

The Biology of Traditions

Models and Evidence

Edited by

DOROTHY M. FRAGASZY

University of Georgia, Athens, USA

and

SUSAN PERRY

University of California, Los Angeles, USA and Max-Planck
Institute for Evolutionary Anthropology, Leipzig, Germany

 **CAMBRIDGE**
UNIVERSITY PRESS

- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., and Boesch, C. 1999. Cultures in chimpanzees. *Nature*, 39, 682–685.
- Wink, M., Hofer, A., Bilfinger, M., Englert, E., Martin, M., and Schneider, D. 1993. Geese and dietary allelochemicals – food palatability and geophagy. *Chemoecology*, 4, 93–107.

“Traditional” foraging behaviors of brown and black rats (*Rattus norvegicus* and *Rattus rattus*)

The brown rat, in particular, appears especially able to develop local traditions, more so perhaps than other more-closely examined mammals, possibly including the anthropoids.

159

STEINIGER, 1950, P. 368

6.1 Introduction

Imagine, if you will, an energetic, young graduate student who has established a study site near Para, Brazil, where she spends 3 years observing a geographically isolated population of capuchin monkeys that no other primatologist has looked at. Imagine further that our graduate student soon finds, to her great surprise and pleasure, that all of the members of one troop of capuchins at Para, unlike any previously studied capuchins, regularly hunt and eat small lizards. Many months of demanding field work show that the lizards are the source of more than 20% of the calories and 36% of the protein ingested by troop members.

Discovering a complex, biologically meaningful pattern of behavior that is unique to a particular population of monkeys would be a significant event in the career of any behavioral scientist. Surely, before very long, our imaginary graduate student is going to want to tell her colleagues, and quite possibly members of the media as well, about her discovery. To do so, she is going to have to decide how to refer to the unusual behavior that her field studies have documented.

If our imaginary graduate student were to make the conventional choice, and there is little reason to doubt that she would, she would soon be referring to the lizard hunting she has observed as “cultural”, as a “tradition” of the capuchins at Para. Her decision may seem a trivial one,

but dozens of similar decisions made over decades have had unintended effects leading the unwary to conclude that intellectual problems have been solved that have not even been addressed.

6.1.1 Defining tradition

The English word "tradition" derives from the Latin *traditio* meaning either the action of handing something over to another or of delivering up a possession (Lewis and Short, 1969). In ordinary speech, a behavior described as "traditional" is one that has been learned in some way from others and is passed on to naïve individuals (Gove, 1971). Consequently, calling a pattern of behavior "traditional" implies (or, at the least, will surely lead a listener to infer) that social learning of some kind has played a role in its development. Those unfamiliar with the literature on traditions of animals may even infer that the behavior described as traditional or cultural is actively transmitted by the knowledgeable to the naïve by teaching, imitation, or some other complex process, as are most elements of human culture (Galef, 1992).

Of course, the word used to describe a phenomenon is of little importance so long as the label does not interfere with understanding, as describing population-specific behaviors as traditional seems sometimes to do (Whiten and Ham, 1992). What is important is that we not allow the use of words from the common language as technical terms to cloud our thinking about behavioral phenomena.

Why field workers have until fairly recently labeled as "traditional" essentially any pattern of behavior common in one population of a species and rare or absent in others is not obvious. Whatever the origins of the practice, it is problematic for those interested in the processes responsible for the development of specific patterns of behavior. Behavioral differences among groups can often be explained as the result of asocial developmental processes (see Ch. 11). Consequently, referring to any population-specific behavior as traditional before it has been established that it is transmitted from individual to individual by social learning conceals the need for developmental analysis.

Tradition, like adaptation (Williams, 1966), is an onerous concept that should be employed only when there is evidence that social learning of some kind actually plays a role in dissemination of the supposedly traditional behavior. Otherwise, description of a behavior as "traditional" serves only to camouflage ignorance of the developmental processes responsible for the spread of behaviors so labeled.

Calling a population-specific behavior traditional before the causes of its development have been identified has a further unfortunate consequence. Those with a primary interest in areas other than behavioral development may assume that once it has been established that a behavior is, in fact, traditional in an animal population (i.e., that it is learned in some way by the naïve as a result of interaction with knowledgeable others), the causes of its diffusion are known.

6.1.2 Tradition and social learning

Gaulin and Kurland (1976, p. 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". Surely, the concept of tradition differentiates those instances of behavioral variance resulting from social transmission from those resulting either from genetic processes or from behavioral differences reflecting response to variation in the asocial environment. Still, Gaulin and Kurland (1976) focused attention on an important issue. Social learning processes, from "teaching" (Caro and Hauser, 1992) to "local enhancement" to "true imitation" (Thorpe, 1963), can result in transmission of behavior from one individual to another. Consequently, for those interested in understanding either behavioral development or social learning processes, calling a population-specific behavior "traditional" answers relatively few questions and raises many.

6.2 Alternative explanations of behavioral variation

Variance among individuals in behavioral development can be conceived of as caused by interaction of three types of information: (a) genetically transmitted information received from parents, (b) information acquired individually as a result of direct transactions with the asocial environment, and (c) information acquired by individuals as a consequence of interactions with conspecifics (Galef, 1976). Obviously, simply discovering a difference in the behavior of two populations does not demonstrate that social learning produced that difference. Less widely appreciated is the converse proposition. Discovery of singular properties of either the gene pool or ecology of a population that exhibits a unique pattern of behavior does not mean that social learning is excluded as a cause of diffusion of that behavior.

The relationship among findings in genetics, ecology, and the study of social learning has produced sufficient misunderstanding (see, for example, the exchange in *Science* between Strum (1975, 1976) and Gaulin and Kurland (1976)) that discussion of a concrete example may prove useful.

6.3 An example: vampire finches of Wolf and Darwin Islands

Measurement of body parts of adult male, sharp-beaked ground finches (*Geospiza difficilis*) on Wolf (Wenman) and Darwin (Culpepper) Islands (40 km apart and 100 km from the closest other island) in the Galapagos Archipelago has resulted in classification of *G. difficilis* on these two islands as a distinct subspecies (*septentrionalis*) (Lack, 1947, 1969; Schluter and Grant, 1982, 1984). Such classification may lead to the inference that the unique morphology of *G. difficilis* on Wolf and Darwin Islands reflects differences between the genotypes of *G. difficilis septentrionalis* and those of *G. difficilis* found elsewhere in the Galapagos. Indeed, DNA analyses in progress at the time this manuscript was in preparation are providing direct evidence that *G. difficilis* found on Wolf and Darwin Islands is genetically distinct from other population of the species (P. Grant, personal communication, September 8, 1999).

Sharp-beaked ground finches found on Wolf and Darwin Islands differ from those found elsewhere in the Galapagos not only in heritable morphological characters but also in their environment and behavior. For example, Wolf and Darwin Islands are not inhabited by the predatory owls and hawks that are found elsewhere in the Galapagos Archipelago. Possibly as a consequence, *G. difficilis septentrionalis* exhibits "a tameness that is most striking" (Bowman and Billeb, 1965, p. 41).

Wolf Island is also the only place in the Galapagos where *Opuntia* (prickly-pear) cacti are found that do not also support species of ground finches (*G. scandens* and *G. conirostris*) that are specialized feeders on *Opuntia*. Perhaps because of the absence of efficient competitors on Wolf Island, *G. difficilis* birds found there, unlike conspecifics elsewhere in the Galapagos, probe *Opuntia* flowers for nectar and pollen.

More startling, *G. difficilis* subspecies 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 boobies' feathers, and feed on blood flowing from the wounds thus created. Also on Wolf and Darwin Islands, but not

elsewhere, *G. difficilis* uses its relatively long bill to pierce seabird eggs and eat their contents (Bowman and Billeb, 1965; Koster and Koster, 1983; Schluter and Grant, 1982, 1984).

In sum, the *G. difficilis septentrionalis* subspecies exhibits four population-specific behaviors: unusual tameness, feeding on cactus flowers, feeding on birds' eggs, and feeding on blood. The last of these four population-specific behaviors is the one most frequently referred to in the literature as a "tradition" of finches on Wolf and Darwin Islands, so I shall focus discussion on it. The question, of course, is whether the wealth of available information regarding the taxonomy, ecology, and natural history of sharp-beaked ground finches is sufficient to determine whether the unique patterns of behavior exhibited by *G. difficilis* on Wolf and Darwin Islands are "traditional" in the strict sense of the term.

6.3.1 Is blood feeding an animal tradition?

To test the hypothesis that the unusual behaviors exhibited by *G. difficilis septentrionalis* are traditional, information is needed about social interactions that might increase the probability that an individual born on Wolf or Darwin Island would exhibit behaviors typical of the *G. difficilis* found there. Although hypotheses relating to the development of such unique behaviors will surely incorporate information about ecology and genetics, their test requires study of behavioral development in individuals. Analyses at population, ecological, or genetic levels are simply not sufficient.

For example, Bowman and Billeb (1965) have suggested, regarding the habit of blood feeding, that (a) during the dry season, when insects (the typical fare of *G. difficilis*) are reduced in numbers, boobies are frequently infested with black hippoboscids that are, at least to a human observer, very conspicuous against the boobies' white plumage, and (b) finches might pursue flies on boobies and develop the blood-feeding habit as a result of accidentally puncturing a booby's skin while attempting to capture a fly.

Although such an account fails to address directly the question of why *G. difficilis* on Wolf and Darwin Islands feeds on the blood of boobies, whereas *G. difficilis* found elsewhere does not, the explanation is at a level of analysis appropriate to that issue. To understand the origins of blood feeding we need information about how the behavior develops in individuals.

Heritable differences in tameness might permit *G. difficilis septentrionalis* to approach boobies when other subspecies of *G. difficilis* would not. Heritable differences in beak shape might increase the ease with which this subspecies gains access to blood. There might also be heritable differences among subspecies of *G. difficilis* in the tendency to attack seabirds. However, ecological differences among islands of the Galapagos Archipelago might make blood feeding particularly valuable to finches on Darwin and Wolf Islands, maintaining a behavior in which all *G. difficilis* subspecies would engage, if they were exposed to similar ecological conditions.

Last, it is also possible that a very rare incident allowed one *G. difficilis septentrionalis* bird living on Wolf or Darwin island to learn to attack boobies and feed on their blood, and that the habit of blood feeding developed in others as a result of learning from this innovator. Indeed, blood feeding may have developed or be maintained in response to all five of the factors mentioned above interacting in complex ways in the unique situation, environmental, genetic as well as social, in which all the birds of this subspecies live. Determining causes of the unusual behaviors of sharp-billed ground finches on Wolf and Darwin Islands would require experiments, in addition to observation and correlational analyses. Such experiments have not been and, given the protected state of the genus, may never be conducted with Darwin's finches. However, behaviors that are engaged in by members of some populations of a species but not others have been found in species less fragile than the ground finches of the Galapagos Archipelago.

6.3.2 Primate traditions

In the anthropological or psychological literatures, particular attention has been given to evidence consistent with the view that at least some of the unusual behaviors observed in only one or a few chimpanzee, capuchin, or dolphin troops may be behavioral traditions (for review see Whiten *et al.*, 1999 and Chs. 13 and 14). However, in apes and in capuchin monkeys, as in the Galapagos finches discussed above, the hypothesis that population-specific patterns of behavior observed in free-living populations are traditional does not rest on experimental evidence. Rather, the conclusion that such species exhibit true behavioral traditions depends largely on exclusion of alternative explanations of the origins of population-specific behaviors (for an exception, see Ch. 5).

6.4 Traditions of rats

It is seldom mentioned in discussions of the possibility of population-specific patterns of behavior in primates that the most convincing evidence of behavioral traditions in free-living, nonhuman animals is to be found not in the geographical distribution of patterns of tool use by our great ape cousins or of social behaviors in our more distant primate relatives but in the singing of passerine birds and the feeding habits of Norway and black rats (for a refreshing exception, see McGrew, 1998).

The fact that evidence of behavioral traditions is not restricted to our close phylogenetic relatives is important because it serves as a reminder that evidence of traditional patterns of behavior in animals, no matter how convincing, is not evidence of mental processes in animals similar to those supporting traditions in humans (Galef, 1992). Indeed, analyses of traditions in nonprimates, particularly in Norway and black rats, have demonstrated repeatedly that animal traditions can rest on rather simple behavioral substrates.

6.4.1 Field evidence of traditions in Norway and black rats

Norway rats (*Rattus norvegicus*) are the most successful, nonhuman mammals on the planet and are found breeding from Nome, Alaska (64° 32' N), where they live on human garbage (Kenyon, 1961), to South Georgia Island (54° 90' S), where they subsist on a diet of tussock grass, beetles, and ground-nesting birds (Pye and Bonner, 1980). Much of the biological success that rats enjoy results from their ability to adapt their foraging to an extraordinary range of ecological conditions.

Not surprisingly, given the plasticity of the foraging behavior of Norway rats, most population-specific behaviors in the species involve foraging of one sort or another. Norway rats living on the banks of ponds in a hatchery in West Virginia catch fingerling fish and eat them (Cottam, 1948). Many members of some colonies of Norway rats living on the banks of the Po River in Northern Italy dive for and feed on mollusks inhabiting the river bottom, whereas no members of nearby colonies with equal access to mollusks prey upon them (Gandolfi and Parisi, 1972, 1973; Parisi and Gandolfi, 1974). On the island of Norderoog in the North Sea, Norway rats frequently stalk and kill sparrows and ducks (Steiniger, 1950), though they have not been reported to do so elsewhere. Colonies of black rats (*Rattus rattus*) thrive in the pine forests of Israel by removing scales from pinecones and eating the seeds that the scales conceal, a

behavior not reported in other populations of black rats (Terkel, 1996), and so on.

6.4.2 Laboratory studies of “traditions” in free-living rats

Numerous instances of possible socially transmitted behavior have been analyzed in laboratory studies of rat behavior: everything from movement in a T-maze to predation on house mice and avoidance of candle flames (e.g., Church, 1957; Flandera and Novakova, 1974; Lore, Blanc and Suedfeld, 1971). However, most systematic, experimental investigations of traditions in rats have involved analyses of instances of population-specific patterns of behavior that, like those mentioned in the preceding section, were first described by those studying free-living rats.

Fortunately, population-specific behavior observed in rats can often be reproduced in the laboratory. Consequently, development of such behaviors can be examined experimentally, and assertions that population-specific behaviors seen in free-living animals are, in fact, traditional can be critically evaluated.

6.4.3 Learning what to eat

6.4.3.1 Field observations

Fritz Steiniger (1950), an applied ecologist who spent many years studying ways to improve methods of rodent control, discovered that it was particularly difficult to exterminate rat colonies by repeatedly placing the same poison bait in a rat-infested area. When Steiniger used the same bait a number of times, despite initial success in reducing pest numbers, later bait acceptance was very poor, and colonies soon returned to their initial sizes (Steiniger, 1950). Young rats that were born into colonies that contained animals that had survived their first ingestion of a poison bait, and had consequently learned not to eat it, avoided the bait without ever even tasting it for themselves. Steiniger (1950) believed (incorrectly, as it turned out) that inexperienced rats were dissuaded by experienced individuals from ingesting potential foods by those that had learned that the bait was toxic.

6.4.3.2 A laboratory analogue

Young wild rats' total avoidance of diets that adults of their colony have learned to avoid ingesting is a robust phenomenon that can be brought into the laboratory with little difficulty (Galef and Clark, 1971a). We captured adult wild rats on a garbage dump in southern Ontario and

placed them in groups of five or six in 2 m² laboratory cages. For 3 hours each day, each experimental colony was provided with two easily distinguished, equally nutritious foods.

To begin a typical experiment, we introduced sublethal doses of a toxin into one of the two foods placed in a colony's cage each day. Under such conditions, colony members rapidly learned to avoid ingesting the poisoned food, and continued to do so even when subsequently offered uncontaminated samples of the previously toxic bait.

After a colony had been trained, we had to wait until a female colony member gave birth and her young grew to weaning age. Then, we could use closed-circuit television to observe adults and pups throughout daily feeding sessions and record the number of times that pups ate each of the two uncontaminated foods in their cage: one of which adult colony members were eating and the other they were avoiding.

We found repeatedly that weaning young ate only the food that the adults of their colony were eating and totally avoided the alternative (Galef and Clark, 1971a). Even when we removed pups from their natal enclosures and offered them the same two foods that had previously been available to them, the pups continued to eat only the food that adults of their colony had eaten (Galef and Clark, 1971a). Clearly, we had a laboratory situation in which young rats showed a population-specific pattern of food choice similar to that shown by the free-living wild rats Steiniger (1950) had studied in Germany two decades earlier.

6.4.3.3 Analysis of the phenomenon

My students and I have spent much of the last 30 years determining how feeding patterns of adult rats influence food choices of the young that interact with them (for reviews see Galef, 1977, 1988, 1996a,b). We have not been working painfully slowly. Rather, we have discovered that there are many ways in which social interactions affect rats' selection of foods and feeding sites, and years of investigation, both in our laboratory and elsewhere, have been required to begin to unravel the complexities involved. Below, I explore briefly some of the processes occurring throughout life that result in rats tending to select the same foods to eat as their fellows.

6.4.3.4 Prenatal effects

A rat fetus exposed to a flavor while still in its mother's womb (as a result, for example, of injection of that flavor into its dam's amniotic fluid) will, when grown, drink more of a solution containing that flavor than will

