

Approaches to the study of traditional behaviors of free-living animals

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I review literature on four different approaches to the study of traditions in animals: observation of free-living animals, laboratory experiment, armchair analysis, and field experiment. Because, by definition, a tradition entails social learning of some kind, it is difficult, perhaps impossible, to establish that a behavior is in fact traditional without knowledge of how it develops. Observations of free-living animals often provide strong circumstantial evidence of a tradition. However, even in the view of several researchers who have studied possibly traditional behaviors in natural populations, observation alone has not proven sufficient to show that social learning contributes to development of behaviors of interest. The relevance of laboratory experiments to the understanding of the development of behaviors in free-living animals is always open to challenge. Armchair analyses of field data can produce interesting hypotheses but cannot test them. Field experiments to determine how behaviors of interest develop in population members provide a promising way forward.

A better mousetrap, or a better automobile, or a better concept of freedom, may seem to occur as inspiration; but no such inspiration is possible unless the inspired mind has first perceived the existing mousetrap, automobile or concept to be inadequate. Criticism, that is to say, and the doubt out of which it arises, are the prior conditions to progress of any sort.

—Philip Wylie, in *Generation of Vipers* (1942)

During the last 30 years, the number of articles devoted to studies of social learning and tradition in animals has grown nearly exponentially. Scientists trained in fields from anthropology to zoology have begun to study phenomena that, 30 years ago, were the primary interest of only a handful of psychologists and biologists.

Happily, interaction among those trained in diverse disciplines has been largely positive, and studies of social learning have benefited immeasurably from collegial exchange reflecting divergent approaches. There has been general recognition that, like other behavioral phenomena, social learning can be analyzed in many different ways and that the approaches of those trained in different disciplines are usually complementary, rather than antagonistic (see, e.g., McGrew, 2001). There are, of course, important issues that remain as sources of controversy, and it is with one of these, the evidence necessary to establish that a behavior is traditional in a free-living population, that this article is concerned.

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). In ordinary speech, a tradition is something that is learned in some way from others and that can be passed on

to naive individuals (Gove, 1971). The labeling of a behavior as traditional thus implies, or at the least may lead others to infer, that social interaction was important in its development (Galef, 1988; Whiten & Ham, 1992). It follows that a behavior can be characterized as traditional with certainty only after something is known of how that behavior develops in the individuals that exhibit it (Galef, 1996b).

Although many behavioral differences that are labeled *cultural* by those observing free-living animals (e.g., Rendell & Whitehead, 2001; van Schaik et al., 2003; Whiten et al., 1999, 2001) are likely to be traditional, an influence of social learning on their development has rarely been demonstrated (see, e.g., commentaries on Rendell & Whitehead, 2001). Consequently, the traditional nature of differences in behavior of allopatric populations remains open to question.

In this essay, I consider four different approaches to the question of whether a behavior is traditional. I begin with field studies. I then describe laboratory studies and logical analyses of differences in the behavior of members of a single species living in different locales, and will conclude with a consideration of field experiments designed to determine the causes of such behavioral variation.

The literature on animal traditions has grown so vast over the last quarter century that a book-length monograph would be required to review all the studies contributing to our understanding of possible traditions in animals. Consequently, this single article must be a selective rather than a comprehensive review. I apologize to all whose contributions are not mentioned. Unfortunately they vastly outnumber those to whose work I have made reference.

STUDIES OF FREE-LIVING ANIMALS

The earliest and, in some sense, most primitive evidence of animal traditions is found in comparisons of the behav-

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ior of geographically separate populations of a single species. Indeed, the modern era in investigations of animal traditions opened with now-classic studies of geographic variation in the song of chaffinches, *Fringilla coelebs* (Marler, 1952), milk bottle opening by British titmice, *Parus spp.* (Fisher & Hinde, 1949), and sweet potato washing and wheat placer mining by Japanese macaques, *Macaca fuscata* (Kawai, 1965). More recent comparisons of entire ethograms of allopatric populations provide impressive circumstantial evidence of traditional behavior in animals (see, e.g., van Schaik et al., 2003; Whiten et al., 1999).

Below, I will describe in detail two recent examples of field studies that provide evidence of traditions. The first is a comparison of the behavior of members of a single species living in different locations, and the second is a study of change in the behavior of a single population over time. Both are relatively recent and have not been discussed previously in the secondary literature. I also refer briefly to studies in great apes that I consider further in discussions of armchair analyses and field experiments.

Caledonian Crows

Differences in the structure of probing tools manufactured from pandanus leaves by New Caledonian crows (*Corvus moneduloides*) living on Grande Terre island have provided evidence that variations in tool design “are probably transmitted between crows and not individually invented” (Hunt & Gray, in press). Caledonian crows manufacture three types of tools from pandanus leaves: wide tools, narrow tools, and stepped tools with varying numbers of steps (Hunt, 2000; Hunt & Gray, 2002, in press). Distribution of the three types of tools is easy to determine, because manufacture of a tool leaves behind a readily identified residual counterpart in the leaf of a living pandanus tree. The relatively sophisticated stepped tools are stiff at the base and pointed at the end used to probe for insects, and are, therefore, possibly better suited for use as insect probes than are the simpler wide and narrow tools.

In 14 study sites in the north of Grande Terre, 98% or more of the tools manufactured were stepped tools with only occasional wide tools being found, whereas in 3 study sites in the south of the island, roughly equal numbers of each of the 3 tool types were found. In three additional study sites just to the north of the most southerly sites, narrow and stepped tools were found in roughly equal numbers, and less than 1% of the tools were wide tools.

Geographical distribution of the three tool types was not correlated with such ecological factors as the availability of raw materials, rainfall, or altitude of study site, and simpler tools were rarely found where sophisticated stepped tools predominated. The data suggest that crows do not gradually learn to produce the more sophisticated type of tool by trial and error (Hunt & Gray, 2002). The circumstantial evidence for social learning of tool manufacture is clearly more than sufficient to support the authors’ suggestion that although “we do not have direct evidence for social transmission of tool design between crows, this seems probable” (p. 873).

However, even the extraordinary quantitative data leave questions unanswered. For example, if the observed geographic pattern of tool manufacture reflects tradition, why is only a single type of tool produced at sites in the north of Grande Terre, whereas several different types are produced in the south? Perhaps different tools are used in different microhabitats or to hunt different prey, and the construction of tools reflects such differences in use.

I will consider experimental evidence concerning the development of a similar behavior, tool use by woodpecker finches, in the laboratory experiments section and in the field experiments section—evidence that the type of tool that animals use can be affected by the type of prey that they pursue. For the moment, I suggest only that without information as to how tool manufacture develops in individual Caledonian crows, focus on tradition as an explanation may be premature.

Song in Galapagos Finches

The near impossibility of using observational data alone to establish the traditional nature of a behavior is well illustrated by the extraordinarily complete set of observations carried out by Grant and Grant (1996). The Grants recorded songs of more than 95% of all male Darwin’s medium ground finches, *Geospiza fortis*, that reached breeding age over a period of 13 years on a small island in the Galapagos archipelago. By comparing the songs of males of known genetic relationship, the Grants were able to calculate a heritability coefficient of .725 for song features passing from father to son. The Grants then examined more than 100 grandson–paternal grandfather pairs and found a significant correlation in song features close to that expected on the hypothesis that they were inherited ($.725^2 = .526$). When they similarly examined more than 100 grandson–maternal grandfather pairs, they found no correlation in the features of the songs of grandfathers and grandsons.

The finding of inheritance from paternal but not maternal grandfathers indicates that song learning in *G. fortis* is either culturally transmitted through the male line or transmitted on sex-linked genes. Despite the extraordinary detail available on song feature distribution, the genetic hypothesis can be excluded only because of what we know from laboratory studies of song development in other passerine birds.

Great Apes

Comparisons of the behavioral repertoires of allopatric populations to identify traditional behaviors has reached exceptional levels of sophistication in recent publications that synthesize decades of observation of chimpanzees, *Pan troglodytes*, and orangutans, *Pongo pygmaeus*, in natural habitats (van Schaik et al., 2003; Whiten et al., 1999, 2001). However, as van Schaik et al. note, “it remains difficult by observation alone to show conclusively that variation in the behavioral repertoires of free-living animals are, in fact, cultural rather than genetically transmitted or environmentally induced” (p. 102). I will return to the con-

sideration of the data on chimpanzee “culture” in the armchair analysis and field experiments sections.

LABORATORY STUDIES OF NATURALLY OCCURRING VARIATIONS IN BEHAVIOR

Courtship Behaviors in Birds

Traditions in bird song have been reported since the time of Aristotle (1984), who noted both that birds of the same species taken from different localities produced different songs and (in “laboratory” studies) that some birds produce their species-typical songs only if reared by conspecifics. However, it was Marler and Tamura’s (1964) experimental analyses of the development of song dialects in white-crowned sparrows, *Zenotrichia leucophrys*, that ushered in the modern age of laboratory experimentation on naturally occurring traditions in animals. Although the artificiality of some of the procedures used by Marler and his students has generated considerable controversy (see, e.g., Baptista & Petrinovich, 1984; Nelson, 1998), their analyses of song remain a cornerstone of our understanding of both developmental processes and traditions in animals.

The literature on song traditions in birds is far too extensive to review here. However, it is worth noting that recent work on the development (West & King, 1996) and functional significance (see Freeberg, 1996, 1998, 2004; Freeberg, King, & West, 2001) of population-specific courtship behaviors of brown-headed cowbirds, *Molothrus ater*, indicate that traditional variation in courtship can affect reproductive success. Males reared in captivity with females from Indiana develop courtship behaviors that Indiana females prefer, and during the breeding season, such males have greater success securing Indiana females as mates than do males reared with females from other localities. In Freeberg’s studies, very large enclosures containing flocks of birds proved to be a useful middle ground between observation in uncontrolled environments and studies in small laboratory cages for investigating the development and analyzing the function of what proved to be traditional behaviors.

Milk Bottle Opening by Titmice

The spread of milk bottle opening behavior through populations of British parids reported by Fisher and Hinde (1949) has been examined in laboratory settings by Sherry and Galef (1984, 1991) with the use of a closely related North American species, black-capped chickadees, *Parus atricapillus*, as subjects. Sherry and Galef’s experiments confirmed the potential importance of social interaction in the induction of bottle opening in parids but failed to provide support for the frequent assertion in secondary sources that the spread of milk bottle opening resulted from learning by imitation. Rather, Sherry and Galef’s results indicated that two simple socially mediated responses—feeding from milk bottles that others had opened and simple presence of conspecifics near milk bottles—facilitated acquisition of milk bottle opening by naive birds. Such simple sorts of social interaction may well underlie many traditional behaviors of animals.

Tool use by Woodpecker Finches

Woodpecker finches, *Cactospiza pallida*, on the Galapagos Islands use twigs or cactus spines, which they hold in their beaks, in several different ways to push or lever arthropod prey out of crevices in bark, although the frequency of tool use by finches varies among habitats. Tool use is rarely seen in humid habitats, where woodpecker finches glean prey from moss and leaves; it is common only in drier regions or during the dry season in humid regions, when *C. pallida* hunts for prey that are concealed under bark and, therefore, difficult to reach (Tebbich, 2000).

In a laboratory study undertaken to explore the role of social learning in the development of this complex behavior, which if seen in a primate or cetacean population would surely be viewed as a possible tradition, no evidence of social learning in the development of tool use was found. All juveniles used tools whether they had observed a tool-using model or not, and adults that were not tool users never learned to use tools either by trial and error or by observing conspecifics use tools (Tebbich, Taborsky, Fessl, & Blomqvist, 2001). The investigators interpreted their results, similar to those of Galef’s (1980) studies, described below, of the development of diving behavior in rats, as suggesting that tool use is based on a “learning predisposition” and develops by trial and error during a sensitive period early in development (Tebbich et al., 2001, p. 2189).

Diving for Food by Norway Rats

Gandolfi and Parisi (1972) reported that most members of some colonies of Norway rats, *Rattus norvegicus*, living along the Po River in northern Italy fed on mollusks that inhabited the river bottom, whereas no members of nearby colonies with equal access to mollusks preyed on them. The distribution of mollusk predation was easily determined, because the rats that ate mollusks produced piles of discarded shells along the river’s banks.

Gandolfi and Parisi (1972) interpreted their observations of localized mollusk predation as suggesting that diving is socially transmitted in colonies with diving members. Galef (1980), in a series of laboratory studies, investigated the importance of social learning by inducing both wild and domestic Norway rats to swim and dive for food. The results were not consistent with the hypothesis that social learning plays an important role in the development of diving behavior in rats.

In the laboratory, all young rats that were given access to water began to swim at an early age, regardless of whether they were reared by a swimming or a nonswimming mother. Furthermore, all young rats that swam also spontaneously dove for food when given opportunity to do so. Adult rats never learned to swim or dive even if they lived with a diving rat, and even rats trained to dive for food did not do so when they had continuous access to rations ashore. This last result is consistent with Parisi and Gandolfi’s (1974) informal field observation that “time dedicated by rats to mollusk capture depends greatly on the availability of other food” (p. 102).

Galef’s (1980) data suggest, as did Hunt’s (2000) findings concerning tool use by woodpecker finches, both a

sensitive period during development when complex behaviors are easily learned and an ecological determination of whether a behavior seen in only some populations of a species is expressed in adulthood.

Poison Avoidance by Norway Rats

Steiniger (1950) attributed to social learning his repeated failures to control pest populations of wild Norway rats by the introduction of permanent baiting stations containing poisoned food into rat-infested areas. Steiniger observed that young rats born to colony members that had survived initial contact with a poisoned bait and had learned not to eat it also avoided eating that bait without ever sampling it for themselves.

Galef and Clark (1971) found that adult wild rats confined in laboratory enclosures also transmit poison avoidance to their young, and Galef (1996a) has described seven independent behavioral mechanisms whereby adult rats' food choices influence the development of juveniles' food choices. Everything from flavor cues contained in mothers' milk to scent trails deposited by adult rats leading from food sources to harborage sites has been found to result in the juveniles' choice of the same foods and feeding sites as the adults with which they interact.

Unexpectedly, although rats can increase one another's preference for safe, nutritious foods in multiple ways, there is no evidence that they can warn one another not to eat toxic or nutritionally deficient foods. Rather, the extreme hesitancy of wild rats to ingest unfamiliar substances, together with their enhanced preferences for foods that others are eating, reduces the probability that they ingest toxins (Galef, 1985). To the contrary, laboratory studies have shown that red-winged blackbirds, *Agelaius phoeniceus*, and cotton-top tamarins, *Saguinus oedipus*, learn to avoid foods that they see conspecifics reject or fall ill after eating (Mason & Reidinger, 1981; Snowdon & Boe, 2003), although there have been no field observations of feeding traditions in either species.

Pine Cone Stripping by Black Rats

Perhaps the most successful of recent laboratory analyses of population-specific patterns of behavior observed in free-living animals is Terkel's (1996) study of social learning of an efficient method of stripping scales from pine cones to gain access to pine seeds by black rats, *Rattus rattus*. The stripping of scales from pine cones in an energetically efficient manner allows rats to inhabit otherwise uninhabitable pine forests in Israel, where the rats subsist on a diet consisting entirely of pine seeds and water (for a review, see Terkel, 1996).

At the ecological level, the absence of tree squirrels in Israel has left open a potential niche for exploitation by other arboreal mammals. At the behavioral level, the experience of naive young rats, when they complete the stripping of scales from pine cones snatched from adults that had begun stripping them using the efficient technique, facilitated young rats' acquisition of the skill. Whereas no naive rats learned to open cones when presented with only

intact cones, approximately 24% of the rats that had been given partially opened cones to complete subsequently acquired the efficient stripping technique (Zohar & Terkel, 1992).

Predator Avoidance by Rhesus Macaques and European Blackbirds

Mineka and Cook (1988) used published comparisons of responses to snakes of both young and old monkeys and laboratory- and wild-reared monkeys to infer that fear of snakes was learned rather than instinctive. They then undertook laboratory studies to investigate the possible role of social learning in the development of snake fear, an issue they argued could not be resolved by field studies alone. Mineka, Davidson, Cook, and Keir (1984) showed that laboratory-reared rhesus monkeys, *Macaca mulatta*, that had observed either live conspecifics or videotapes of conspecifics responding fearfully to snakes subsequently exhibited a range of avoidance and fear responses to snakes and snake-like objects not seen in conspecifics lacking such exposure (Cook & Mineka, 1989, 1990).

Curio (1978) referenced Lorenz's earlier observation of young jackdaws learning to avoid a cat after witnessing their parents harassing one as a starting point of his elegant studies of cultural transmission of enemy recognition in blackbirds, *Turdus merula* (reviewed in Curio, 1988). In brief, naive blackbirds viewing a neutral object while hearing the alarm calls or viewing the mobbing behavior of a conspecific subsequently made the alarm call when shown the neutral object (Curio, Ernst, & Vieth, 1978). The formerly naive birds could then serve as models for other naive birds, and a multigeneration tradition of antipredator response to the previously neutral object was established in a laboratory population. Laland and Plotkin (1990a, 1990b) and Galef and Allen (1995) have provided evidence of multigeneration traditions in the foraging behavior of Norway rats in the laboratory.

ARMCHAIR ANALYSES

As was noted above, systematic differences in the behavioral repertoires of members of a single species living in different areas provide circumstantial evidence that such differences in behavior are traditional. However, careful reading of field reports can often reveal issues that need to be resolved before the hypothesis that social learning underlies the development of observed differences in the behavior of allopatric populations can be accepted.

As might be expected, skeptical examination by outsiders of plausible interpretations of field data is not always welcomed by those who have done the hard work of observing free-living animals and who may hold strong views concerning the role of social learning in the development of the behaviors that they have observed at first hand. However, reconsideration is not undertaken to reject interpretations proposed by those who did the original work. Rather, such secondary analysis serves to identify issues that need to be resolved before rich interpretations

