CHAPTER

31

From Material to Symbolic Cultures: Culture in Primates

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Abstract

Recent wild animal studies have led to the realization that some of the population differences observed in some species possess close similarities to human cultures. This has inflamed a long-standing debate about the uniqueness of human cultural abilities. The accumulation of such detailed observations from wild animal populations has provided more and more convincing details about the cultural skills in different animal populations, which has resulted in a shift away from the question, "do animals possess culture?" to the question, "what differentiates humans' cultural abilities from other animals'?" The growing body of evidence of cultural differences, not only in chimpanzees but also in macaques, capuchin monkeys, orangutans, and other primate species, opens the way to a precise ethnography of culture in different species. Chimpanzee culture is observed as well in the material domain as in the symbolic and social ones and is disseminating by social-learning mechanisms, allowing in some cases for cumulative cultural evolution. To further a precise understanding of the social-transmission mechanisms involved in cultural transmission combining detailed field observations with ecologically and socially valid experimental studies would be timely and welcome.

Keywords: Culture, symbols, cooperation, cumulative cultural evolution, ecological validity, chimpanzees, humans, primates.

Culture is probably the single most central concept in twentieth-century anthropology, as noted by the *Oxford Encyclopedia of Social and Cultural Anthropology* (1996). Although not wanting to attempt to formally define "culture," this encyclopedia mentioned that "culture is what a person ought to acquire in order to become a fully worthwhile moral agent" (p. 136). This illustrates one side of the culture debate, which has been raging for decades as a consequence of the increasing number of observations of behavioral differences seen between populations in different primate species. Although these have been labeled as "cultural differences" by primatologists (Goodall, 1970; Boesch, 1996, 2003; McGrew, 2004; Panger et al., 2002; Perry & Mason, 2003; Van Schaik et al., 2007; Whiten et al., 1999), for many anthropologists and psychologists, culture applies only to human beings, and, therefore, a direct reference to ourselves is often implicitly made when defining the concept (e.g., Barnard, 2000; Kuper, 1999; Galef, 1992; Tomasello, 1999; Povinelli, 2000). For many others, however, culture is first and foremost a social process and should be defined as such without reference to any particular species (e.g., Borner, 1980; Kummer, 1971; Boesch & Tomasello, 1998; Whiten & Boesch, 2001).

The tone of the culture debate has, in a sense, been set by Marshall Sahlins, in his famous 1976 book titled *The Use and Abuse of Biology*, in which the reluctance of some in the human sciences to discuss humans with an open comparative eye was clearly formulated. This seems to reflect some people's fear that by opening anthropological concepts to other species, human beings might be "threatened" in their humanity. For example, when the famous anthropologist Louis Leakey learned about spontaneous tool use in wild chimpanzees in the early 1960s, he remarked, "Ah, now we must redefine tool, redefine man—or accept chimpanzees as humans!" A century earlier, after learning about Darwin's theory of evolution, the wife of the Bishop of Worcester said, "Humans descended from the apes! My dear, let us hope that it is not true, but if it is, let us pray that it will not become generally known." Interestingly enough, this view was still expressed in a paper published in *Science* in 2009 when White et al. (2009) wrote that a new description of *Ardipithecus ramidus* showed that "humans did not evolve from chimpanzees." However, this is a view that biologists have never expressed. As Desmond Morris said so wisely in his book *The Naked Ape*, humans' "climb to the top has been a get-rich-quick story, and, like all nouveaux riches, we are very sensitive about our background." At the same time, we may very well be the only species that is curious to know what makes us different from other species, and, therefore, many biologists and anthropologists feel that it is important to keep an open approach. Only in this way can we progress in answering the question, "what makes us human?"—instead of relying on just-so stories that do not reflect our humanity.

Culture as It Happens

I shall adopt this last attitude in the present chapter and will present some of the knowledge that has been gained in the last three decades, as a result of field studies of primates in their natural environments. For the first time in history, this research has allowed us to gain a detailed view of what primates really do in the wild. For this purpose, following a broad consensus, a behavioral trait is considered to be cultural once we have shown it to be a group-specific socially acquired trait (e.g., Kummer, 1971; Bonner, 1980; Galef, 1992; Kuper, 1999; Barnard, 2000). It is often also required that these behavioral traits should be independent of any genetic and ecological factors; however, if the first aspect make sense, the second is never required when talking about humans and its relevance to the cultural debate should therefore be questioned (Boesch, 1996, 2003; Laland & Hoppitt, 2003). The example of potato washing in Japanese macaques will nicely illustrate this aspect of the cultural debate.

Imo the Culture Wall-Breaker

Imo, a juvenile female Japanese macaque, was a member of the Koshima troop, which lived on a small islet in the Japanese archipelago. This troop was provisioned by animal keepers, who threw sweet potatoes on the beach for them daily. The macaques rapidly learned to come to the beach and eat the potatoes, and at the same time tolerated the close presence of human observers. One day, Imo carried a sweet potato from the sandy beach into the water, and after washing the sand off the potato, ate it. This new behavior, which resulted in sand-free and saltier-tasting potatoes, was performed by Imo again the next morning. Interestingly, until this time, the macaques avoided the water, but this new innovation required that they now, at a minimum, come into contact with water. The peer playmates of Imo were the first to copy her behavior, and next were the infants in the troop. Later, the mothers of the different potato washers also learned the behavior. In the end, other than some of the large adult males from the troop, everyone acquired Imo's innovation. Remarkably, while potato washing, the macaques started to enter deeper and deeper into the water, so that the newborn babies lost any kind of aversion to the water, and started to play and swim. A few years later, the same Imo invented a new behavior: she collected a handful of wheat grains that the caretakers were throwing on the sand and carried them to the water where she threw them all in. Only the wheat grains floated on the surface of the water and she was able to eat them much more rapidly than if she had had to sort them from the sand, as before. This new invention also propagated to the majority of the group. Thanks to Imo's innovations, several new cultural traits, including potato washing, wheat grain throwing, and bathing, playing, and swimming in water, spread through the troop.

When reporting these observations as far back as the 1950s, the Japanese observers did not hesitate to use the word "culture" without limiting its application to humans (Imanishi, 1952; Kawai, 1965; Kawamura, 1959, 1965). This was because they were less affected by the anthropocentric glasses that we tended to wear in the occidental world (de Waal, 2001). They were not disturbed by the fact that such changes resulted from human interventions, as, for generations, the macaques had been living in contact with humans in Japan and they had become part of the Japanese culture. To them and to many others in the fields of anthropology and psychology throughout the world, Imo and her playmates' behavior opened the door to discussions of culture in animal species other than humans for the first time. However, not everybody shared our enthusiasm!

Some recent reviews of the concept of culture in the field of anthropology do not even mention these observations, and consequently, there is also no hint of a discussion about the possibility that cultures might be observed in other animal species (Kuper, 1999; Barnard, 2000). Others have looked carefully at the speed of acquisition of these new behaviors and have suggested that the transmission was too slow to warrant the designation of cultural transmission (Galef, 1990, 1992; Heyes, 1994; Tomasello, 1999; Laland & Hoppitt, 2003; *but see* McGrew, 1992; Boesch, 2003 for alternative social explanations for this).

It remains impressive that Imo invented two new techniques that spread through her social group and that resulted in a series of behavioral changes related to water. If precise analyses of the spread of the behavior are important to characterize how innovation spreads in macaques, it should not distract us from the fact that macaques have this ability to learn from others, and totally new behavior patterns can be acquired by most group members within a few years. These observations show that macaques exhibit important behavioral flexibility that was previously thought to be restricted to humans. To many, this is a nice example of cultural change!

The Cultural Debate after Imo's Breakthrough

Although the primatological community reacted positively to such new developments, some psychologists adopted a more critical stance and reminded us that, as cultural traits disseminate within social groups through a social-learning process, we should expect this to happen "relatively" quickly (Galef, 1990, 1992; Heyes, 1994). This has led to endless discussions about how quickly a behavioral trait should spread within a social group when it is supposed to be cultural transmission, and how we can differentiate such a social-transmission mechanism from a pure individual learning process (e.g., Lefebvre, 1995; Boesch, 1996; Tomasello, 1999; Laland & Janik, 2006). It should come as no surprise that in the absence of any rational argument about the expected speed of such a spread, opinions would diverge; some believed that the macaque observations show that the speed of spread indicates the absence of cultural transmission (e.g., Galef, 1990, 1992; Heyes, 1994; Tomasello, 1990), while others saw it as strong support for a cultural spread as the spread followed precisely the social interactions network prevailing within a macaque group (e.g., Kawai, 1965; Whiten, 2005; Boesch, 1996; Leca et al., 2007).

From another perspective, some psychologists have argued that cultural transmission requires *faithful copying* of the behavioral trait and have claimed that this can only be guaranteed through imitation or teaching (Galef, 1992; Heyes, 1994; Tomasello et al., 1993). They argued that other social-learning mechanisms, such as social facilitation or emulation, whereby individuals copy the context or the way objects are used but not the behavior itself, might lead to the acquisition of a behavior but with much less fidelity. In their view, neither had been shown in the case of the Japanese macaques and, therefore, that although the acquisition of potato washing was impressive, it could not be labeled as "cultural." Others rapidly argued that human data did not show that cultural transmission required either of these mechanisms but, instead, that other forms of social learning equally contributed to cultural transmissions (Boesch, 1996; Waal, 2001). Following the arguments of the Japanese researchers, biologists, on the other hand, have argued that the sheer presence of such invention and propagation within a social group is strong evidence of the cultural abilities of this species (Bonner, 1980; Waal, 2001).

More generally, psychologists tend to argue that animals' abilities to adapt to the ecological constraints they face in their daily life are well-documented, and that both present and past small *ecological factors* could have affected the occurrence of specific behavioral patterns. Furthermore, they suggest that, in natural settings, it would be almost impossible to exclude such ecological effects and that natural observations, therefore, do not allow us to make any claims about the cultural abilities of animals (Galef, 1990, 1992; Heyes, 1994; Tomasello, 1990, 1999). This view has become dominant in some circles of experimental and comparative psychology and has led to an increase in studies done in captive settings.

PROBLEMS WITH "CULTURE OUTSIDE OF CULTURE" STUDIES

However, such studies of "culture outside of culture" falter on their two key assumptions. First, they assume that captive animals face the same social-learning challenges as their wild counterparts, and second, they assume that all behavior patterns are learned via the same learning mechanism, independent of the ecological relevance of the behavior. For example, they would argue that captive macaques would learn to rake food within arm reach of a human model based on the same copying mechanism and motivation as Imo's playmates learn to wash potatoes. The stance a scientist takes toward experimental data with captive animals is a function of their stance on these two assumptions. For a number of experimental psychologists, these assumptions are perfectly reasonable and broad claims made from such experimental studies have been thought to reveal limitations in the cultural abilities of different animal species.

On the other side, the validity of this "culture outside of culture" approach has been viewed much more critically by the majority of behavioral ecologists, anthropologists, and philosophers, and the broad claims made from such artificial studies with animals who are often socially impaired are greeted with skepticism (Byrne, 1995, 2007; de Waal, 2001, 2006; Bekoff et al., 2002; Allen, 2002, 2004; Boesch, 2007, 2008; McGrew, 2004). For one, the "artificial" nature of the ecology of captive settings has no parallel in nature and, therefore, no one can really assess the "ecological validity" of such studies. To some, this renders captive experiments useless. Furthermore, the artificial nature of the social groups in captive settings is patent and the effect of this is again very difficult to assess, although we know that early social upbringing conditions have a large influence on later cognitive development. At the very least, this should require one to carefully assess the validity of captive studies in contributing to our understanding of the culture phenomenon in primates.

Chimpanzees as Culture Generalists

As this debate was developing, new data was being published on what has emerged as the most major discovery in chimpanzee behavior of the two last decades, namely the unexpectedly large behavioral diversity observed among different wild populations. This was observed in a diverse assortment of contexts, including the sexual, social, demographic, tool-use, and hunting contexts. This important dimension of chimpanzee behavior was the center of three international conferences, which each resulted in an edited volume. These were titled *Understanding Chimpanzees* (Heltne & Marquardt, 1989), *Chimpanzee Cultures* (Wrangham et al., 1994), and *Great Apes Societies* (McGrew et al., 1996). This has progressively placed the chimpanzee in a special position, as the more we are learning about wild chimpanzee population diversity, the more similarities we are finding between chimpanzee and human cultures. This has been mainly possible thanks to the special treatment of chimpanzee studies in primatology; because of the genuine interest we have in our closest living relatives, more different populations living in diverse habitats have been studied in chimpanzees than in any other primate species.

It is important to realize from the start that the study of culture in chimpanzees has followed a different approach than the one adopted with macaques; if a *dynamic diffusion approach* based on the acquisition of novel behavior caused by human intervention was central to the study of culture in macaques, an *ethnographic approach,* in which established behavior patterns in different populations were compared, has been taken with the study of culture in chimpanzees. Such an ethnographic approach to culture proceeds by exclusion, whereby ecological and genetic influences must be excluded before any behavior is proposed to be cultural (*see* Goodall, 1973; Nishida, 1987; Boesch & Boesch, 1990; Nishida et al., 1993; Boesch, 1995, 1996, 2003; McGrew, 1992; Boesch & Tomasello, 1998). The main rationale for utilizing such a different approach lies in the fact that, since wild animal populations live in stable ecological conditions, it is extremely rare to see the acquisition and dissemination of new behavior elements within a social group. Hence, the ethnographic approach is often the only one available.

In the case of the chimpanzees, this approach has proven very successful, in the sense that it has allowed for the first time to gain more precise knowledge of important characteristics of the cultural phenomenon in this species. Here, I will go through what researchers have seen as some of the key elements of the culture phenomenon in chimpanzees over the years:

1) *Large cultural repertoire*: First, field researchers have started to compare aspects of the behavioral repertoires of their study populations with the knowledge gained by others on other populations and have proposed an ever-growing list of potential cultural elements (Goodall, 1973; McGrew, 1992; Boesch, 1996). Then, in an attempt to understand the breadth of the variability in the cultural repertoire of each population, field workers who followed eight different populations of wild chimpanzees in different regions of Africa gathered together to compare their knowledge about chimpanzees. This resulted in a preliminary list with 38 behavioral traits that were proposed to be cultural in the

species and independent of any ecological influences (Whiten et al., 1999, 2001). At the time of writing, a second similar exchange between field workers is underway. This meeting includes the addition of researchers who study three new chimpanzee populations, so that a much more extensive list of putative cultural elements is been produced (Whiten et al., in prep.).

The main lesson to be taken from such a listing exercise is that, in chimpanzees, *each* population can be distinguished from the others thanks to a specific cultural repertoire, which always includes a multiple complex of different behavioral elements. Like a fingerprint, knowledge of these elements makes it possible to determine the population origin of any individual chimpanzee with certainty. The map of the original publications presented here illustrates the distribution of the 38 cultural elements across six wild chimpanzee populations (Fig. 31.1). For example, Taï chimpanzees exhibit 26 of the 38 cultural traits, while Gombe chimpanzees perform 24 of them, but only 16 of these are shared with the Taï chimpanzees. Similarly, the Bossou chimpanzees, whose territory is only 200 kilometers north of the Taï forest, exhibit 11 of the 38 elements, and share only six with Taï and four with Gombe chimpanzees. So, each population of chimpanzees is characterized by multiple different cultural elements, and it is this mix that is population-specific.

The second point is that cultural differences are not merely a question of presence or absence of a trait, but also a question of the *form and context* under which the trait is performed in each population. For example, ant dipping (the third icon from the top of the map, in the left column of each population cultural card) is performed with short sticks and one hand in Taï chimpanzees, but with longer sticks and both hands in Gombe chimpanzees

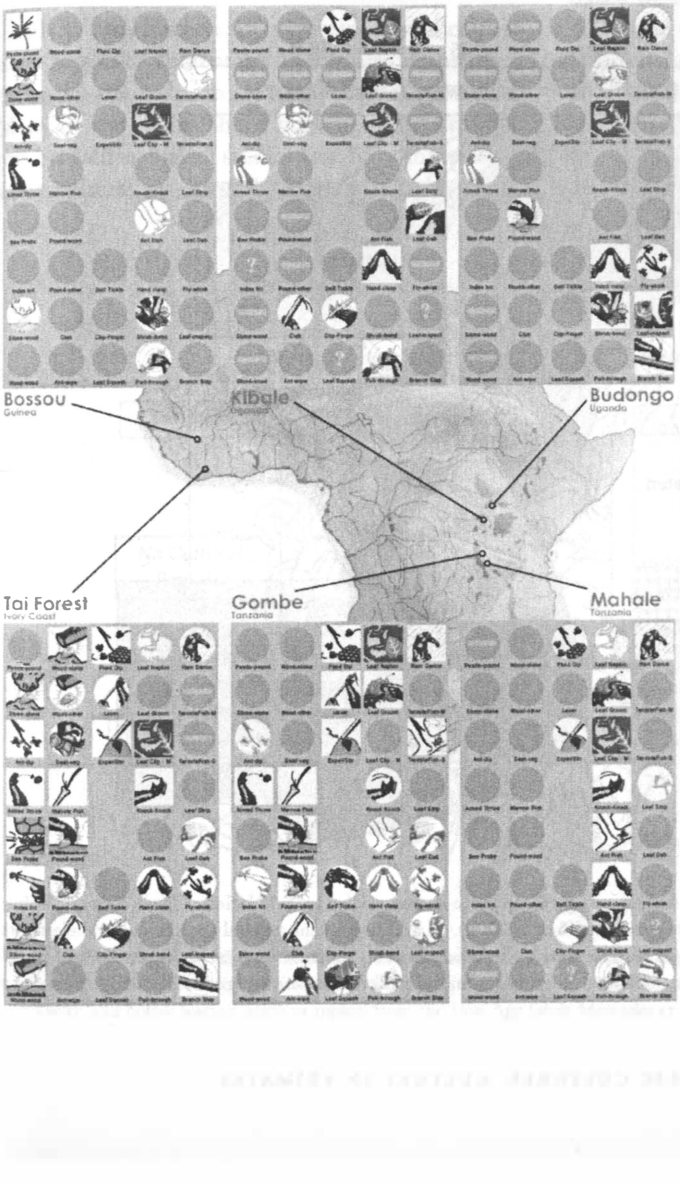

Figure 31.1 The cultural repertoire of six different chimpanzee populations (Whiten et al., 1999). For each population, the repertoire is synthesized on a card with the 38 potential behavior elements, where each element present in that population is earmarked with a colorful icon; a square icon stands for the element being observed in the population, a circle icon stands for an alternative form of the behavior element, and a blue circle indicates the element was not seen in the population with no obvious ecological reason. When a clear ecological reason explained the absence of the element, a horizontal minus bar is marked in the blue circle.

(Goodall, 1968, 1970; Boesch & Boesch, 1990). This is illustrated by the icon on the map with a squared or round shape, as can be seen for ant-dip. On the other side, for example, leaf-clip (the second to last icon from the right in the third row from the top) is performed in a very similar way in each population but the context and its attached meaning varies extensively (see below).

2) *Cultural fidelity*: In some limited instances, researchers have followed and made detailed observations about two neighboring chimpanzee groups living in the same forest block. For example, in the Mahale Mountains of Tanzania, field researchers followed two neighboring chimpanzee communities, the K- and the M-Group, and the larger of the two, the M-Group, was seen to push the smaller K-Group out of their range during certain seasons of the year (Kawanaka & Nishida, 1968). They have found behavioral differences that persist despite the very close proximity of the two groups, and exchanges of individuals between the two groups have been recorded. As such groups are neighbors, we can be certain that genetic differences do not explain these observations, and additionally, it is straightforward to control for possible ecological differences. This has allowed researchers to make strong claims about cultural differences (Boesch, 2003, in press; Whiten et al., 1999; Langergraber et al., 2010).

In the Taï forest, three neighboring communities have been followed and reveal strikingly important cultural differences in 11 behavior elements. These behavior elements have been seen as well in the material domain, related to the acquisition of food, as in the symbolic domain, related to courtship and play initiation (Fig. 31.2) (Boesch, 2003).

The important aspect here is that, in chimpanzees, *cultural transmission and fidelity within groups*

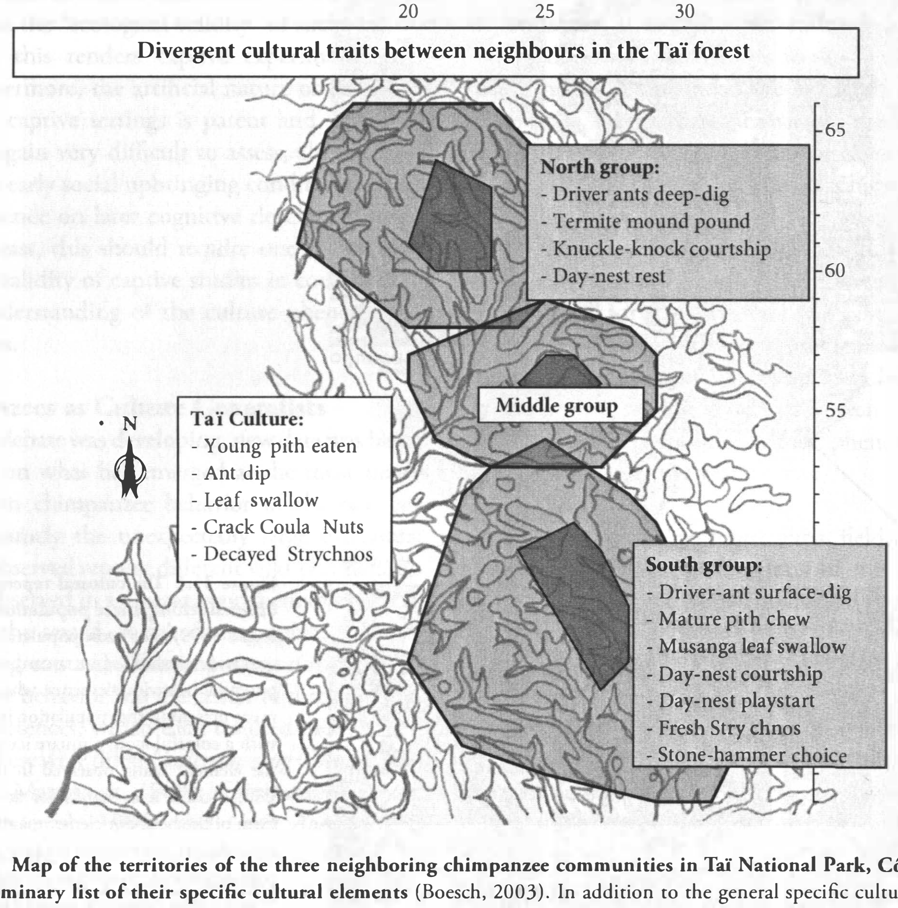

Figure 31.2 Map of the territories of the three neighboring chimpanzee communities in Taï National Park, Côte d'Ivoire, with a preliminary list of their specific cultural elements (Boesch, 2003). In addition to the general specific cultural elements shown already in Figure 31.1, Taï chimpanzees possess community-specific cultural elements, both in the material and social domain, that show a high level of conformity, being observed in all community members, and a strong level of fidelity, prevailing for many years.

persist for extended periods of time, despite females transferring between communities at menarche. This dispersal pattern could lead to a homogenization of the behavior patterns across neighboring communities over a very short period of time, as females who transfer from their natal community to a new one, at an age when they have already acquired the full behavioral repertoire of their natal group, could continue to perform it in their new group. However, the opposite was observed in both Mahale and Taï chimpanzees, in the sense that community-specific culture elements remain extremely stable and the new immigrants adapt rapidly to the culture of the new group (Luncz & Boesch, in prep.). It is too early to say anything about either the mechanisms making the immigrant females adopt the behavioral culture of their new community or about the benefits of doing so. In conclusion, high fidelity to group-specific cultural traits and conformity to new group-specific cultural habits are characteristics of chimpanzee culture.

3) Cultural history: An important part of culture is its historical dimension as this also emphasizes the social transmission aspect of the behavior trait. Many of the claims about human cultural fidelity rest on archaeological studies that have shown that some cultural products, like arrows, hammers, or shelters, have maintained themselves for numerous generations in human groups. However, detecting the age of a behavior pattern is impossible, unless it produces long-lasting artifacts. The nut-cracking behavior of chimpanzees may well be the only primate behavior that might allow for such a study, as it is a cultural behavior in which chimpanzees often use stone hammers or anvils to crack nuts.

To answer the question of how long nut-cracking behavior has been present in chimpanzees, we initiated an archaeological project with the hope of uncovering some old nut-cracking sites (Mercader et al., 2002, 2007). By applying traditional archaeological methods to a *Panda* tree, where we had seen regularly chimpanzees crack nuts, we could show that they had been cracking at that particular tree for over 150 years (Panda 100 in Fig. 31.3), and had left hundreds of stone flakes behind. In a closely adjacent area, we were able to reach old soil layers dated to 6,000 years old, and found stone artifacts produced by cracking nuts in layers that were between 2,200 and 4,300 years old (site Noulo in Fig. 31.3) (Mercader et al., 2007). These artifacts were found mixed with some typical Iron Age human artifacts and the older samples were found below the human occupation layer. This represents a first estimate that could be shifted back in time once excavations are

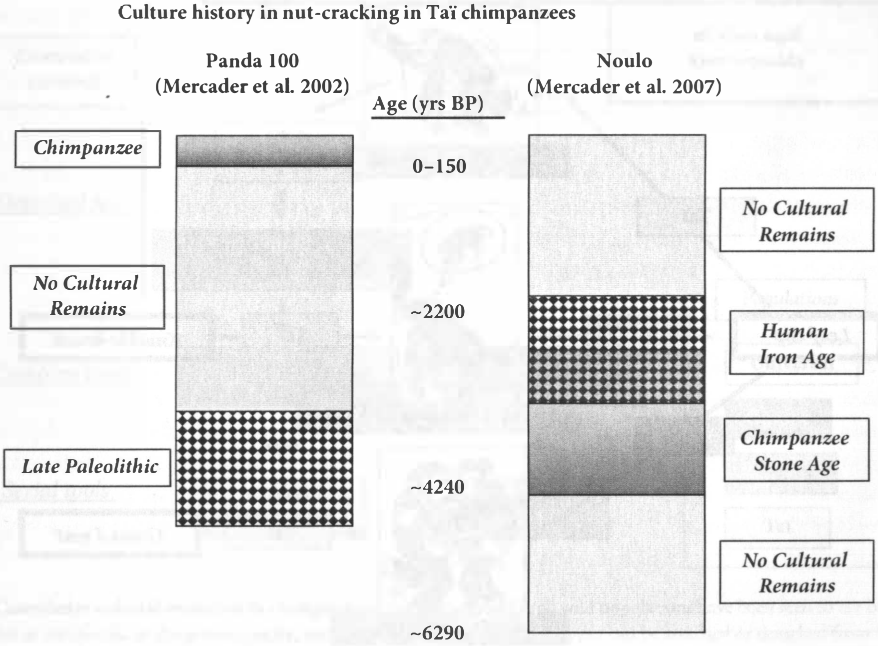

Figure 31.3 Stratigraphy of two excavation sites in the Taï Forest. The first on the left represents a known recent Panda nut-cracking site (Panda 100), and the second is at an old nut-cracking site (Noulo), where chimpanzee stone artifacts that were uncovered were partly mixed with and below human artifacts typical from the Iron Age (after Mercader et al., 2002, 2007).

done on older soil layers. However, this result already shows that, in the case of nut cracking, chimpanzees have used a cultural behavior in a very similar way for over 200 generations. To give an idea of the time interval this represents, the human Iron Age began in this region of Africa about 2,500 years ago, and so the *Chimpanzee Stone Age predated the Human Iron Age* by some thousands of years.

This behavior remains the only cultural behavior trait where it is possible to show that chimpanzee culture has been transmitted over hundreds of generations. However, that simple observation suggests that the ability to copy a behavior pattern over generations is present in chimpanzees and may be observed in many other cultural traits.

4) *Symbolic culture*: Communicative behavior elements are used to convey information between social group members and, therefore, by definition are based on some shared meaning if they are to be of any use. In chimpanzees, some communicative traits follow some group-specific norms, by which it is the meaning of the trait that differs and not the form (Boesch, 1995, 1996, 2003, 2008). The most complex example is the leaf-clipping behavior element that is present in three of the six well-studied populations: In Taï chimpanzees, leaf-clip is used by adult males just before a display to signal their intention; in Bossou chimpanzees, it is often used by youngsters to get others' attention and invite others to play; and in Mahale chimpanzees, it is used by sexually active males to attract estrus female to mate with them (Nishida, 1987; Sugiyama & Koman, 1979; Boesch, 1995) (*see* Fig. 31.4). So, within a group, one behavioral element can acquire a specific meaning that is shared between all members, although the form of the behavior and the sounds produced remain exactly the same and do not refer to the meaning. In other words, the meaning of a behavior element results from a social construct that is shared between group members in chimpanzees.

The flexibility of these social meanings in chimpanzees is further revealed by the fact that a similar meaning can be expressed by different behavior elements in different social groups (Fig. 31.4). For example, although leaf-clip means "I want to have sex with you" in Mahale chimpanzees, this specific meaning is expressed by knuckle-knock in Taï chimpanzees. Leaf-clip in Taï chimpanzees means something different than in Mahale chimpanzees, while this last meaning is performed by knuckle-knock. To complicate this further, leaf-clip in Bossou chimpanzees, which means "I want to play with you" is

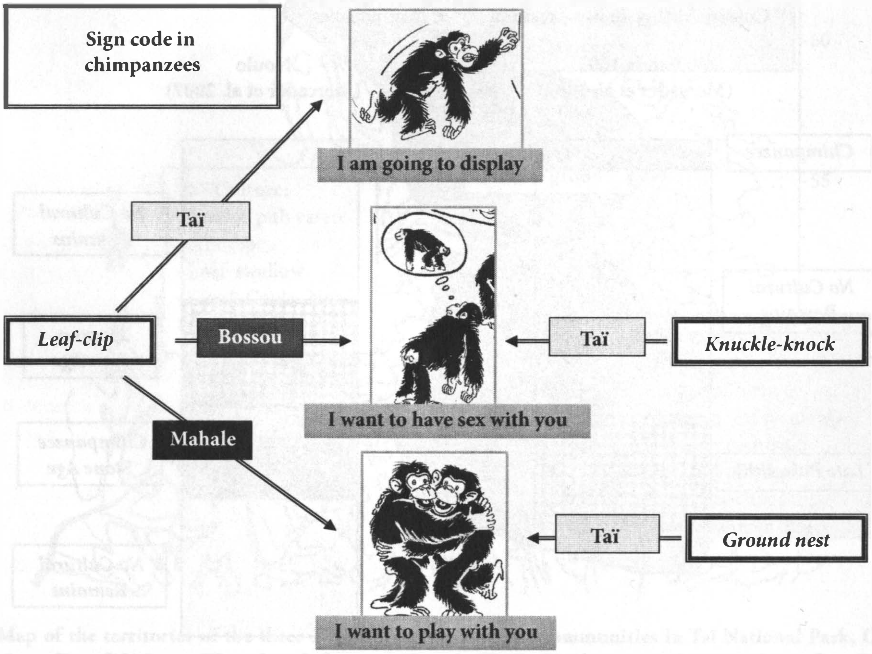

Figure 31.4 Symbolic culture in wild chimpanzees. The three behavioral elements performed by chimpanzees in three populations are framed in bold with the name of the population indicated on the arrow specifying the meaning the element has in this population. Two of the meanings have been seen to be supported by different signs in different populations.

also used by Taï chimpanzees, but is expressed by making a coarse day-nest on the ground (Boesch, 1995, 2003).

Arbitrary shared meanings that are group-specific are obviously among the main characteristics of human language, and it is very intriguing to find that behavior signs in wild chimpanzee populations have similar properties. If the example of leaf-clip is still a long way from being a language, we need to keep in mind that uncovering such a "sign code" (*see* Boesch, in press) in another species requires from the human observers an expertise in this code, something no one anticipated to be present. In other words, if it was hard for Europeans to decipher Egyptian hieroglyphs, doing so for sign code differences between Taï and Gombe chimpanzees may prove even harder. Thus, the leaf-clip sign codes might be just the tip of the iceberg in a new dimension of chimpanzee communication still unknown to us, or it may remain what it appears to be now—an intriguing sophistication that never developed. Until specific studies comparing chimpanzee populations are done with expert eyes, we will not know.

5) *Cumulative cultural evolution*: Some of the cultural elements proposed in chimpanzees are characterized by a relatively high level of technological complexity, in the sense that they incorporate different elements that each produce a behavior element that fulfills a function on its own and is seen to be used in only some populations. For example, all chimpanzees in all studied populations pound hard-shelled fruits against hard surfaces in order to break them open and get at the seeds or the flesh found inside. Some chimpanzee populations in Western and Central Africa have incorporated the use of a hard tool in this universal behavior pattern, whereby the tool is hammered against the hard-shelled fruit to pound it open (Fig. 31.5) (Boesch & Boesch, 1984, 1990; Morgan & Abe, 2006). The integration of a second object in the pounding movements, as seen in Bossou and Taï chimpanzees, allows the chimpanzee to crack open much smaller and harder fruits that would not have been accessible with the first, simpler technique. Finally, in regions where roots, which are used as anvils, are hard to find, as in Bossou, chimpanzees have been seen to place nuts on mobile stone anvils instead (Fig. 31.5) (Matsuzawa, 1999).

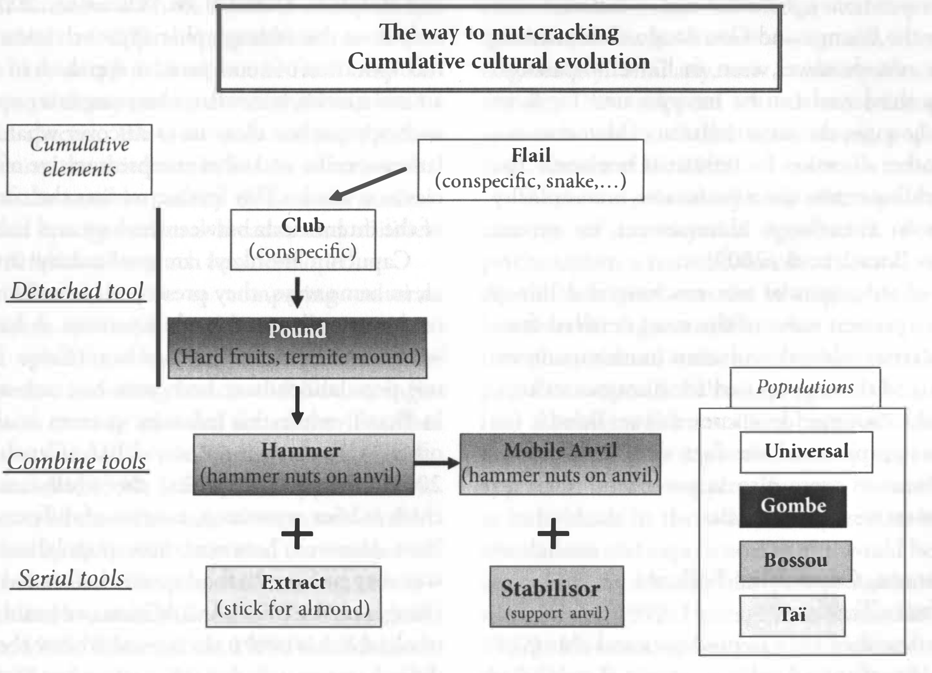

Figure 31.5 Cumulative cultural evolution in chimpanzees: All chimpanzees in all wild populations have been seen to use branches, clubs, or saplings to hit at conspecific or dangerous species, such as snakes or wild cats. This object can be attached or detached from their substrate. As a second innovation, a food source could directly be pounded against a hard surface, as seen in Gombe, Bossou, and Taï chimpanzees. Third, a hammer has been added to the behavioral sequence to pound harder food sources in Bossou and Taï chimpanzees, while only Bossou chimpanzees have been observed to use mobile anvils that they can transport to the nut-producing trees. Furthermore, chimpanzees in Taï and Bossou have been seen to use other tools to either extract more of the kernel out of the shell or to stabilize the mobile anvil.

But from there on, we saw two additional incorporations that are possible, either the use of sticks to empty nuts as seen in Taï chimpanzees, or the use of a second stone to stabilize mobile anvils in Bossou chimpanzees (Fig. 31.5).

An additional, very complex example of cumulative cultural evolution in chimpanzees is seen in the honey-extracting techniques performed by Central African chimpanzees (*see review* Boesch et al., 2009; Sanz & Morgan, 2009). Here, different elements have again been progressively integrated in the technique, so that each step in this cumulative process produces an efficient technique seen to be used in some chimpanzee populations (Boesch et al., 2009). As seen in the nut-cracking example, chimpanzees add innovations to a universal technique, in this case, the common behavior for chimpanzees extracting a food resource from a hole in either a tree trunk or the ground with their hands. In some chimpanzee populations, we observed the first incorporation of a tool in the technique, either a twig for ant dipping in Gombe, Goualougo, and Taï chimpanzees, or a sturdy branch, a pounder, to break open bee nests for honey in Goualougo, Loango, and Taï chimpanzees. Then, after they succeeded in breaking open the nest with the first tool to extract tree honey, a second tool, a collector, was added by the Loango and Goualougo chimpanzees. This was not, however, seen in Taï chimpanzees. Finally, a third tool can be incorporated for large nests. In Loango, the accumulation of elements can go in another direction for terrestrial bee nests. The Loango chimpanzees use a perforator, a complexity not seen in Goualougo chimpanzees, to extract honey (*see* Boesch et al., 2009).

New observations of nut cracking and honey extraction present some of the most detailed cases of cumulative cultural evolution in chimpanzees, analogous to those proposed for human artifacts, such as the hammer or a screwdriver. Boesch (in press) has emphasized the fact that such cumulative processes were also apparent in different communicative cultural traits.

Orangutans, Capuchins Follow the Culture Track

Once described only in macaques and chimpanzees, the idea of animal culture has gained credibility in larger circles in science, and biologists have garnered the courage to look for culture in other animal species and have adopted a similar approach by comparing behavior patterns in different populations. It follows then that ideas about the uniqueness of human culture have lost some of their preeminence, and in their place, the urge to understand the distribution of different animal species' cultural practices has arisen. The legitimacy of culture in animals was gained through an ethnographic approach, by which the behavioral repertoire of different populations within one species was compared to the ecological conditions they were facing. By excluding ecological factors, the ethnographic approach suggested that the potential differences were of a cultural nature. The main requisite to the implementation of such an approach is the necessity of detailed studies on enough different wild populations in a given species. Even today, this situation exists for only a handful of species, and, therefore, our understanding of the real distribution of the cultural phenomenon in animals remains limited by definition.

The ethnographic approach applied to wild populations has uncovered fascinating new facts about important population differences that exist within a species, and cultural abilities have been proposed in such diverse species as orangutans (van Schaik et al. 2001), capuchin monkeys (Perry & Manson, 2003; Panger et al., 2002; Visalberghi et al., 2007), macaques (Leca et al., 2007), as well as in whales and dolphins (Rendell & Whiteside, 2001). Not only does the ethnographic approach stimulate the incorporation of a comparative approach in different animal species, but, when observing one population, such approaches allow us to discover what is population-specific and what is representative of the species as a whole. This further stresses the complexity of the interactions between ecology and culture.

Capuchin monkeys are particularly interesting as, in some ways, they present very similar patterns to the ones observed in chimpanzees. A handful of wild-bearded capuchin monkey (*Cebus libidinosus*) populations have been seen to crack wild nuts in Brazil, while this behavior pattern is absent in others (Visalberghi et al., 2007; Canale et al., 2009). In another species, the white-faced capuchins (*Cebus capucinus*), a series of differences have been observed between three populations in the way they process 20 food species before eating them (Panger et al., 2002). In addition, a certain number of social behavioral traits have also been observed to differ between populations, such as hand sniffing of others, sucking on the body parts of others, and the "finger-in-mouth" game (Perry & Manson, 2003). Some cases of new social games were invented when researchers were around and the diffusion within the group could be followed (Perry & Manson, 2003). From these and other primate species observations, we see that some of the simpler forms of cultural abilities seem to have been present very early on in our evolutionary history and that abilities proposed to be uniquely human in the past are possibly shared with many in the primate family lineage.

The Cultural Debate after the Wild Animal Culture Explosion

The important progress made in recent years to our understanding of the cultural phenomenon in different animal species has led to a second shift, one that is still in progress. The central question in the culture debate has become, "what distinguishes the cultural practices in different species?" rather than, "is culture a uniquely human ability?" This shift in focus in the culture debate has been enthusiastically adopted by primatologists and some behavioral ecologists, while contemplated with more skepticism in some human science circles (Boesch, 2003; Whiten et al., 2003; Laland & Janik, 2003; Byrne, 2007).

This shift in trying to understand the width of cultural diversity in different species is still underway but there are many stumbling blocks. The first is sample size, as this differs dramatically between species. In humans, we have access to observations from hundreds of different populations or more, while we have detailed observations from only 12 populations of chimpanzees, the second-most-studied animal species. There are only six populations of orangutans, the third on the list. In other words, because of the terrible paucity of data on nonhuman animal species, cultural breadth and abilities might by definition be much less-developed.

An additional hurdle to comparing cultural abilities across species is that, since adaptation to ecological conditions has long been observed in animal species, including insects and fish, ecological influences must be excluded for a behavior to be recognized as cultural in nonhuman animals (Galef, 1992; Tomasello, 1990; Laland & Hoppitt, 2003). The addition of this criterion, never considered in humans, has by definition decreased the number of potential behavioral elements that could be considered as cultural in animals (Boesch, 1996; Boesch & Tomasello, 1998; Whiten et al., 1999; Van Schaik et al., 2003). However, we all know that a vast part of human culture includes artifacts, clothes, foraging tools, and many other items that are all related to the specific ecological conditions a population faces. For example, many of the differences in material culture between Eskimos and Pygmies are, first and foremost, because of the drastically different ecological conditions that they face. It is important to bear in mind that if we want to compare cultural abilities between different species, we need to use the same set of criteria to define culture. Sadly, such an aspect has rarely been considered in the conclusions made when comparing the cultural abilities of humans with other species.

Two ways of progressing toward a fairer comparison have been pursued. The first solution to narrowing this gap was to address the sample size issue by studying more and new groups of wild populations belonging to species known for their cultural abilities. The gaps in our knowledge in chimpanzees have been especially dramatic, as the largest population of this species lives in Central Africa, and they have been totally neglected for decades. It is only very recently that two long-term studies have been initiated to fulfill this gap, the first in the Goualougo Triangle in the Republic of Congo (Sanz & Morgan, 2007, 2009; Sanz et al., 2004) and the second in the Loango National Park in Gabon (Boesch et al., 2007, 2009). Both have already unraveled surprising new and sophisticated forms of tool use that have not been described before. This nicely illustrates how much our knowledge of chimpanzees, a species who we have studied so much, is still very fragmentary. Similarly, new studies with capuchin monkeys have adopted a much more comparative approach and included many more populations (e.g., Canale et al., 2009).

The second solution directly addressed the shortcomings of experimental approaches. For many psychologists, a transmission mechanistic approach should be favored over the ethnographic approach, based on the argument that what counts in the culture phenomenon is not necessarily the end result of population-specific behavioral patterns but, instead, how a behavior is transmitted between individuals. Furthermore, they argue that only an experimental approach is able to identify such a mechanism, as individuals in the wild are exposed to so many simulations and experiences that it would be almost impossible to identify the precise mechanisms at work (Galef, 1992; Heyes, 1994; Tomasello & Call, 1997). However, it has been difficult to interpret the results of experimental studies on social learning of novel behavior patterns, which showed strong limitations in this ability in captive chimpanzees (Tomasello et al., 1987; Heyes, 1994; Povinelli & Vonk, 2003). The favored experimental procedure was to present a single individual in an isolated room with a demonstrator located in another room through a window. To prevent any uncontrolled influences, the social dimension of cultural learning was completely excluded. Furthermore, the novelty of the tasks was more important than their ecological validity, so individuals were tested with artificial tasks such as throwing sand or raking food (Tomasello et al., 1987). Nevertheless, to some, a consensus developed that such experiments were enough to prove that culture, as understood in humans, was not present in nonhuman primates and that the population-specific behavior observed should be based on a totally different process (Povinelli, 2000; Tomasello & Call, 1997; Tomasello, 1999). However, such a conclusion remained in strong contrast to observations in the wild and no attempt was made to explain the differences between the ethnographic approach and the captive experimental studies.

The impressive array of cultural behavior differences documented in wild primates concerning group-specific socially learned behaviors has led other psychologists to question the validity of the above-mentioned experimental procedures and to develop alternative ones, in which some of the aspects presented to the tested individuals would be as similar as possible to the situations faced by wild animals in the cultural domain. One of the most innovative procedures was done by keeping the individuals within their normal social setting during the experiments rather than isolating them. In this way, the social transmission of a novel behavior as well as the development of group-specific traditions could be mimicked in captive social groups (*see* Whiten et al., 2005, 2007, 2009; Horner et al., 2006; Hopper et al., 2007, 2008; McGuigan et al., 2007). This proved to be very successful as it was possible to follow the whole chain of social transmission from one expert individual to all group members and then from one group to up to four different neighboring groups. Such dispersal of novel behavior was accompanied by a strong fidelity to the expert's behavior, which maintained itself over long periods of time and during the dispersal process between groups. In other words, some of the key aspects of cultural transmission could be reproduced in such innovative cultural diffusion experiments.

This success has led the team to explore another aspect of culture that was proposed to be unique to humans, namely the ability to imitate one another. Some have proposed that culture can develop only as a result of imitation, as this was suggested to be the only social-learning process that guaranteed a high level of fidelity in the copied behavior (Galef, 1990, 1992; Heyes, 1994; Tomasello, 1990; Tomasello et al., 1993). However, in the absence of a complete theory as to when and why imitation should be used within a species, experimenters have been looking for imitative evidence with behavioral tasks selected randomly with mixed results. Although the results of group diffusion experiments have convincingly shown that imitation is not required to reach a high level of fidelity in copying a behavior pattern in chimpanzees, it was found that chimpanzees copy more by imitation when the individual cannot understand all the physical complexities of a task (e.g., when copying the way to get access to food contained in an opaque version of a box), while they will use more individual skills if they can understand them (e.g., when facing a similar but transparent version of a box with food inside) (McGuigan et al., 2007). In both cases, the demonstrator was the highest-ranking female of the group and therefore a trustful social partner. This convincingly showed that imitation and transmission are social behaviors and that chimpanzees are very sensitive to this. Without taking great care to preserve the social dimension, the results of experiments are not very helpful.

The main lesson about such studies is that culture is a social phenomenon and that the "culture outside of culture" approach adopted in so many captive studies has shown very strong limitations in its ability to understand the cultural abilities in nonhuman animal species (Boesch, 2007, 2010; de Waal, 2001). The main progress to experimentally understanding some aspects of cultural transmission was achieved when the social dimension could be reintroduced into the experiment paradigm. This social approach was so successful that it could be replicated in other primate species, such as capuchin monkeys (Dindo et al., 2009). Field studies remain the prime source of information about the breadth of the culture spectrum and the cultural abilities.

Conclusion

Being as selfish as we are, the question of human uniqueness has always drawn a lot of attention and been an area with numerous unsupported strong claims (e.g., de Waal, 2001; Whiten et al., 2003; Boesch, 2009). To avoid such well-known pitfalls, I shall try to limit myself to comparisons between species for areas where direct observations are available, as reviewed above, and avoid anthropocentric claims as much as is humanly possible. The newest data on wild animals reveal that, in many species, cultural differences are present. Such cultural traits that are concentrated on feeding techniques and therefore contribute directly to an individual's survival represent important characteristics of life. In other cases, cultural traits are also observed in the social and communicative domains but these tend to be less common than those seen in the material domain (Boesch, in press). For the first time, this progress offers some hope toward a resolution of what parts of the culture phenomenon are uniquely human.

This review would open the way to distinguishing some of the differences observed between animal species in their cultural abilities. To do this, I tried to include all we know about wild animal cultural behavior as well as some important experimental results. This review allows us to propose that, at a minimum, humans share the following attributes with many animal species:

- Acquisition of spontaneous group-specific behavior traits,
- Presence of cultural traits that are not influenced by ecological and genetic conditions,
- Social learning of cultural traits from group members,
- Persistence of cultural traits for extended period of time,
- Presence of nonadaptive cultural traits.

In addition, I propose that the overlap between human and chimpanzee cultural abilities is larger, as they include the following attributes:

- Cultural cumulative evolutions in material and social domains,
- Multi-generational history in cultural traits,
- Faithful copying from dominant prestige-carrying models,
- Conformity to new social groups,
- Active teaching and imitation of cultural traits,
- Symbolic social norms in cultural behavioral traits.

At this stage, it would be tempting to argue that those cultural abilities not listed here are uniquely human. This may be true, but we should not forget that our knowledge of other animal species fares very poorly compared to what we know about humans, and, therefore, more observations will certainly increase the list of similarities. I fully realize that such a statement is very frustrating, as all primate species are threatened in one way or another, and because of this, we may never fully know how similar our abilities are.

Wild animal studies have led to the realization that some of the population differences observed in some species possess close similarities to human cultures. The accumulation of such detailed observations from wild animal populations have provided more and more convincing details about the cultural skills in different animal populations, which has resulted in a shift away from the question, "do animals possess culture?" to the question, "what differentiates human cultural abilities from other animals'?" The growing body of evidence of cultural differences, not only in chimpanzees but also in macaques, capuchin monkeys, orangutans, and other primate species, opens the way to a precise ethnography of culture in different species.

By turning away from wild animal studies, comparative psychology faces the risk of eventually reaching an impasse, as only experimental studies with captive animals are considered without any concern for the ecological validity of such approaches. Luckily, studies have recently been started that will, in complement to wild animal studies, help us to address the question of animal cultural abilities. However, time is running out and all primate species suffer from habitat degradation and direct hunting against them, which could prevent us from collecting enough data on them before we can determine the specific cultural abilities of human and nonhuman primate species.

Future Directions: Toward a Resolution of Understanding Human Uniqueness

One way to find a provisional answer to the question of human uniqueness is to look for cognitive abilities unique to humans that are important for cultural transmission and acquisition. This would include speech, which is notably absent in other animal species, as well as modern human means of communication like writing, radio, and Internet. These communication media allow for the transmission of cultural traits between individuals who do not meet face-to-face, either because they are not visible to one another or because one of them might already be dead (Boesch, 2008). In addition, even in a face-to-face situation, such improved communication permits the cultural transmission of skills out of context, namely without having to demonstrate or practice the skill. Such cultural transmission modes, which are not available to any other animal species, would facilitate the transmission of more complex cultural traits.

Another possible way to answer such a question will come from careful and ecologically valid comparisons between how chimpanzees and humans learn social skills from group members. Recent work on imitation reveals that, although both species readily imitate, humans have a much stronger tendency to overimitate than chimpanzees, in the sense that they will faithfully copy unnecessary or irrelevant actions (Lions et al., 2007; Whiten et al., 2009). This tendency to blindly imitate irrelevant actions in adults might contribute to a stronger tendency in humans to adopt irrelevant and maladaptive cultural traits (Whiten et al., 2009). In a process similar to mate choice in birds, where individuals have been seen to simply copy the choice of others rather than to select the best mate, humans may be copying what they see group members doing without going through the time-consuming process of evaluating the benefit of each cultural trait, and thereby nonadaptive or opaque cultural traits can spread more readily in humans than in chimpanzees.

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