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of Animal
Culture

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This chapter focuses on two questions: (1) What kinds of evidence suffice to establish that social learning contributes to maintenance of behavioral variation among allopatric populations of a species, and (2) given current evidence, should we accept the hypothesis that traditions observed in free-living, nonhuman animals (hereafter animals) are precursors of culture in *Homo sapiens*?

Part 1: Do Animals Have Traditions?

Criticism . . . and the doubt out of which it arises are the prior conditions to progress of any sort.

(Wylie 1942)

All scientific hypotheses should be poked and prodded, tested and retested, and made to stand up to the available observations.

(White 2006, p. 472)

Titles of recent publications in prestigious journals boldly assert that differences in the behavioral repertoires of allopatric populations of a single species demonstrate culture in animals (e.g., Whiten et al. 1999, 2001; van Schaik, Ancrenaz et al. 2003). This use of the term "culture" to refer to variability in behavior among allopatric populations of animal species has proved contentious (Whiten 2005).

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learning by imitation are frequently mentioned sources of culture in humans that appear to play, at best, a very limited role in the behavioral development of other animals (e.g., Galef 1992, 1996; Tomasello 1994, 2000, this book). Such emphasis in definitions of culture on behavioral variation resulting from imitation and tuition is based on logical arguments that indicate that only imitation and teaching can support the cultural "ratcheting" (the gradual accumulation of socially learned variants) that seems to many to be a critical characteristic of human cultures (e.g., Heyes 1993; Tomasello 1994; Richerson and Boyd 2005). This apparent inability in principle of the types of social learning that are commonly seen in animals to support cumulative behavioral change in a population provides the rationale for focusing attention on the social learning processes in discussions of animal "culture."

Types of Social Learning

Like imitation, local enhancement (defined as "apparent imitation resulting from directing the animal's attention to a particular object or particular part of the environment"; Thorpe 1963, p. 134) can lead to uniformity in behavior among members of a group. However, although local enhancement directs the attention of individuals toward a particular portion of the environment local enhancement leaves each individual to then develop *de novo* its responses to that aspect of the environment that others have made salient. Consequently, local enhancement cannot produce cumulative behavioral change in a population (Heyes 1993).

Emulation, like local enhancement, does not involve learning about the particular behaviors in which others engage; rather, emulation involves learning about outcomes of those behaviors. For example, a focal individual may learn that a tool can be used to gain access to food by observing another use the tool to produce food, and the focal individual may then attempt to produce the same outcome by devising its own way of using the tool (Tomasello et al. 1987; Tomasello 1998, this book). A naïve individual's attention is directed toward a goal and, possibly, to the utility of a tool in achieving that goal, but as in the case of local enhancement, the individual must develop *de novo* its own means of achieving the goal, so again no ratcheting is possible.

In contrast, imitation, defined as "learning to do muscular acts from seeing [others] do them" (Thorndike 1898, p. 76), allows an individual to acquire the details of behavior developed by others (Heyes 1993). An imitator can directly incorporate a model's learned motor patterns into

its own behavioral repertoire and then innovate, using the model's behavior as a platform or scaffolding (Wood et al. 1976) upon which to elaborate. Thus imitation (and a similar argument can be made concerning tuition) can support cumulative culture, whereas other forms of social learning cannot.

It has been proposed that "mechanisms are of secondary importance" (de Waal 1999, p. 636; de Waal and Bonnie, this book) in defining culture. I disagree. Distinguishing homology from analogy requires attention to details of mechanism, as well as to function, and distinguishing analogy from homology is critical to exploring hypotheses concerning the evolution of traits, whether those traits are morphological or behavioral.

The issues raised in the preceding paragraphs will become particularly important in the second part of this chapter, "Animal Tradition; Human Culture." I mention them here because analysis of the behavioral mechanisms that support social learning and traditions in animals has been the foundation of my own approach to the study of behavioral traditions and colors all that follows.

Social Learning and "Culture"

Despite considerable controversy concerning use of the term "culture," all students of animal behavior seem to agree that involvement of social learning of some sort in the development of a behavior is a necessary condition for it to be defined as "cultural" (e.g., Galef 1988; Whiten and Ham 1992). Consequently, an obvious first step in discussion of "culture" in animals (which, for reasons explicated in part 2 of the present chapter, I shall refer to hereafter as "tradition") is to establish which purportedly traditional behaviors involve social learning in their development. If there is no social learning, there is no tradition. Unfortunately, although establishing that social learning has played a role in development of a behavioral variant is critical in determining whether that variant is traditional, showing that social learning is involved in development is often more difficult than it appears to be at first glance.

Animal Traditions

In the following sections I discuss several purported instances of traditions in animals that illustrate the difficulty of determining whether social learning has actually played a role in development of patterns of behavior observed in some populations and not in others. I also indicate

species to inhabit islands where *Opuntia* cactus grow and ground finches that specialize in feeding on cactus (*G. scandens* and *G. conirostris*) are not present (Grant 1986).

Behavior. The behavioral repertoires of *G. difficilis* finches on Wolf and Darwin islands are quite different from those of others of their species. *Septentrionalis* finches are unusually tame (Bowman and Billeb 1965) and are the only *G. difficilis* finches to either eat *Opuntia* cactus regularly or probe *Opuntia* flowers for nectar and pollen (Lack 1969).

More spectacularly, only *G. difficilis* finches on Wolf and Darwin islands feed on the blood of living seabirds. The finches land on the backs of boobies (large white-bodied, dark-winged seabirds of the genus *Sula* that nest throughout the Galápagos), peck at the base of the boobies' wing feathers, and feed on blood that seeps from the wounds that they have created (Bowman and Billeb 1965; Figure 10.1). Also on Wolf and Darwin islands, but not elsewhere, *G. difficilis* finches pierce seabirds' eggs and eat the eggs' contents (Bowman and Billeb 1965; Koster and Koster 1983; Schluter and Grant 1984). Several *septentrionalis* finches were even once filmed "working together" to roll an egg 3 meters from a booby's nest, knocking the egg against a rock until it cracked and then feeding on it (Koster and Koster 1983, pp. 6–7).

If observation of patterns of behavior without obvious ecological correlates restricted to a single population of a species provides evidence of culture (Whiten et al. 1999), then *G. difficilis* finches are "cultural" birds indeed, only one of many avian species that have been reported to exhibit population-specific patterns of foraging behavior (e.g., Lefebvre and Bouchard 2003; Emery 2006). For example, the tools that New Caledonian crows (*Corvus moneduloides*) manufacture and use to forage for insects vary from one part of the island to another (Hunt 1996, 2000; Hunt and Gray 2002), and carrion crows (*Corvus corone*) in Japan have learned to use automobiles as nutcrackers (Nihei and Higuchi 2001).

Blood feeding. Only a handful of the several thousand extant avian species take blood from living animals. Three of that handful, *G. difficilis* and two species of mockingbird (*Nesomimus parvulus* and *N. macdonaldi*), are indigenous to the Galápagos. Consequently, it might be suspected that the mockingbirds learned blood feeding from the finches or vice versa by cross-species social learning, a mechanism for transmission of innovative behaviors

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Figure 10.1 A sharp-beaked ground finch (*G. difficilis*) on Wolf Island feeding on the blood of a seabird. Copyright David Parer and Elizabeth Parer-Cook/AUSCAPE. Modified and printed with permission.

that was widely accepted in the nineteenth century (e.g., Romanes 1882) but has seldom been considered since then (for exceptions, see Werner and Sherry 1987; Carlier and Lefebvre 1997; Lefebvre et al. 1997; for review, see Seppanen et al. 2007). However, although Galápagos mockingbirds and *G. difficilis* finches are coresident on six islands (Bowman and Billeb 1965; Grant et al. 2000), the finches feed on blood only on Wolf and Darwin islands (Bowman and Billeb 1965), and the mockingbirds only on Española and Santa Fé islands (Curry and Anderson 1987), where *G. difficilis* is currently absent.

Discussion. The relatively simple and well-described ecology of the Galápagos, together with detailed knowledge of the genetics, morphology, and behavior of *G. difficilis*, should make it relatively easy to determine which, if any, of the unusual behaviors of *septentrionalis* are in some way socially learned. However, without direct evidence that social learning plays a role in development of the unique behaviors of *septentrionalis*,

we are left to guess at the causes of observed behavioral diversity in *G. difficilis*.

Probably, *septrionalis* feeding on *Opuntia* can be attributed to the absence of cactus-feeding competitors on Wolf and Darwin islands (Lack 1969). Removal of specialized competitors often results in "character release" in the less specialized of two sympatric species (e.g., Robinson et al. 1993). Of course, it remains possible that social learning has promoted diffusion of *Opuntia* feeding among *G. difficilis* on Wolf and Darwin islands.

Other ecological factors may play a role in emergence of blood feeding on Darwin and Wolf islands. Perhaps blood feeding is a response to demands of the low-lying, dry habitat where *septrionalis* finches live. However, if so, explaining why only mockingbirds that reside on relatively elevated and damp Española and Santa Fé islands feed on blood is difficult, as is the observation that *G. difficilis* finches that live on Genovesa Island, which is relatively dry and low lying, do not feed on the blood of seabirds that nest there.

Perhaps the exceptional tameness of *septrionalis* finches (possibly reflecting relaxed selection for wariness on predator-free Wolf and Darwin islands) allows *septrionalis* finches to approach seabirds and feed on ectoparasitic hippoboscids that live among the seabirds' feathers. Accidental puncture of a seabird's skin while hunting flies could lead individuals to learn independently to feed on blood (Bowman and Billeb 1965).

Perhaps all *G. difficilis* finches have blood feeding in their behavioral repertoires, but seasonal loss of alternative sources of protein on Wolf and Darwin islands releases the behavior. Possibly some other ecological difference between the islands is critical in expression of blood feeding. Perhaps an interaction between the unique genotype of *septrionalis* and the ecology of Darwin and Wolf islands results in blood feeding. Perhaps the unusually long bill of the finches on Wolf and Darwin islands is necessary to puncture the skin of seabirds or their eggs. Perhaps "the habit [of feeding on blood] is . . . learned and is transmitted by tradition from one generation to the next" (Bowman and Billeb 1965, p. 42). Perhaps many things. We just do not know. Simple observation of differences in the behavioral repertoires of allopatric populations of a species cannot, in itself, provide strong support for the hypothesis that social learning played a role in development of behavioral variants.

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septrionalis finches (possibly introduced predator-free Wolf and Darwin islands) approach seabirds and feed on the blood of seabirds' feathers. Hunting flies could lead in blood (Bowman and Billewicz 1965).

Blood feeding in their behavioral repertoire. Sources of protein on Wolf and Darwin islands possibly some other ecological factors. Expression of blood feeding. Genotype of *septrionalis* results in blood feeding. Perhaps Wolf and Darwin islands is for their eggs. Perhaps "the blood" is transmitted by tradition (Bowman and Billewicz 1965, p. 42). Perhaps observation of different populations of a species supports the hypothesis that social learning promotes avian variants.

Potential routes to understanding. Cross-fostering of nestling *G. difficilis* finches from Wolf and Darwin islands and nestlings from one of the four islands where both *G. difficilis* and seabird colonies are found, but blood feeding is not, could prove informative. If some cross-fostered chicks behaved like their natural rather than their adoptive parents, then blood feeding could not be a result either of social learning or of interaction with particular environments. If cross-fostered chicks behaved like their adoptive parents, then genetic explanations of blood feeding would be excluded, but effects of social learning and environment would not be distinguished.

Nestling *G. difficilis* finches could also be transferred from Wolf and Darwin islands to low-lying, dry Genovesa Island, where no blood feeding occurs. If such transfers, but not those of nestlings from Wolf and Darwin islands to moist islands, resulted in blood feeding, evidence would be provided of a genotype-environment interaction responsible for development of the behavior.

Potentially most conclusively, adult *septrionalis* finches could be transferred both to Genovesa and to one of the three other islands where *G. difficilis* finches are found, but blood feeding is not. If some members of populations of *G. difficilis* that received immigrants from Wolf and Darwin islands began to feed on the blood of seabirds, social learning would be proved to be an important contributor to current distribution of the behavior.

If, as is likely, moving *G. difficilis* finches from island to island proved impossible, options are more limited, but useful work could still be done. A small experiment carried out during the dry season (when arthropod prey are relatively infrequent on Wolf and Darwin islands) to examine the effect of providing high-protein liquids to some *septrionalis* finches on frequency of occurrence of blood feeding might prove informative. If provisioned birds stopped harassing sea birds, while unprovisioned birds did not, an important ecological contribution to expression of blood feeding could be inferred.

Further, observations that cast light on the development of idiosyncratic feeding behaviors can be useful in identifying truly traditional behaviors. For example, individual Cocos finches (*Pinaroloxias inornata*), the only Geospizine found outside the Galápagos Archipelago, specialize in different foraging behaviors; some feed predominantly on insects gleaned from leaves, others on insects gleaned from branches, and so on. Foraging preferences are not correlated with either the time or place

where foraging occurs or the age, sex, or morphology of the forager (Werner and Sherry 1987). Rather, Cocos finches appear to learn their idiosyncratic feeding behaviors socially. "Throughout the year, we repeatedly observed ($n=20$) a juvenile finch follow an adult . . . and alternately watch the adult, then imitate its feeding, often in precisely the location vacated by the adult" (Werner and Sherry 1987, p. 5509). Providing a desirable food to Cocos finches in a container that required an unlikely behavior to open it and then observing spread through a marked population of container-opening behavior could provide evidence of a capacity for social learning of foraging specializations in the species but would not, of course, show that any naturally occurring foraging variant was in fact socially learned.

WHAT CAN WE LEARN FROM ROOF RATS?

The power of controlled experiments to determine the causes of purportedly traditional behaviors is beautifully demonstrated in a series of studies by Terkel and his colleagues.

Observation. Aisner and Terkel (1992) discovered that black rats (*Rattus rattus*) living in the pine forests of Israel subsist on pine seeds that provide the sole source of nutriment in an otherwise sterile habitat. Extracting pine seeds by stripping scales from a pinecone and eating the seeds the scales protect permit rats in Israel to occupy an ecological niche occupied in other pine forests of the world by tree squirrels (*Scuiridae*) that are absent from Israel.

Experiments. Rats captured in Israel's pine forests continue to strip pinecones in captivity, whereas rats captured elsewhere in Israel, and therefore unfamiliar with pinecones, fail to open pinecones even if they are offered insufficient alternative food. Laboratory studies have shown that to gain more energy from pine seeds than is expended in extracting them from cones, rats must take advantage of the structure of the cones. The rats must first strip scales from the base of a cone and then spiral up and around the cone's shaft to its apex, removing one overlapping scale after another (Terkel 1996; Figure 10.2).

Investigations of development of this energetically efficient method of feeding on pine seeds revealed that only 3 percent of rats reared in the laboratory learned by trial and error to strip pinecones efficiently even when they were provided for weeks with an insufficient amount of rat chow together with an excess of pinecones. The other 97 percent of

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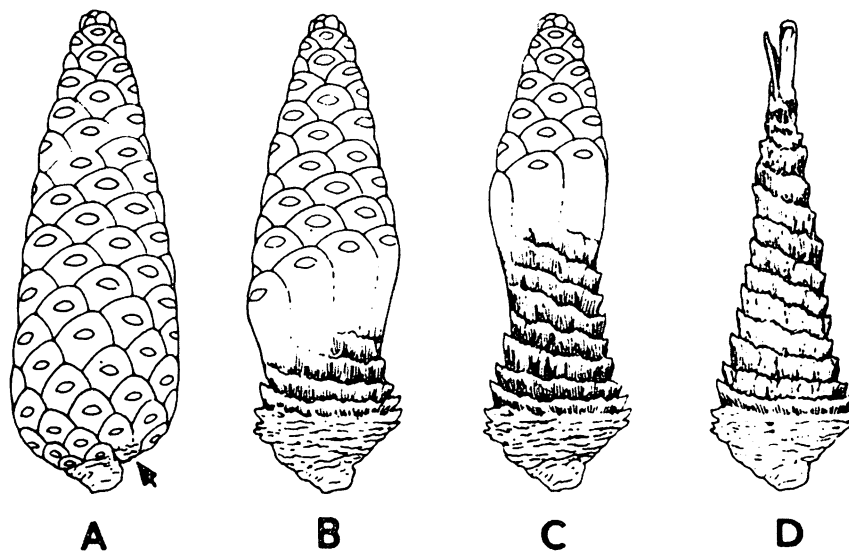


Figure 10.2 Pinecones in different stages of efficient opening, with the number of rows stripped of scales increasing from left to right. From Terkel (1996); reprinted with permission of the author and Academic Press.

subjects either ignored cones or recovered seeds in a way that led to en-
 ergy loss from eating pine seeds (Zohar and Terkel 1992).

Rats born in the laboratory to dams that efficiently stripped pinecones
 and foster reared by dams that did not failed to open cones efficiently,
 whereas more than 90 percent of pups reared by a foster mother that
 opened pinecones in their presence learned the efficient method of strip-
 ping cones (Aisner and Terkel 1992). Further experiments showed that 70
 percent of young rats became efficient exploiters of pinecones following
 experience completing the stripping of pinecones started appropriately by
 either an adult rat or a human experimenter using pliers to copy the initial
 stages of an adult rat's pattern of scale removal (Terkel 1996; see Figure
 10.2). When a rat mother stripped scales from a pinecone, young gathered
 around her and attempted to grab seeds as she uncovered them. As the
 young grew older, they snatched partially opened cones from a feeding
 adult and continued the process that the adult had started (Terkel 1996).

Discussion. Despite the overwhelming evidence that pinecone stripping is
 socially learned by young rats and is therefore traditional in forest rats,

occurrence of the behavior also reflects the absence from Israeli pine forests of tree squirrels, specialized competitors for pine seeds that exclude rats from pine forests elsewhere in the world, another possible example of character release similar to that discussed earlier in reference to *G. difficilis* finches on Wolf Island feeding on *Opuntia* cactus. Indeed, recent observations of black rats on the island of Cyprus, an area that, like Israel, is free of tree squirrels, indicate that they, like the rats of Israel, can survive in pine forests by feeding on pinecones (Landova et al. 2006). Thus the observed difference in the behavioral repertoires of Israel's rats and those living elsewhere has to be understood as an interaction between social learning and ecology, not as a result of social learning alone. As Laland, Kendal, and Kendal (this book) suggest, traditions are not purely socially determined. Both environmental variability and social learning contribute to observed variance in behavior. Second, although social learning clearly contributes to variability in the behavior of allopatric populations of rats, neither teaching nor imitation is involved in diffusion of this complex motor skill.

No other study of a traditional behavior exhibited by free-living members of any species, even humans, has been carried out with the rigor or elegance of Terkel's analysis of pinecone opening by rats (McGrew 1998). The combination of observation in the field and laboratory experiment provides all-but-incontrovertible evidence of social transmission of a complex motor skill from one generation to the next.

NEW CALEDONIAN CROWS

The importance of studies of development in critical examination of purported instances of animal "culture" is particularly clearly revealed in Kenward et al.'s (2005) recent study of development of tool use in New Caledonian crows. These corvids manufacture tools from leaves and use these tools to retrieve food hidden in crevices. Differences in both the types of tools and number of types of tools found in different areas in New Caledonia suggest that there may be traditions of tool use in crow populations (Hunt 2000; Hunt and Gray 2002).

However, when Kenward et al. (2005) hand-reared four New Caledonian crows in captivity, giving the maturing birds no opportunity to interact with tool-using conspecifics, all four hand-reared birds developed the ability to use twig tools, and one of the four both cut a simple tool from a leaf and used it to obtain hidden food. At the time of Kenward et al.'s (2005) publication, none of the hand-reared crows had produced tools as sophisticated as some found in nature. A shortage in the United Kingdom, where

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the experiment was conducted, of appropriate leaves for tool manufacture by crows had prevented regular inspection of the ability of the still-maturing, hand-reared crows to manufacture sophisticated tools (Kacelnik, personal communication, 2006). Nevertheless, "The fact that an inherited predisposition can account for a complex behavior such as tool manufacture highlights the need for controlled investigation into behavioral ontogeny in other species that show culturally transmitted tool use" (Kenward et al. 2005, p. 121; see also Thouless et al. 1989; Tebbich et al. 2001).

Animals with Large Brains

The same problems that bedevil purely observational studies of purported traditions in animals with small brains are common in studies of the better-known "traditions" of larger-brained species. The studies of "traditional behavior" of dolphins and chimpanzees, discussed later, surely provide evidence consistent with the hypothesis that population-specific behaviors are traditional in the populations that exhibit them. However, we still have some way to go before we know which purported traditions actually reflect social learning processes and which are not dependent on social learning for their development.

TOOL USE IN BOTTLENOSE DOLPHINS

Some wild bottlenose dolphins (*Tursiops* sp.) resident in Shark Bay, Western Australia, carry marine sponges while foraging in deepwater channels (Mann and Sargeant 2003). The sponges are believed to be used to protect the rostrum of animals as they probe the sea floor to locate small, bottom-dwelling fishes, and sponge-using females have higher calving success than females that do not use sponges when foraging (Mann, personal communication, 2006).

Analyses of mitochondrial DNA of the Shark Bay dolphins show that sponge use occurs almost exclusively within a single matriline, in which most daughters (and a few sons) of sponge-carrying females adopt the habit (Krützen et al. 2005). Although a genetic explanation of such results seems plausible, Krützen et al. (2005, p. 8942) argue that examination of several possible modes of genetic inheritance makes it "extremely unlikely that a genetic propensity" is responsible for the observed distribution of the behavior. Further, the finding that only some of the many female dolphins that forage in the deepwater channels use sponges while foraging there makes it unlikely that exposure to deep channels in itself results in sponge use (Sargeant et al. 2007). The investigators conclude

that social learning is the sole determinant of the observed variability in behavior in sponge use by dolphins in Shark Bay.

Although some researchers, including some experts in dolphin behavior, have proposed alternative explanations for the data from Shark Bay (see Laland and Janik 2006), the effort that investigators working in Shark Bay are making to examine effects of genotype (Krützen et al. 2005) and environment (Sargeant et al. 2007) in producing the observed distribution of sponge use in dolphins is worthy of emulation.

TRADITIONS IN CHIMPANZEES?

In landmark articles Whiten et al. (1999, 2001) provided a list of 65 behaviors that vary in frequency of occurrence in seven geographically separate populations of chimpanzees (*Pan troglodytes*), each studied for many years. As in *G. difficilis* and *R. rattus*, there are not only substantial ecological differences among sites where populations of interest reside, since chimpanzees live in habitats that range from dry, sparsely wooded savanna to moist forest, but also substantial genetic variation among populations.

Whiten et al. (1999, 2001) sort behaviors of potential interest into four categories: (a) patterns present at all sites, (b) patterns not achieving habitual frequency at any site, (c) patterns the absence of which can be explained by ecological factors, and (d) patterns customary or habitual at some sites but absent at others with no ecological explanation. Perhaps surprisingly, given the exceptionally broad range of habitats that chimpanzees inhabit, only three patterns of behavior are listed in category c (but see Whiten this book).

Differences across populations in frequency of occurrence of behaviors listed in category d are treated as "cultural" on the assumption that the observed differences in behavioral repertoires are a result neither of genetic differences between populations nor individual trial-and-error learning about differences in ecological circumstances. Presumably, at some time in the past a member of a population discovered a behavior in category d, and other members of the innovator's group subsequently acquired that behavior by interacting with the innovator. Members of groups that fail to exhibit a behavior in category d either never stumbled upon the relevant innovation or for some reason (other than a difference in ecology) did not copy an innovator.

However, there are reasons to question the assumption that some behaviors in category d are not a result of genetic or ecological differences

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Second, Whiten et al. (1999, 2001) do not discuss their interesting finding that 22 of the 39 behaviors assigned to category d are “common” or “habitual” in one or more populations but only “present” in others. For example, fishing for termites by using a leaf midrib is present at Bossou, common in the K group at Mahale, and absent at five sites (three with ecological explanation and two without). The challenge is to explain the difference in frequency of occurrence of such behaviors at the sites where it has been observed.

Possibly, by chance, long-term study of chimpanzees at Bossou and Mahale has taken place just when use of leaf midribs has saturated the population at Mahale and is beginning to spread among Bossou chimpanzees. Such chance occurrence is a reasonable explanation for any one of the 22 behaviors assigned to category d that are common or habitual in one group and only "present" in one or more others. However, chance occurrence is a very unlikely explanation for all 22 behaviors that share the characteristic of infrequent occurrence in some populations and frequent occurrence elsewhere. It seems more reasonable to suppose that the variable frequency of occurrence of these 22 behaviors in the various groups in which they are found results from differences in ecology (McBeath and McGrew 1982 provide evidence of effects of habitat on tool use by chimpanzees).

If ecological variables as yet undiscovered account for the differences in the frequencies with which a purportedly cultural behavior is expressed in populations that exhibit it, then ecological variables might also explain complete absence of the same behavior in other groups. Nonoccurrence is just the lower limit of uncommon occurrence.

Ant dipping at Bossou. Much attention has been focused on different methods used by allopatric populations of chimpanzees to dip for driver ants, frequently described as one of the strongest examples of culture in chimpanzees (e.g., Boesch and Boesch 1990; McGrew 1992). At Gombe in Tanzania (East Africa) chimpanzees that are dipping for ants hold a long wand in one hand, introduce one end of the wand into an underground nest of driver ants, and then quickly withdraw the wand as the ants stream up it to attack. The chimpanzee then sweeps the length of the wand with its free hand, collecting the ants in a loose ball that it then pops into its mouth (McGrew 1992). In the Taï Forest in the Ivory Coast (West Africa), an ant-dipping chimpanzee uses a short stick to collect a small number of ants and then pulls the stick directly through its mouth. The Taï technique results in capture of far fewer ants per unit time than the Gombe technique (Boesch and Boesch 1990).

Boesch (1996a) examined ecological factors at Taï and Gombe that might favor different ant-dipping techniques, but could find none. However, Sugiyama (1995, p. 203) had previously proposed that the length of the wand, the dipping technique employed, and the working position of chimpanzees when ant dipping "must be determined by the

of chimpanzees at Bossou and leaf midribs has saturated the to spread among Bossou chimpanzees. A plausible explanation for any one of these behaviors is that they are common or habitual for all 22 behaviors that share in some populations and more reasonable to suppose that these 22 behaviors in the various species from differences in ecology and evidence of effects of habitat on

ered account for the differences in cultural behavior is when ecological variables might influence behavior in other groups. uncommon occurrence.

has been focused on different chimpanzees to dip for driver strongest examples of culture in (1990; McGrew 1992). At Gombe, chimpanzees that are dipping for ants hold a wand into an underground nest and withdraw the wand as the ant enters. The ant then sweeps the length of the wand in a loose ball that it then pops out. In the Ivory Coast (West Africa), chimpanzees use a short stick to collect a small ant directly through its mouth. The ant enters the mouth and the ant dies per unit time than the ant (1990).

factors at Tai and Gombe that chimpanzees use, but could find none. It has previously proposed that the technique employed, and the working hypothesis "must be determined by the

characteristic features of the prey and, to some extent, tradition of the chimpanzee group."

It seems unlikely that the efficient foraging technique of ant dipping used at Gombe was never discovered at Tai. Chimpanzees at Bossou in Guinea (West Africa), like chimpanzees at Gombe, use long wands and use their hands to wipe ants from probes, which suggests that discovery of the Gombe technique is not a rare event. More intriguing, chimpanzees at Bossou not only use both the Tai and Gombe ant-dipping techniques but also use the Tai technique more frequently than the Gombe technique despite the alleged greater efficiency of the Gombe technique.

Humle and Matsuzawa (2002) investigated the role of nonsocial factors in determining use of short and long probes in ant dipping by chimpanzees at Bossou. They found that (1) chimpanzees at Bossou fed on several different species of ant, and (2) the aggressiveness of different ant species was correlated with the technique that chimpanzees employed in dipping for them. Use of long tools (and the corresponding use of the hand to remove ants from wands) was associated with dipping in risky contexts, for example, when feeding on black ants that delivered more painful bites (at least to humans) than did red ants, or when feeding on bivouacked ants that were more aggressive than were those at lower densities. A simple experiment in which humans used wands of different lengths to dip into nests of red and black ants revealed that black ants swarmed up the probe in greater numbers than did red ants. Not surprisingly, the chimpanzees at Bossou probe nests of black ants by using long wands and the pull-through-the-hand method and probe nests of red ants using the short tool and pull-through-the-mouth method.

Of course, the finding that the ant-dipping method is affected by prey behavior at Bossou does not show that the different ant-dipping techniques used by chimpanzees at Gombe and Tai reflect differences in the behavior of ants at the two sites. Indeed, results of experiments described in a very recent paper by Mobius et al. (2008) indicate that differences in the aggressiveness of preyed-upon ant species will not explain all of the differences in ant-dipping techniques used by chimpanzees in different areas. Nonetheless, the Humle and Matsuzawa (2002) finding does raise questions that need to be answered before cultural explanations of differences in ant-dipping techniques at Tai and Gombe are accepted.

That so obvious a potential explanation of differences in ant-dipping behavior as the nastiness of prey, previously mentioned in the literature

(Sugiyama 1995), escaped attention is particularly problematic because environmental correlates of variation in behavior can be far more subtle than those reflected in differences in aggressiveness of ants of different color. For example, seasonal variability in the rate at which chimpanzees at Gombe hunt for colobus monkeys has been attributed to seasonal variability in the frequency with which foraging chimpanzees encounter colobus troops. This encounter rate is, in turn, affected by seasonal patterns of fruit availability that determine both the distance traveled by foraging chimpanzee troops each day and the likelihood that both monkeys and apes simultaneously exploit the same resource (Stanford 1998).

Development of termite fishing at Gombe. Failure to detect ecological or genetic correlates of differences in the behavior of members of allopatric populations provides, at best, indirect evidence that those differences are cultural. Direct studies of development of behaviors of interest are clearly both needed and generally lacking. There are, however, exceptions.

Lonsdorf (2005; Lonsdorf et al. 2004) has reported results of a 4-year field study of development of termite fishing in wild chimpanzees at Gombe. Lonsdorf's analysis of her observations revealed, first, that male and female chimpanzees differ significantly both in the rate at which they acquire each behavioral component of termite fishing and in the age at which they become successful fishers for termites, with female chimpanzees achieving success, on average, more than 2 years before males. Infant (less than 4 years old) females spent significantly more time watching adults termite fishing than did infant males, who spent more time while at termite mounds playing than watching adults feed. Across both sexes time spent watching in the preceding year, but neither investigating mounds nor contacting mounds with tools, was correlated with age at first successful fishing. However, females, but not males, showed a distribution of the depths to which they dipped tools into termite mounds that was correlated with the distribution of dipping depths used by their respective mothers

Lonsdorf (2005, p. 681) concluded that "development of termite fishing includes social learning processes as well as individual trial-and-error learning . . . Male and female offspring learn from their mother that the termite mound is the object to which attention should be directed . . . Once the mother starts to termite-fish male and female learn that the goal of the behaviour is to capture termites . . . Male offspring then develop their own method of achieving this goal, while females

cularly problematic because behavior can be far more subtle than the obviousness of ants of different species. The rate at which chimpanzees learn has been attributed to seasonal changes in the foraging chimpanzees encounter, affected by seasonal patterns in the distance traveled by foraging chimpanzees and the likelihood that both monkeys learn from a source (Stanford 1998).

Failure to detect ecological or behavioral differences of members of allopatric populations suggests that those differences are not behaviors of interest are clearly defined, however, exceptions. As reported results of a 4-year study of wild chimpanzees at Gombe revealed, first, that male chimpanzees both in the rate at which they learn to fish for termites and in the age at which they learn to fish for termites, with female chimpanzees more than 2 years before males. Second, female chimpanzees spent significantly more time watching adults feed. Across the study year, but neither investment in tool use, was correlated with age, but not males, showed a significant dip in dipping depths used

that "development of termite fishing as well as individual trial-and-error learning from their mother which attention should be directed to fish male and female learn to fish for termites . . . Male offspring learn this goal, while females

learn something of the form of the behaviour . . . For both sexes, individual trial-and-error learning follows, as the offspring learns how to withdraw the tool without dislodging prey." There is thus evidence that social learning contributes to development of termite fishing in females but plays a lesser role (if any) in development of the same behavior in males. And if male chimpanzees learn independently to fish for termites, the role of social learning in development of termite fishing by females would be merely facultative rather than obligate, and termite fishing in chimpanzees would have little to do with "culture."

Nut cracking in the Ivory Coast. Observations of differences in the behavior of social groups separated by geographic barriers, particularly rivers, that prohibit social contact while perhaps permitting gene flow between groups provide another potential route to discriminating behaviors that are traditional from those that are not (Boesch et al. 1994; van Schaik 2004, 2006). For example, although wild orangutans (*Pongo pygmaeus*) on both sides of the impassable (for orangutans) Alas River in Sumatra feed on *Neesia* trees, only orangutans to the west of the river use twigs as tools to remove the fat-rich seeds from *Neesia* fruit, thus increasing their feeding efficiency (van Schaik 2004, 2006).

Similarly, chimpanzees to the west of the N'Zo-Sassandra River in the Ivory Coast use hammers and anvils to crack open nuts of five tree species, whereas those to the immediate east of the river do not (Boesch et al. 1994). This distribution of nut-cracking behavior could not be explained by differences in density of chimpanzees, density of nut-bearing trees, or frequency with which objects suitable for use as hammers or anvils are encountered. However, Morgan and Abwe (2006) have recently discovered troops of chimpanzees living some 100 miles to the east of the N'Zo-Sassandra River in Cameroon that use stone hammers and anvils to crack nuts. The finding raises potentially important questions concerning previous interpretations of the distribution of use of hammers and anvils in the Ivory Coast.

Inoue-Nakamura and Matsuzawa (1997, p. 172), in discussing results of their 4-year study of development of nut cracking by young chimpanzees at Bossou, concluded that imitation and teaching did not play a role in development of the behavior. Juveniles did not copy either the motor patterns of their mothers or other adult group members or the "way to relate nuts and stones." Instead, the authors conclude, young chimpanzees learned from observing the behavior of accomplished nutcrackers

"the general functional relations of stones and nuts and . . . the goals obtained by the demonstrator." However, the only observation that Inoue-Nakamura and Matsuzawa (1997) provided in support of their proposal of even a limited role of social influence in acquisition of nut cracking by young chimpanzees was that infants frequently watched adults crack nuts and took pieces of nuts that others had cracked. Such observations may be consistent with the view that chimpanzees learn to crack nuts socially, but they prove little (Galef 1996).

Inoue-Nakamura and Matsuzawa (1997) also provided evidence inconsistent with the hypothesis that use of stones in nut cracking is socially learned. Adults frequently chased away juveniles that tried to take stones and nuts, and rearing by a mother who did not crack nuts did not slow acquisition of the behavior by her offspring. Indeed, Inoue-Nakamura and Matsuzawa (1997, p. 172) concluded their article by stating that "in summary, the members of the community provided only the infants with the opportunities to freely access stones and nuts. These opportunities could facilitate the individual experience of stone-nut manipulation and result in the apparent social transmission of the tool-use behavior among the wild chimpanzees." A role for social learning beyond local enhancement in development of nut cracking remains to be demonstrated.

Social conventions in capuchin monkeys. Perhaps the most convincing field evidence of traditional behaviors in nonhuman primates is provided by the work of Perry, Baker et al. (2003; Perry this book) on differences in the social behaviors of groups of capuchin monkeys (*Cebus capucinus*). Because of the relatively brief lifespan of some capuchin social conventions, Perry, Baker et al. (2003) could document both the spread of idiosyncratic social behaviors from individual to individual within a group and the decline of those behaviors when key individuals either died or emigrated. For example, Gaupo, a subdominant, young adult male, introduced the "finger-in-mouth game" into group LB-AB. The game involved one monkey putting its finger into another's mouth. The recipient then clamped down on the inserted finger hard enough that the owner of the finger could not easily withdraw it and had to "go through various contortions" to pry open the recipient's mouth and free its finger. After a finger was freed, it was sometimes reintroduced, or the two players reversed roles, with the game continuing through several iterations.

Before 1993 all finger-in-mouth games involved Gaupo. In 1993 others began to play the game without Gaupo, and in time roughly half the

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dyads in the LB-AB group did so. Because adult male capuchins regularly move from one social group to another, a genetic basis for behavioral differences between groups seems unlikely, and such social conventions are sufficiently arbitrary that it seems all but impossible that members of a social group would have acquired them independently.

The tendency of adult male capuchins to migrate between groups has a further potentially useful consequence. With luck, it should be possible to determine whether a male that migrates into a new group brings idiosyncratic social conventions of his old group with him. If so, evidence of the traditional nature of social behaviors in capuchins would be irrefutable.

Conclusion to Part 1

I expect that some, if not many, behavioral differences between populations of chimpanzees (Whiten et al. 1999), orangutans (van Schaik, Ancrenaz et al. 2003; van Schaik this book), monkeys (Perry this book), and various cetaceans (Mann and Sargeant 2003; Sargeant and Mann this book; Rendell and Whitehead 2001; Whitehead this book) currently discussed as traditions are, in fact, products of social learning of some kind. I would also wager that many purported traditional differences between allopatric populations of species are not, in fact, a consequence of social learning. It behooves us, as students of animal social learning, to do our best to go beyond a simple cataloguing of differences in the behavioral repertoires of allopatric populations to identify truly traditional differences in the behavior of free-living animals.

Identification of behavioral differences between populations is certainly an important and useful first step in the discovery of animal traditions. However, labeling a difference in the behavior of two populations as cultural is an assertion about how that behavior develops. Studies of development of population-specific behaviors are thus essential for determining which purported instances of culture truly reflect social influences on behavioral development. Developmental studies are few and far between (e.g., Whiten et al. 2005) and are still producing contradictory outcomes, sometimes providing evidence of the spread of techniques through a population and sometimes not (e.g., Hopper et al. 2007). Claims of "culture" in chimpanzees need to follow, not to precede, such investigations. Last, the question whether imitation rather than emulation is involved in laboratory demonstrations of social learning of foraging behaviors needs to be resolved (Tomasello 1999a, this book) so that,

as discussed later, the relationship of animal traditions to human culture can be clarified.

Part 2: Animal Tradition; Human Culture

No animal comes close to having humans' ability to build on previous discoveries and pass the improvements on. What determines those differences could help us understand how human culture evolved.

"What are the roots of human culture?" (2005, p. 99)

We must not overestimate the situation and say that "monkeys have culture" and then confuse it with human culture.

Hirata et al. (2001, p. 489).

Labeling ape behavior as "culture" simply means that you have to find a different word for what humans do.

Marks (2002, p. xvi)

Similarities or Differences?

The first of the three preceding quotations is taken from a list of 100 "things we don't know that we need to know" proposed by the staff of *Science* magazine. The quotation suggests that at least with respect to the interests of the staff at *Science*, discussions of animal culture have been moving in quite the wrong direction. Attention has been focused almost entirely on what the similarities rather than the differences between human culture and animal traditions might tell us about the evolution of human culture.

Animal tradition and human culture serve similar functions. Both provide naïve individuals access to adaptive behaviors that others of their species have invented. Although interacting with others engaged in some behavior can facilitate acquisition of adaptive (and sometimes maladaptive) behaviors by animals from insects to apes (Heyes and Galef 1996), *Homo sapiens* has taken such social learning much further than has any other species.

Using different terms to refer to the products of social learning in nonhumans and humans simply reflects curiosity as to why, for example,

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our chimpanzee and bonobo cousins, after millions of years of experi-
ence, still sit naked, exposed to tropical downpours, while humans have
gone on to build cathedrals and walk on the moon. We will never know
why the ability of humans and animals to develop traditions has such
different consequences unless we remain curious about differences, as
well as similarities, between animal and human "culture." Whether "cul-
ture" in animals is referred to as animal culture, subculture (Kawamura
1959), preculture (Kawai 1965; Menzel 1973a), or tradition (Galef
1992) is a matter of indifference. However, until we know better, it
might be wise to consider seriously the possibility that "culture" in our
species and "culture" in other species are different phenomena. In poli-
tics, assuming differences where none exist can prove dangerous (de
Waal 2001). In science, the reverse is as often the case.

Thinking about differences between traditions in animals and culture
in humans need not reflect some sort of Western philosophical commit-
ment to existence of an unbridgeable chasm between animals and hu-
mans that can be contrasted with an Eastern belief in the continuity of
life (de Waal 2001). As suggested by the second quotation at the head of
the present section, Japanese researchers introduced and still use the
term "preculture" when discussing the traditions of monkeys at Koshima
to indicate that in their view, monkey "culture" and human culture dif-
fer significantly (Kawai 1965; Watanabe 1994).

Demonstrating functional similarity is simply not sufficient. We need
to know whether the "cultural" behaviors of animals and humans are
products of similar underlying processes, and consequently whether ani-
mal tradition and human culture are analogs or homologs (e.g., Galef
1992; Tomasello 1994; Byrne et al. 2004). Using different terms to refer
to the "culture" of animals and of humans focuses attention on the pos-
sibility (apparently a fact to the staff at *Science*) that there may be im-
portant mechanistic differences, as well as important functional
similarities, between social learning in animals and in humans.

Teaching

Caro and Hauser (1992) proposed that teaching be defined as occurring
when (1) a teacher incurs some cost as a result of modifying its behavior
when in the presence of a naïve individual, and (2) the modified behavior
of the teacher causes the naïve individual to acquire some behavior more
rapidly than it otherwise would. Caro and Hauser's definition thus treats
teaching as an altruistic act and consequently brings teaching within the

purview of neo-Darwinian approaches to the study of behavior (Galef et al. 2005).

A handful of possible instances of teaching by apes and cetaceans have been provided in the literature (e.g., Caro 1994; Rendell and Whitehead 2001). However, many find these examples unconvincing (e.g., Janik 2001; Maestriperi and Whitham 2001). Perhaps most informative is that with the exception of two instances of possible teaching of nut cracking by chimpanzees (Boesch 1991), there have been no reports of teaching in chimpanzees or bonobos despite tens of thousands of hours of observation (Matsuzawa 2001). Consequently, Franks and Richardson's (2006) recent report that the ant *Temnothorax albipennis* exhibits behavior that exceeds the criteria for teaching proposed by Caro and Hauser (1992) came as something of a surprise.

In Franks and Richardson's (2006) experiment leader ants, but not their followers, knew where to find food. When a leader ran to food with a follower in attendance, the leader ran rapidly only after being tapped by the antennae of a follower. The consequent irregular movement of leaders running with followers resulted in a fourfold increase in the time leaders took to reach food (the cost to the teacher), and followers found food significantly sooner after engaging in running with a knowledgeable leader than did ants that searched for food on their own (the benefit to the pupil).

A second recent study, this one concerned with the role of social interaction in the development of predation in wild meerkats (*Suricata suricatta*), provides similar evidence of behavior that meets the criteria of Caro and Hauser (1992). Meerkat helpers at the nest respond to changes in the begging calls of maturing meerkat pups by altering the frequency with which they provide the pups with disabled, potentially dangerous prey (scorpions). The experience of the pups with disabled scorpions accelerates the young meerkats' learning to handle intact scorpions without being stung or bitten (Thornton and McAuliffe 2006).

Both tandem runs by ants and provisioning of young meerkats with disabled prey meet the criteria Caro and Hauser (1992) proposed to define teaching. However, although the functional similarity of teaching in ants, meerkats, and humans is striking, teaching in ants and meerkats provides essentially no insight into evolutionary precursors of teaching in humans and would not even if ants, meerkats, and *Homo sapiens* were phylogenetically close. The behavioral mechanisms that support teaching in the three species appear so different from one another that it is all but

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impossible to conceive of one evolving into the other. Indeed, no one has yet proposed that teaching in ants and meerkats provides insight into the evolution of teaching in humans.

The Evolution of Culture: Analogs and Homologs

The question whether chimpanzee tradition is the evolutionary precursor of human culture requires attention to the same issue as does the evolution of teaching. If the far more complex "culture" of humans than of chimpanzees reflects elaboration of behavioral processes that support traditions in chimpanzees, then chimpanzee tradition and human culture are homologous, and there is no reason to use different terms to refer to them. If, to the contrary, tradition in chimpanzees is the expression of fundamentally different behavioral processes than is human culture, then "culture" in the two species is analogous and tells us nothing about the evolutionary origins of human culture.

Much of human culture in the developed world clearly depends upon imitation, teaching (or pedagogy *sensu* Csibra and Gergely 2006), and language (the extent to which indigenous cultures depend on these processes for transmission of behavior from generation to generation remains to be determined). Present evidence suggests that chimpanzees essentially never teach and have no symbolic language unless they are taught one by humans.

Chimpanzees, like many other animals, are susceptible to effects of local enhancement and can emulate. How often and how precisely chimpanzees imitate (e.g., Whiten et al. 1996; Whiten this book) are both controversial (Horner and Whiten 2005; Call et al. 2005; Tomasello this book) and important in determining the relationship between human culture and chimpanzee tradition. As explicated more fully earlier in the present chapter, only a very few behavioral processes can support the cumulative culture that is characteristic of all human social groups. The total absence of such cumulative culture in even our closest relatives (Tomasello this book) suggests that there are fundamental differences between animal traditions and human culture.

Are Animal Traditions the Evolutionary Precursors of Human Culture?

Perhaps, in time, we shall discover that differences between social learning processes in humans and animals are trivial rather than profound, and that small differences in capacity have resulted in huge differences in

performance. Until then we need to ask both in what ways animal tradition and human culture are similar and in what ways they are different, not to sweep potential differences between culture in humans and traditions in animals under the rug in the name of Darwin or continuity. Using different terms to refer to the traditions of animals and the culture of humans should maintain a simultaneous focus on potential differences, as well as potential similarities. Both are of importance.

It is even possible that the cumulative culture that is characteristic of our own species requires either the linguistic capabilities unique to humans (Donald 1991) or the neural architecture that evolved to support human language. Such precursors of the social learning processes that support human culture may have emerged only in the ancestral hominid line that diverged from that of the great apes toward the end of the Miocene, some 7 million years ago. Szathmáry (2006, p. 307) has suggested that "it is perhaps no accident that cooperation in large non-kin groups, a developed theory of mind, tool use, teaching . . . and natural language go together in our species." Perhaps we should subtract tool use from, and add culture to, Szathmáry's list of possibly distinctively human characteristics. Despite the close phylogenetic relationship between *Homo sapiens* and the extant great apes, traditions of animals may have little to do with the evolution of human culture. We need to know.