use particular motor

skills in problem-solving situations. Consequently, I have no reason to believe that behaviors associated with fishing for termites are cultural in chimpanzees. Surely, given the current state of the evidence, termite fishing by chimpanzees does not warrant discussion as a prototypical example either of imitation or of culture in animals.

CONCLUSIONS

Those who favor a conservative approach to description and analysis of animal behavior, as I do, find little satisfactory evidence that animals either teach or learn by imitation. Locale-specific behaviors, common in animal populations, do not provide evidence either of tuition or of imitation (Galef 1990). Both analyses of field reports and laboratory studies of social-learning phenomena suggest that animal traditions rest on processes quite different from those supporting culture in humans. Animal traditions are, therefore, analogs rather than homologs of human culture. Consequently, it can be misleading to speak of an evolution of culture in animals (e.g., Bonner 1980); this usage suggests homology when there is evidence only of analogy.

It might be argued that it is no more misleading to talk about "culture" in animals and humans than it is to discuss the "wings" of birds and bats or the "eyes" of vertebrates and insects. All three cases involve using the same label for analogous features rather than for homologous ones. There is no problem with using the labels "wings" or "eyes" to refer to analogous structures, however, because no one suggests that bat wings evolved from bird wings or that vertebrate eyes evolved from invertebrate ones. Would that the same were true in discussions of "culture" in animals and humans.

Discussion of animal analogs of human culture as though they were homologs of human culture has the potential to lead students of culture into the same error made by comparative psychologists during the 1950s and 1960s, when they tried to create a phylogeny of intelligence by ordering the learning capacities of animals (turtles, goldfish, pigeons, rats, monkeys, etc.) from diverse evolutionary lineages. As Hodos and Campbell (1969) made clear in a devastating critique of the entire enterprise, only representatives of a common evolutionary lineage provide a firm foundation for inferences concerning the evolution of behavior. Representatives of diverse lineages provide information about general mechanisms of adaptation, not about evolutionary history.

Animal tradition and human culture serve similar functions. If, as the present review suggests, animal tradition and human culture are only

analogous features of the behavioral repertoires of vertebrates, then culture is not a trait whose antecedents can be traced back into the early reaches of the vertebrate line and beyond. We do not know when the intellectual abilities necessary for learning by imitation and for teaching first arose. Indeed, as Sahlins (1976) suggests, the intellectual abilities supporting learning by imitation, teaching, symbolic language, etc., may have developed to the point where culture could develop only within the hominid line; there may, in fact, have been no culture before the hominid line evolved.

Given this view, there is no reason to treat culture as a trait that evolved out of primitive antecedents. Through evolutionary time, a population of our direct ancestors may have become increasingly likely to express culture as a consequence of selection for increased sophistication in intellectual processes that served other functions and only later came to play a role in cultural transmission. After the thresholds for culture had been crossed, once our hypothetical ancestral hominid was able to imitate or to teach, then selection for increased ability to participate in culture (for increased "docility," in Simon's [1990] terminology) would have led to elaboration of intellectual processes supporting cultural transmission. In this model, continuity would be found in the evolution of psychological processes necessary for culture, not in culture itself.

Darwin remarked both that "there is no fundamental difference between man and the higher mammals in their mental faculties" (1871:35) and that "the difference between the mind of the lowest man and that of the highest animal is immense" (1871:104). One hundred and twenty years later, our understanding of the relationship between the "mental faculties" or "minds" of humans and of their closest phylogenetic relations is little more consistent than was Darwin's. In the preceding discussion of culture, I have emphasized differences in human and animal mental processes, where others might choose to emphasize similarities. Further explorations in comparative psychology provide our only means to improve our understanding of why the behavioral capacities of members of our own species appear both so similar to and so different from those of our fellow primates.

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