See also: Description and Prescription; Post-Bloomfieldians.

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## **Traditions in Animals**

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More than 50 years ago, James Fisher and Robert Hinde (1949) documented the spread of a tradition of milk-bottle opening among British birds. Shortly thereafter, Satsue Mito discovered that several members of a troop of macaques living on Koshima Island in southern Japan would take dirt-covered sweet potatoes to a nearby stream and wash the dirt from them (Kawai, 1965). Geographical dialects in the songs of birds (see Dialects in Birdsongs) have long been a subject of discussion by ornithologists (Armstrong, 1963), and idiosyncratic feeding behaviors in various populations of Norway rats have been reported for many decades (for a review, see Galef, 2003b). Such observations provided the first evidence that members of a single species living in different areas exhibit differences in their behavioral repertoires that are not readily explained in terms of differences in either their genotypes or their ecological circumstances. The evidence, fragmentary though it was, led to a resurgence of interest in laboratory studies of the behavioral processes supporting social learning in animals as well as extraordinary efforts to describe differences in the behavior of geographically distinct populations of free-living primates.

Evidence from the field of differences in the behavior of geographically distinct populations within a species is now overwhelming not only in the great apes and other mammals, but in fish and birds as well (e.g., Box and Gibson, 1999; Fragaszy and Perry, 2003). For example, chimpanzees at Gombe National Park in east Africa hold a long stick in one hand and use the other to wipe ants from the probe and transfer the ants to their mouths. Chimps living in the Tai Forest in west Africa use a short stick to collect ants and their mouths to remove ants from the stick (McGrew, 1992; Whiten *et al.*, 1999). Studies of orangutan populations scattered across Southeast Asia have revealed similar differences in behavior

among geographically distinct populations (Van Schaik et al., 2003). Important articles have appeared in the scientific literature using the term 'culture' to describe the local-specific behavioral repertoires of populations of chimpanzees and orangutans (Whiten et al., 1999; Van Schaik et al., 2003), suggesting fundamental similarities in the traditions of humans and great apes.

There is disagreement as to the appropriateness of such a usage. Some argue that although human culture and animal traditions share certain features, until we have a better understanding of how behavior is transmitted in both animals and humans, it is premature to assume that they are equivalent (Galef, 1992). Others feel that the specific mechanisms involved in the diffusion of behaviors through populations can be ignored when discussing traditions or culture because the evolutionary consequence of social learning, however it occurs, is always the same: behavior is transmitted (de Waal and Tyack, 2003).

From the perspective of those interested in language and linguistics, the differences between the traditions of animals and those of humans appear profound indeed. Although there has been relatively little study of the way in which humans acquire traditional patterns of behavior, many aspects of human culture, especially those involving the acquisition of complex skills, appear to depend on language, on teaching, and on imitation for their propagation.

Although ages have the capacity to manipulate a symbolic system invented and given to them by humans and to communicate with it (see Cognitive Basis for Language Evolution in Non-human Primates), there is no evidence that free-living apes communicate in a similar way. Anecdotal reports suggest that chimpanzees may engage in activities that can be interpreted as deliberate tuition of their young. However, teaching, as we know it in humans, appears to play a limited role, if any, in the development of the behavioral repertoires of apes. Chimpanzees and orangutans probably can imitate to some extent, but the contribution of imitation of others to the development of behavior of free-living animals is not known. If even our closest phylogenetic relatives rarely transmit behavior as we do, how is the existence of traditions in animals to be understood?

Like humans, nonhuman animals provide conspecifics with whom they share an environment with information useful in determining which of many possible behaviors is likely to be successful. In some cases, the traditions of animals are shaped and maintained by signals (behaviors evolved for the purpose of communication) emitted by one animal that influence the behavior of another. For example, male cowbirds from different geographical areas sing different variants of male-cowbird song, and these 'song dialects' are maintained by differences in the response of females from different areas to the songs that males produce. Although male cowbirds normally sing all of the various songs in their repertoires without repetition, after a female cowbird gives a wing stroke display in response to a male's song, he repeats that song several times in succession. During the breeding season, males tend to produce songs that previously caused females to give wing stroke displays and thus increase their access to females (West and King, 1988). Other contributors to this encyclopedia have discussed, either in detail or in passing (see Animal Communication: Overview; Animal Communication: Vocal Learning; Cognitive Basis for Language Evolution in Non-human Primates; Communication in Marine Mammals; Dialects in Birdsongs), traditions that similarly involve signals shaped by natural selection for the purpose of communication. I focus here on 'communications' between animals that do not involve signals that evolved for communicative purposes. Animals can learn from others not because those others actively provide information, but because stimuli that others emit as byproducts of activities necessary for their own maintenance incidentally direct the behavior of recipients in profitable directions (e.g., King, 1994). For example, the rasping sounds that an agouti makes as it gnaws on a nut carry for many tens of meters through the forests of Central America, attracting both other agouti and the occasional predator to a promising feeding site. A vulture descending to feed from a carcass lying on the Serengeti Plain attracts both others of its kind and competing species to a recent kill. It does not seem reasonable to suppose that, in such cases, individuals that have discovered a food source emit signals to announce their finds. Still, the feeding behavior of one agouti or vulture provides an unambiguous cue to those sufficiently alert to detect and exploit it.

Sometimes the behavior of one animal results in residual changes in the environment that affect the behavior of conspecifics. As a Norway rat moves about its home range, it creates paths through the undergrowth that influence the behavior of those that come after. As it feeds, it deposits residual olfactory cues in the saliva it leaves on its food and in the feces it voids in the location where it eats. Such residual signs are attractive to other rats and strongly bias their choice of feeding site (Galef, 2003b).

Sometimes, the effects of environmental modification of the behavioral development of others are quite sophisticated. For example, the pine forests of Israel are inhabited by colonies of roof rats that live on a diet of pine seeds and water. Laboratory observation of roof rats captured either in pine forest or elsewhere in Israel reveals that although all of the former animals are able to extract pine seeds from cones in a way that provides more energy than it consumes, few rats captured outside the pine forest can do so. The efficient method of harvesting pine seeds takes advantage of the architecture of cones and involves starting at the base of a cone and removing, in succession, the spiral of scales that run from the base of a cone to its apex. Regardless of genetic background, rat pups reared by dams that open pinecones in their presence usually develop the efficient technique, whereas few pups reared by dams not given access to pinecones do so. Experience of young rats in completing the removal of scales from cones started in the right way by an adult rat (or by a human stripping scales from the base of a cone in imitation of a proficient adult) allowed most of them to acquire the efficient technique (Terkel, 1995). Clearly, socially produced residual changes in the environment provide the necessary substrate for diffusion of behavior through rat populations.

In discussion of the development of behavioral traditions in members of our own species, the role of information acquired as a result of observation of the activities of others as they go about behaviors necessary for self-maintenance is easily overlooked. We talk, we teach, we confer, we advertise. It is easy to forget that we also act and that our activities provide useful, often unambiguous messages for others, modeling behaviors that are likely to be rewarded in a shared environment. Extraction of information from the life-sustaining activities of others and the residues such activities leave in the environment, rather than from signals that have an explicitly communicative function, can prove useful, even for humans.

There has been considerable discussion among behavioral ecologists as to whether signals passing from one animal to another provide a recipient with honest information or are designed to manipulate the behavior of a signal recipient to the sender's advantage (see Animal Communication: Deception and Honest Signaling). Information extracted from observation of the life-sustaining activities of others is less likely to misinform than information extracted from signals evolved for communicative purposes. No animals other than humans, and perhaps chimpanzees, have been shown to modify behaviors involved in their own maintenance so as to mislead others. Consequently, information extracted from signs and cues emitted by others, rather than information extracted from signals that evolved for purposes of communication, is likely to be particularly useful.

Information extracted from the behavior of others can both introduce novelty into behavioral

repertoires and lead to homogeneity in the behavior of members of a population (Galef, 2003a). However, like other elements in the behavioral repertoires of individuals, behaviors acquired by extracting information from signs or cues produced by others are rewarded or punished during subsequent interaction with the physical and social environments. Consequently, socially acquired behaviors will increase or decrease in frequency of expression in a population as a function of their costs and benefits relative to alternative behaviors in the repertoires of population members. There is no reason to believe that there is anything special about behaviors that are acquired socially. Like behaviors acquired as the result of individual experience, continued expression of a socially learned behavior depends on the reward it produces relative to alternative related behaviors in an individual's repertoire. Still, information extracted from others as they go about the mundane tasks necessary for self-maintenance, like the signals that other contributors to this encyclopedia discuss, can bias the development of behavioral repertoires of nonverbal species (Boyd and Richerson, 1985).

See also: Alarm Calls; Animal Communication: Deception and Honest Signaling; Animal Communication Networks; Animal Communication: Overview; Animal Communication: Parent–Offspring; Animal Communication: Vocal Learning; Apes: Gesture Communication; Bee Dance; Birdsong; Cognitive Basis for Language Evolution in Non-human Primates; Communication in Grey Parrots; Communication in Marine Mammals; Development of Communication in Animals; Dialects in Birdsongs; Individual Recognition in Animal Species; Non-human Primate Communication.

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## Trager, George L. (1906-1992)

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Trager was born on March 22, 1906 in Newark, NJ, and died on August 31, 1992 in Pasadena, CA. He is well-known for his contributions to structural linguistics, phonetics, American Indian languages, Romance philology, and Slavic and Germanic linguistics.

The young Trager, whose parents emigrated from Russia via Germany, grew up speaking Russian and German at home, and English in his Newark neighborhood and in school. An excellent student in the public schools of Newark, he was awarded a full state scholarship to attend Rutgers University in 1922. Although his first declared major was chemistry, he graduated in 1926 with a B. Litt. in Romance languages. He received both his A.M. (1929) and Ph.D. (1932) in Romance Philology from Columbia University. His dissertation (Trager, 1932) was supervised by H. R. Muller, with L. H. Gray serving on his committee. Although his forte was in Romance, he was also competent in Slavic (see Trager, 1933, 1942). Two classic studies deal with French morphology (Trager, 1944, 1955), a particular strength of his, and he taught French at Brown University and Columbia University.

Trager was a Research Associate of the International Auxiliary Language Association from 1931-1934. He taught every foreign language offered at Adams State College in Alamosa, CO, from 1934-1936. It was during this period that he began his lifelong fieldwork on Taos, a Tanoan language spoken about 100 miles from Alamosa. He was a postdoctoral scholar at Yale University from 1936-1938, and a research fellow there from 1936-1941. He was Lecturer in Phonetics for 1937-1938 (see Trager and Bloch, 1940; Trager, 1950a, 1964, e.g., for his special expertise in that subject). He later served there as Assistant Professor of Slavic Languages (1942–44). During the Yale years, he came in contact with numerous superstars of the structuralist era: E. Sapir, M. Swadesh, C. Osgood, F. Edgerton, E. H. Sturtevant, M. B. Emeneau, C. F. Hockett, B. L. Whorf, and also L. Bloomfield. He collaborated with Whorf, B. Bloch, and with others (e.g., H. L. Smith, Jr.) in a long and distinguished career.

Trager was Chief Linguistics Secretary for the U.S. Board of Geographical Names from 1944-1946. He then was Professor of Linguistics at the University of Oklahoma, Norman, from 1946–1948, followed by a stint as Professor of Linguistics at the Foreign Service Institute from 1948–1953. He also served as Director of Linguistic Research at the Institute of Languages and Linguistics, Georgetown University from 1950-1953, and was Visiting Professor there for 1954-1955. After Georgetown, he became the Assistant Director of the Human Relations Area Files, Washington Bureau, American University, for 1955-1956. He became Professor of Anthropology and Linguistics, University of Buffalo, 1956-1957, and