The Biology of Traditions

Models and Evidence

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6

"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.

<div align="right">STEINIGER, 1950, P. 368</div>

<div align="right">159</div>

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 hippoboscid flies 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

control rats lacking such prenatal experience (Smotherman, 1982). More realistically, feeding garlic to a pregnant rat enhances the postnatal preference of her young for the odor of garlic (Hepper, 1988).

6.4.3.5 Effects while suckling

Evidence from several laboratories has indicated that flavors of foods that a rat dam eats while lactating affect the flavor of her milk, and exposure to such flavored milk affects the food preferences of weaning pups (Galef and Henderson, 1972; see also, Bronstein, Levine, and Marcus, 1975; Galef and Sherry, 1973; Martin and Alberts, 1979).

Clearly, a process is at work during the nursing period that can increase the probability that successive generations of rats will choose to eat the same foods. As weaning proceeds, both the number of such processes and the magnitude of their impact of food choice increases.

6.4.3.6 Effects while weaning

Galef and Clark (1971b) used time-lapse videography to observe each of nine wild rat pups take their very first meals of solid food. All nine pups ate for the first time under exactly the same circumstances. Each took its first meal at the same time that an adult member of its colony was eating and each ate at the same place that the adult was feeding, not at an alternative feeding site a short distance away.

Further studies revealed that weaning rat pups do not follow adults as they move to feeding sites but instead use visual cues to detect and approach feeding adults from a distance (Galef and Clark, 1971b). In fact, anesthetizing an adult rat and placing it near one of two otherwise identical feeding sites makes the site occupied by the anesthetized adult far more attractive to pups than the unoccupied site, and young pups both visit and eat more at the occupied site than at the unoccupied one (Galef, 1981).

6.4.4 Residual olfactory cues

6.4.4.1 Feeding site selection

Adult rats do not need to be physically present at a feeding site to cause conspecific young to prefer to feed there. As rats leave a feeding site, they deposit scent trails that direct young rats seeking food to locations where food was ingested (Galef and Buckley, 1996). Also, feeding adult rats deposit residual olfactory cues both in the vicinity of a food source

(Galef and Heiber, 1976; Laland and Plotkin, 1991) and on foods they are eating (Galef and Beck, 1985). These odors are attractive to pups and, like the presence of an adult rat at a feeding site, cause young rats to prefer marked sites to unmarked ones.

Normal response to residual cues found around a feeding site depends on preweaning experience of pups with their dam and siblings. Pups reared without contact with conspecifics (Hall, 1975) do not find feeding sites marked with feces of adult rats attractive; pups reared in social isolation and given a few days to interact with a lactating female and pups are subsequently attracted to a feeding site by the presence there of fecal material (Galef, 1981).

6.4.4.2 Feeding site selection and food choice

Although both adult rats and residual olfactory cues present at a feeding site increase a site's attractiveness to weaning rats, such effects are, obviously, not in themselves sufficient to produce socially transmitted food preferences. However, if feeding sites that are used and marked by adult rats contain foods different from those found at sites that adults are not exploiting and marking, then socially learned food preferences can result from socially learned feeding site preferences (Galef and Clark, 1971a).

Wild Norway rats are extremely hesitant to ingest any potential food that they have not previously eaten (Barnett, 1958; Galef, 1970), and young wild rats socially induced to eat their first meals at a site containing a food become familiar with that food and are very reluctant to eat anything else (Galef and Clark, 1971a). Consequently, social influences on feeding site selection may act indirectly (Galef, 1985) to produce traditions of food preference and avoidance in rats of the kind Steiniger (1950) described.

6.4.4.3 Direct transmission of flavor preferences

After a naïve "observer" rat interacts with a recently fed conspecific "demonstrator", the observer exhibits substantial enhancement of its preference for whatever food its demonstrator ate (Galef and Wigmore, 1983; Posadas-Andrews and Roper, 1983; Strupp and Levitsky, 1984). Both food-related odors escaping from the digestive tract of a demonstrator and the scent of bits of food clinging to its fur and vibrissae allow conspecifics to identify foods others have eaten (Galef, Attenborough and Whiskin, 1990; Galef, Kennett and Stein, 1985; Galef and Whiskin, 1992). However, socially enhanced food preferences depend on rats experiencing food odors together with other stimuli emitted by live conspecifics (Galef et al.,

1985, 1988; Galef and Stein, 1985; Heyes and Durlach, 1990). For example, rats exposed to pieces of cotton batting dusted with a food and moistened with distilled water do not develop a preference for the food. However, rats exposed to the same food either dusted on the head of an anesthetized conspecific or on a piece of cotton batting that has been moistened with a dilute carbon disulfide solution (carbon disulfide is a constituent of rat breath) exhibit strong preferences for the food to which they were exposed (Galef *et al.*, 1988; Galef and Stein, 1985).

Such effects of exposure to a recently fed rat on the food choices of its fellows are surprisingly powerful (Galef, Kennett, and Wigmore, 1984; Richard, Grover, and Davis, 1987). If observer rats first taught to avoid totally ingesting a diet by following its ingestion with an injection of toxin are then placed with a conspecific demonstrator that has eaten the diet to which an aversion has been learned, these observers frequently totally abandon their aversion to the diet associated with illness. Further, most rats that interact with conspecifics fed a diet adulterated with cayenne pepper, which is inherently unpalatable to rats, subsequently prefer peppered diet to unadulterated diet (Galef, 1986a). However, as the degree of aversiveness of a food increases, the impact of social influences on its acceptance decreases (Galef and Whiskin, 1998a).

6.4.5 Multigenerational traditions

Evidence that rats can influence one another's choice of foods is overwhelming. However, for a "tradition" to become established in a population, at least some individuals who acquire the traditional pattern of behavior must engage in it long enough to induce others to behave similarly.

As Heyes (1993) has pointed out, socially learned behaviors are not insulated from modification by individual learning during the time between their acquisition and transmission. Consequently, demonstrations that socially transmitted behaviors are sufficiently stable to permit repeated retransmission, and consequent diffusion through a population, are necessary to establish the sufficiency of social learning to support behavioral traditions (Laland, Richerson, and Boyd, 1993). In part because of the expense of maintaining large numbers of animals in the laboratory, such demonstrations are few in number.

6.4.5.1 Digging for food

Laland and Plotkin (1990, 1992) employed a procedure in which a rat that had learned socially to dig for buried food served as a model for a naïve rat,

which, after learning socially to dig for buried food, became a model for another naïve rat etc. Such chaining captures some features of diffusion of socially learned behaviors through free-living populations of animals. However, Laland and Plotkin's (1990, 1992) procedures involved simple iteration of a basic social learning situation (in which a naïve individual learns by interaction with a trained model) and failed to capture many features of life outside the laboratory that might interfere with propagation of behavior. In particular, there was no opportunity for individual learning about alternative behaviors in the interval between social acquisition and transmission of digging behavior, and the presence of alternatives is of considerable possible importance in determining the fidelity of transmission of a socially learned behavior (Galef and Whiskin, 1997, 1998b).

6.4.5.2 Food preferences

Galef and Allen (1995) established small colonies of rats and trained all members of each colony to eat only one of two equipalatable foods available *ad libitum*. After training, one member of the trained colony was removed every 24 hours and replaced with a naïve individual. The process was continued long after all original colony members had been removed, with replacement each day of the colony member that had been in the colony longest. Colonies maintained the food preferences taught to their founders for weeks after all the founders had been replaced (Fig. 6.1).

The longevity of such traditions of food choice was affected by a number of factors, including colony size, rate of replacement of colony members, and number of hours each day that colony members had access to foods (Galef and Allen, 1995; Galef and Whiskin, 1997).

6.5   Summary

Results of more than a quarter century of research demonstrate unequivocally that, under laboratory conditions, rat colonies can maintain stable traditions of food preference. Consequently, we know that at least some of the many mechanisms for social learning about foods uncovered in laboratory studies of social influences on food choice have the potential to support traditions of food preference of the sort Steiniger (1950) described in free-living rats. Although we do not yet know which processes demonstrated in the laboratory to support social learning of food preferences are actually responsible for feeding traditions in free-living populations of rats (Galef, 1984), we do know that social learning can lead to traditions
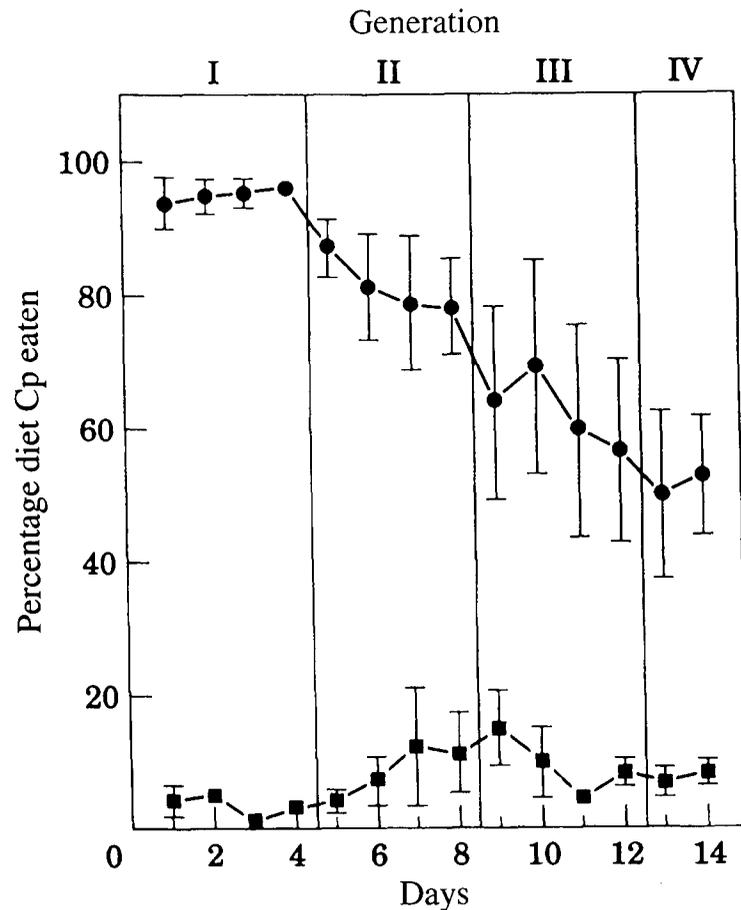
Generation

Fig. 6.1. The amount of cayenne-pepper-flavored diet (diet Cp) as a percentage of total amount (mean ± SEM) eaten by subjects offered both diet Cp and wasabi-flavored diet in colonies whose founding members ate only diet Cp or wasabi-flavored diet. On day 1, enclosures contained only founding members, on days 2–4 both founding colony members and replacement subjects, and on days 5–14 successive generations of replacement subjects (Galef and Allen, 1995; by permission of Academic Press).

in these animals, something that has not been demonstrated in any other genus of nonhuman mammal.

6.6   Learning how to eat

Field observations suggest that social influences can affect not only what rats eat, but how they eat as well.

6.6.1 Diving for food in nature

Gandolfi and Parisi (1972) reported that most members of some colonies of Norway rats living along the banks of the Po River in Italy would dive in the river and feed on mollusks on the river bottom, whereas no members of nearby colonies with equal access to mollusks did so. Gandolfi and Parisi (1972) interpreted their findings as consistent with the hypothesis that predation on submerged mollusks spreads through colonies by social learning. If discovery of mollusks on the riverbed were a rare event, and colony members could learn to dive for mollusks by observing other rats doing so, then the reported bimodality in frequency of diving in rat colonies along the Po could be explained.

Although the hypothesis that the habit of diving in shallow water for food spreads through colonies of wild rats as a result of social learning is attractive, confirmatory evidence has proved difficult to collect even in seminatural settings. Nieder, Cagnin, and Parisi (1982) observed mollusk predation by rats in a large (22 m × 10 m) outdoor enclosure built over a branch of the Po River. The enclosure provided opportunity for unobtrusive observation of mollusk predation in a small population of rats. Unfortunately, although the data collected in the enclosure did suggest that social learning of some sort might have been involved in diffusion of the habit of mollusk predation through a rat population, they are ambiguous.

6.6.2 Diving for food in the laboratory

The potential contribution of social processes to development of the habit of diving for food in shallow water has also been examined under controlled conditions (Galef, 1980). The experiments involved simplified laboratory analogues of the natural situation and, therefore, cannot be extrapolated uncritically to the more complex uncontrolled environment. However, results of the experiments did provide evidence bearing on the issue of whether it is necessary to invoke social learning to explain the distribution of the habit of diving for food reported by Gandolfi and Parisi (1972, 1973).

Second- and third-generation laboratory-bred female wild rats captured on garbage dumps in southern Ontario were placed together with their offspring in enclosures with separate nesting and diving areas connected by meter-long tunnels. In the diving area, subjects could retrieve pieces of chocolate from beneath 15 cm of water.

Adult rats that had not been explicitly trained to dive for food never dived, even if housed with a rat that had been trained to dive for food by

placing chocolate squares in an empty tank and, over a period of weeks, increasing the water level to 15 cm. However, approximately 20% of juvenile wild rats reared in the enclosures came to dive for food. Juveniles were as likely to learn to dive whether their dam regularly dived and retrieved chocolates from under water or never did so. Such results suggest that observation of a diving conspecific does not, in itself, induce rats to dive.

6.6.2.1 Social learning of swimming?

In a subsequent study, young wild rats were trained to swim across the surface of a small body of water to reach food. When introduced into enclosures connected to a diving area, where food was available below 15 cm of water, more than 90% of subjects trained to swim spontaneously dived for food.

The finding that swimming rats are effectively diving rats limits the potential role of social learning in the spread of diving behavior through a population. If rats learn to swim independently, and if swimming rats dive, then social learning could serve only to direct rats to dive in one area rather than another. However, development of swimming might itself be socially influenced. If so, then social learning might indirectly potentiate propagation of diving behavior by facilitating propagation of swimming behavior.

An experiment in which wild rat pups were reared by dams that either swam or did not swim to food in an apparatus where highly palatable food could be reached by swimming 1.7 m down an alley revealed no difference in the age of initiation of swimming by pups as a function of whether their dam swam. All pups began to swim before they reached 40 days of age.

6.6.3 Relating laboratory to field studies

The findings that, at least in the laboratory, wild rat pups readily learn independently to swim and that almost all swimming wild rat pups spontaneously dive for food in shallow water suggest that absence of diving by members of some colonies that live along the Po River may be in greater need of explanation than the diving exhibited by members of other colonies.

Conceivably, all rats living along the Po River know how to dive for mollusks, but they do not dive when sufficient nutriment is available ashore. If so, one might expect rats that had been trained to dive for food to cease diving if adequate rations were made available to them on land. In fact,

rats that reliably dived for food while food was available on land for only 3 in 24 hours stopped diving when given *ad libitum* access to food ashore, even if the food available on land was considerably less palatable than that available under water (Galef, 1980).

Taken together, the laboratory results offer little support for the hypothesis that the distribution of the habit of diving for food observed among colonies of rats living along the Po River results from social leaning of the habit in some colonies, but not others. To the contrary, the laboratory data suggest that all rats may know how to dive for food, but they do so only when adequate food is not available on dry land.

In retrospect, some observations made in the field are consistent with the notion that availability of food on land may be the major determinant of whether members of rat colonies living along the banks of the Po River feed on submerged mollusks. For example, Gandolfi and Parisi (1973, p. 69) reported that in those locations where mollusk predation occurs, mollusks "represent one of the main sources, if not the main source of food for rats" and Parisi and Gandolfi (1974, p. 102) suggested that "the time dedicated by rats to mollusk capture depends greatly on the availability of other foods".

Our laboratory findings suggest that these informal field observations may be more informative than those who made them realized. Possibly, members of colonies that regularly dive for mollusks would stop diving for food if palatable food were available in their territories, and removal of food from the territories of colonies whose members do not normally dive might cause them to start diving. The relevant field experiments have not been carried out, but obviously could be, and might, at least in principle, exclude social learning as an explanation of the distribution of diving behavior along the Po.

6.7 Stripping pinecones for seeds

6.7.1 Field observations

Some years ago, Aisner and Terkel (1992) discovered that black rats (*R. rattus*) living in the pine forests of Israel subsist on a diet of pine seeds in an otherwise sterile habitat. Extraction of pine seeds by stripping pinecones of their scales and eating the seeds the scales concealed allows black rats in Israel to fill a niche occupied elsewhere in the world by tree squirrels, which are not present in the Middle East.
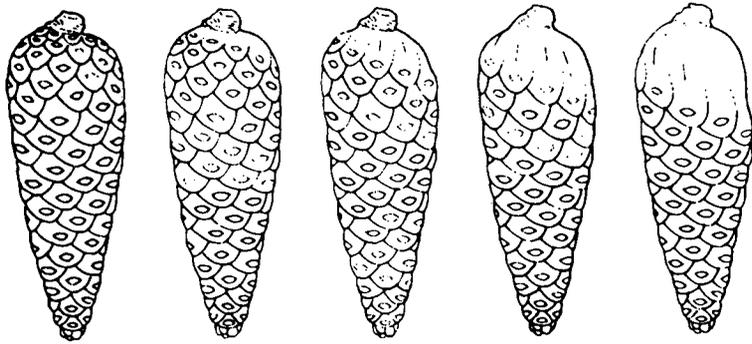
Fig. 6.2. Pinecones in different stages of opening with the number of rows of previously stripped scales increasing from left to right (Terkel, 1996; by permission of Academic Press).

6.7.2 Laboratory analyses

Laboratory studies of pinecone stripping by wild-caught rats revealed that it is difficult for rats to remove the tough scales from pinecones and gain access to the energy-rich seeds they protect and, in doing so, gain more energy from eating the seeds than is expended in acquiring them. To harvest pine seeds efficiently, rats must take advantage of the physical structure of pinecones, first stripping scales from the base of a cone and then removing the scales spiraling around the cone's shaft to its apex one after another (Terkel, 1996; Fig. 6.2).

Laboratory studies of development of the energetically efficient pattern of stripping pinecones found that only 6 of 222 hungry laboratory-reared wild rats given access to a surplus of pinecones for several weeks learned the efficient pattern of cone stripping for themselves (Zohar and Terkel, 1995). The remaining 216 animals either ignored the pinecones altogether or gnawed at them in ways that did not lead to a net energy gain from eating pine seeds. Similarly, pups gestated by dams that efficiently stripped pinecones of their seeds, but reared by foster mothers that did not strip cones, failed to learn to strip pinecones (Aisner and Terkel, 1992). However, more than 90% of pups came to open cones for themselves when reared by a foster mother that stripped pinecones efficiently in the presence of her foster young. Clearly, some aspect of the postnatal inter-action between a dam stripping pinecones and the young she rears suf-fices for transmission of the efficient means of pinecone stripping from one generation to the next (Aisner and Terkel, 1992; Zohar and Terkel, 1992).

Additional experiments led to the conclusion that experience of young rats in completing the stripping of pinecones started appropriately by ei-ther an experienced adult rat or a human experimenter, who used a pair of pliers to imitate the pattern of scale removal by a rat, starting to strip a cone efficiently, enabling 70% of young rats to become efficient strippers (Terkel, 1996).

Terkel's (1996) observations indicated that when a black rat mother opens pinecones by stripping scales and eating exposed seeds her young gather around her and attempt to obtain seeds. Once the young are old enough, they snatch partially opened cones from their mother and con-tinue the stripping process by themselves. Thus, activities of feeding mother rats appear to facilitate acquisition of pinecone stripping by their offspring, first, by focusing attention of juveniles on pinecones as poten-tial sources of food and, later, by providing their young with partially opened pinecones that the young can learn to exploit as sources of food (Terkel, 1996).

As McGrew (1998), a leading proponent of the view that apes exhibit culture, pointed out, no study of a traditional behavior exhibited by the free-living members of any species, even humans, has been carried out with the rigor or elegance of Terkel's analysis of the social transmis-sion of pinecone stripping by black rats. Consequently, today, as 50 years ago when Steiniger made the statement that serves as an epigram for this chapter, we have a better understanding of the origins of behavioral traditions in free-living rats than in any other nonhuman, mammalian species.

6.8   Conclusions

Analyses of behavioral processes resulting in population-specific patterns of behavior often require numerous experiments each involving dozens of animals with similar prior life histories (e.g., Galef, 1980, 1996b; Terkel, 1996). It is relatively easy to procure the numbers of experimentally naïve rodents, birds, fishes, or insects needed for such studies. Almost always, it is impossible to procure similar numbers of primates (for example, see Ch. 7) or cetaceans (see Ch. 9). Consequently, analyses of behavioral pro-cesses supporting traditions in relatively simple systems are likely to be more complete than analyses of traditions in species with large cortices, and lessons learned from analyses of such simple systems will have to inform our understanding of more complex, but less-available species.

Some of these lessons are now discussed and their possible relationship to analyses of some primate "traditions".

6.8.1 Simple mechanisms, complex outcomes

Terkel's studies of rats stripping pinecones of seeds show that social transmission of complex motor patterns can rest on simple social learning processes. Adult rats direct attention of conspecific young to pinecones and provide young with partially opened cones to exploit. Young take advantage of these affordances and learn for themselves the sequence of motor acts needed to strip cones efficiently. No imitation, no teaching, no emulation, and no observational conditioning (Galef, 1976; Whiten and Ham, 1992) are involved in transmission from one generation to the next of a motor skill possibly as complex as that exhibited by apes ingesting difficult vegetable foods (Byrne and Byrne, 1994).

Mediation of social learning by environmental affordances is not unique to pinecone opening by black rats, although the complexity of the motor patterns involved in consumption of pine seeds makes the example a particularly striking one. For example, Norway rats create trails as they move through underbrush on trips to and from foraging sites. These trails lead to traditional patterns of space utilization within colonies (Calhoun, 1962; Telle, 1966).

6.8.2 Environment determination of expression of behavior

6.8.2.1 Pinecone stripping by rats

A few rats in every hundred given pinecones learn independently to strip cones efficiently (Zohar and Terkel, 1995). However, the behavior is common, so far as is known (Smith and Balda, 1979), only in areas where rats do not have to compete with squirrels for pine seeds. Even though pinecone-stripping behavior is clearly socially learned by the majority of rats that eat pine seeds, environmental influences suffice to explain why Israeli black rats strip pine cones and black rats living elsewhere do not (Galef, 1995). There is no need to imagine a "genius" Israeli rat that discovered the proper method for opening pinecones and whose remarkable innovation is the origin of pinecone stripping by Israeli rats.

6.8.2.2 Diving rats

The effect of food distribution on expression of diving behavior in Norway rats in the laboratory is direct and obvious. Rats that can find adequate food ashore refuse to dive even when they have experience of more palatable food under water. Whether a similar process is responsible for the observed distribution of diving behavior in natural circumstances remains to be determined.

6.8.2.3 Chimpanzee culture

In a publication likely to have significant impact on future discussions of traditions in animals, Whiten et al. (1999) provided a list of 65 behaviors that vary in frequency of occurrence in seven geographically distinct, free-living populations of chimpanzees, each studied for many years. The authors subdivide their list of candidate "traditions" into four categories: (a) patterns absent at no site, (b) patterns not achieving habitual frequency at any site, (c) patterns for which absence can be explained by local ecological factors, and (d) patterns customary or habitual at some sites yet absent at others with no ecological explanation.

The 39 behaviors listed in category (d) are discussed as "cultural", the implication being that the distributions of these 39 behaviors across populations, unlike behaviors listed in categories (a–c), result from social learning, rather than from environmental causes. Whiten et al. (1999) did not discuss the implications of the fact that 22 of these 39 behaviors are "common" or "habitual" in one or several populations but only "present" in others. For example, "ant fish" (a probe used to extract ants) is "common" in two populations, "present" in two populations, and "absent" in three.

If ant fishing is "cultural", then explanation is required for why ant fishing is common in only two of the four populations where it has been observed. Such explanation is likely to be ecological, as is the case in pinecone-stripping and diving rats. Perhaps all chimpanzees learn to fish for ants, but the probability that members of different populations ant fish varies from 0 to 100 depending on local environmental conditions, which determine the relative efficiency of ant fishing as a means of obtaining nutrients (Galef, 1992).

The data from chimpanzees are quite different from those emerging from van Schaik's studies of orangutan use of tools to secure food (Ch. 11). Here there is quite convincing evidence that social learning rather than ecology is responsible for population differences in behavior. All members of each of van Schaik's two study populations either do or do not exhibit tool use in exploiting a resource that is exploited by members of both populations.