# Is Culture a Golden Barrier Between Human and Chimpanzee?

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Culture pervades much of human existence. Its significance to human social interaction and cognitive development has convinced some researchers that the phenomenon and its underlying mechanisms represent a defining criterion for humankind. However, care should be taken not to make hasty conclusions in light of the growing number of observations on the cultural abilities of different species, ranging from chimpanzees and orangutans to whales and dolphins. The present review concentrates on wild chimpanzees and shows that they all possess an extensive cultural repertoire. In the light of what we know from humans, I evaluate the importance of social learning leading to acquisition of cultural traits, as well as of collective meaning of communicative traits. Taking into account cross-cultural variations in humans, I argue that the cultural abilities we observe in wild chimpanzees present a broad level of similarity between the two species.

Stephen Jay Gould said once that humanity has an unfortunate tendency to erect "golden barriers" to set us apart from the rest of the animal kingdom. Is culture becoming one of those golden barriers? For many of us, material culture constitutes most of the external world we encounter in our daily lives. In the occidental world, material culture is so pervasive

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Evolutionary Anthropology 12:82–91 (2003) DOI 10.1002/evan.10106 Published online in Wiley InterScience (www.interscience.wiley.com). that for some of us it is the main goal of life. If, however, we were Bwa pygmies living in a tropical rainforest or Aborigines living in the open plains of Australia, our material belongings would be much more limited. This comparison indicates the extreme variability that exists in human material culture. However, human cultures are not only material, but also include beliefs, social rules, knowledge, and language. As a result of the incredible complexity of human cultures, we praise ourselves as distinct from other living beings for our uniquely rich and complex beliefs, thoughts, and knowledge. Indeed, all humans on earth are cultural animals, living in societies with specific cultural rules and traditions that infiltrate all aspects of our life. This fact has been elevated to a dogma, making humans the only living beings on earth with culture. Culture frees us from the natural world, whereas all others living animals are mainly influenced by nature. But is that dogma really so?

Recently this golden barrier has come under question, as increasing evidence from primates, birds, and even marine mammals supports the existence of repeated population differences in behavior patterns, the acquisition of new behavior patterns learned from group members, and the presence of flexible material cultures.<sup>1–5</sup> Other contributors to this special issue on culture will address these aspects, and I refer interested readers to their contributions.<sup>6,7</sup> The topic I particularly want to address here is the general attributes that chimpanzee culture may share with human culture, as a step toward better understanding of how and to what degree they differ.

Primatologists first became receptive to the notion of culture in animals when they observed the invention of potato-washing behavior by the young macaque, Imo, and saw it acquired by her playmates.8,9 Imo's actions shook a golden barrier and opened the way to examining cultural differences in a variety of species. Since that time, research on wild chimpanzees has reached the stage where it is now possible to compare behaviors of different well-known populations living in different places throughout the African range of this species.<sup>1</sup> I will use this information to extract the cultural attributes that are apparent in chimpanzees.

To compare chimpanzee and human cultures, we first need to decide what is meant when speaking of culture. Anthropologists have argued over this concept since the beginning of their discipline and agreement remains minimal.<sup>10–12</sup> Many definitions include the world "man," and thereby exclude any other species a priori and make any studies about the emergence of cultural phenomenon in any other species impossible or illegitimate. However, culture is not the exclusive property of anthropologists; other fields of science have, in the meantime, started to examine various

aspects of culture. For example, psychologists have concentrated on understanding the different learning processes involved in the cultural transmission of information.<sup>13–16</sup> At the same time, biologists have started to show a great interest in culture evolution as a much more rapid alternative to genetic evolution, because of its independence from reproductive events.<sup>17–20</sup>

Despite the different approaches among the three disciplines, a high level of consensus can be found on some basic concepts: First, culture is learned from group members; it is not transmitted genetically nor does it represent simply an adaptation to particular ecological conditions. Because it is transmitted socially, cultural practices have the potential to change rapidly if a new social model becomes available. Second, culture is a distinctive collective practice. This rather vague formulation implies that a culture observed in one group or society is distinct, so that we can actually know the origin of individuals by their socially learned practices. Third, anthropologists tend to speak of a symbolic system to express the fact that culture is based on shared meanings between members of the same group or society.

I shall investigate if chimpanzee cultural abilities share with humans the fact that they are diverse, innovative, and group-specific. Then I shall analyze on what mechanism cultural learning is based and see if the collective practice includes shared meanings. Finally I shall discuss aspects of possible cultural evolution in chimpanzees. This might deepen our understanding of culture in different species. Before we start, one point needs to be kept in mind. Our knowledge of chimpanzee behavior is very fragmented compared to our knowledge of human behaviors. Long-term studies on wild chimpanzees started only in the early 1960s.<sup>21,22</sup> Since the 1960s, field work has increased, but only a few chimpanzee populations have been studied for more than one decade. In a recent survey of culture in chimpanzees we found only seven chimpanzee populations on which enough detailed observations existed to answer simple questions such as whether a behavior pattern was present and, if so, in how many individuals.<sup>1</sup> Thus, we should be aware throughout this discussion that one thing we are certain about with respect to chimpanzee culture is that we strongly underestimate its breadth and complexity.

## CULTURAL DIVERSITY AND CREATIVITY

When Imo, a young female Japanese macaque, introduced potato washing into her population, it was a breakthrough. Nevertheless, it might well seem a bit simple to qualify as a culture. Human cultures are charac-

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terized by a large number of different cultural traits in a variety of domains (social, technical or symbolic). Imo might well be a groundbreaker, but her two inventions fall short of such cultural breadth. However, culture is a collective practice, and we should not expect one single individual to create it. How rich are cultures in chimpanzees? Are they able to innovate?

As early as 1973, Jane Goodall listed thirteen differences in tool use as well as eight differences in social behaviors between the Gombe chimpanzees and other chimpanzee populations. She proposed that some of them were cultural in origin. The most conspicuous one was nut cracking, which is absent in the Gombe chimpanzees, in spite of the presence of oil-palm nuts. Observations of this behavior were first reported in the 1840s in Liberian chimpanzees.23 With increasing observation time, the discovery of additional behavior differences between chimpanzee populations made it feasible to begin drawing up charts of cultural variations. McGrew,24 in his book Chimpanzee Material Cultures. listed nineteen different kinds of tool use that varied in their expression in different communities, while Mike Tomasello and I25 listed twenty-five behavior patterns as potential cultural elements in wild chimpanzee populations. In the last attempt to categorize chimpanzee cultural variation, no less than thirty-nine behavior patterns were proposed as cultural variants, including various forms of tool use, grooming techniques, and courtship gambits.<sup>1,3</sup> This cultural richness in chimpanzee far exceeds anything known for any other species of animal except humans. However, new analyses on other species such as the orangutan<sup>26</sup> are under way, stressing the possibility that rich cultures might be more prevalent than previously was thought.

Anthropologists present culture as releasing individuals to some extent from the ecological constraints under which they live. The invention of nut cracking in chimpanzees illustrates this effect with respect to diet. Nut cracking accounted for 33% of the total feeding time of the chimpanzees during certain seasons at Bossou<sup>27</sup> and more than 40% of it at Taï, supplying the nutcrackers with more than 3,000 calories per day during the four months when nuts were available.28 Further, twenty-two of the thirty-nine cultural variants found for chimpanzees relate to feeding, illustrating how cultural their diet is. More specifically, Taï chimpanzees use twenty types of tools regularly, while Budongo and Kibale chimpanzees on Uganda use only six and five, respectively. Not only does this larger repertoire of tool use in Taï allow the chimpanzees to gain access to many more insect products (larvae, grubs, and honey) than do Budondo and Kibale chimpanzees, but it suggests an underlying "core

cultural orientation" toward technology in Taï chimpanzees, which is manifested in a disposition to innovate and to learn socially about a variety of forms of tool use.<sup>2</sup>

Cultural creativity in chimpanzees is documented by innovations. On the January 7, 1990, the Bossou chimpanzees, which have been under study since 1979, were observed pestlepounding the top of an oil-palm tree to eat the apical bud for the first time. In the following three years, this behavior spread to eight of the sixteen individuals of the group.<sup>29</sup> On March 7, 1999, I first observed an adult female in the Taï forest chewing the pith of adult leaves from young oil-palm trees, whereas such behavior had not been observed in the previous nineteen years of study. In the following days, I saw this behavior performed by four more individuals.

Some observations emphasize that innovation is a regular event in wild chimpanzees. Between 1988 and 1991, I saw Taï chimpanzees use tools in seven new ways.30 In the subsequent four-year period, from 1992 to 1996, I observed eight new behaviors, six of them related to tool use. By "new," I mean a behavior never observed during the course of the study and for which simple ecological explanations, such as using a tool for a new food source that was available for the first time, could be excluded. In other words, the chimpanzees of this community invented, on average, two new behavior patterns per year.

Thus, chimpanzees have the ability to regularly invent new behavioral patterns, many of which increase their freedom from environmental constraints. In addition, we see that many of the cultural variants they use help to shape their environment. Humans also have this ability, although societies vary greatly in this tendency to shape their environment through culture.31 This relatively high rate of invention begs the question of why cultural invention seems so rare in chimpanzees. This represents the "cultural paradox" whereby some cultures are very stable when they could potentially be rapidly changing.<sup>25</sup> Two explanations have been proposed: either group conservatism prevents the introduction of a new variant, or the social learning mechanism is too imprecise for the acquisition of some of the innovations.

# CULTURAL LEARNING

One defining feature of culture in human societies is the acquisition of cultural traits in naïve individuals through social learning. Learning abilities have been subject to many studies with captive individuals.<sup>32–36</sup> As expected, such studies show that chimpanzees and other animals use different mechanisms, both individual and social, to learn different be-

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haviors. Since nobody proposes that one individual learns all the behavior patterns in his repertoire with a single mechanism, we are still left with the question of what learning mechanisms wild chimpanzees use for acquiring cultural traits. Surprisingly enough, up to now only one cultural trait, nut-cracking behavior, has been subject to such study.<sup>28,37–39</sup>

The main nut species cracked in the Taï forest, *Coula edulis*, is an important food source during the fourmonth dry season between December and March.<sup>28</sup> The nuts are cracked with the help of naturally occurring hammers, which include stones or branches, and anvils that are normally surface roots. Chimpanzees as young as two years old show a strong interest in manipulating hammers and in learning to open nuts. In addition, mothers share the nuts they open with their infants for many years, thus creating a situation in which learning attempts and food sharing occur simultaneously. The learning of nut cracking seems to proceed through three distinct phases. First, the youngsters make unsuccessful attempts by hitting the nuts. Typically, during this phase, youngsters do not understand the relationship between the various components of the task and make mistakes such as selecting an incorrect hammer, such as a hand or another nut, or not placing the nut on the anvil. The second phase is reached at the age of three years when they understand relationships between the elements. Then they crack nuts only when all three elements are present, but they lack the muscular strength to open the nuts. The third phase starts when they have gained the musculature necessary to crack the nuts open. Through practice, progress is quite rapid, and youngsters achieve 42% of the adult efficiency for the Coula nuts within two seasons.

What is the role of social learning during this period? If social learning is at work, the nut-cracking attempts of the youngsters should be similar to the behavior they have observed in expert nutcrackers. If, however, social learning is absent, youngsters would be expected to use a wider variety of behavioral techniques than expert nut crackers. To distinguish between these mechanisms, I compared the behavior of young chimpanzees in the Taï forest with that of naïve captive chimpanzees that were provided with the three elements of the task-nuts. hammers, and anvils.40

Despite the fact that the ecological conditions in the tropical rainforest are much richer than those of a zoo, the zoo chimpanzees used twice as many behaviors (fourteen in total) to open the nuts as the Taï chimpanzees did. Interestingly, some of the methods seen in zoo chimpanzees were similar in form to behaviors used by Taï chimpanzees in contexts outside of nut cracking, such as throwing the hammer on the nut (which Taï chimpanzees did at leopards), rubbing the nuts (which Taï chimpanzees did with hairy fruits), or stabbing the nuts with a stick (which Taï chimpanzees did at leopards). We argue that Taï youngsters never used these methods in this context because they never saw them used by experts when cracking nuts. In other words, a strong social canal*ization* is at work in Taï that limits the individual learning attempts to those methods observed in adults. The nutcracking movements seen in expert individuals are copied by all youngsters, and the variations observed concern mainly the object to be used as a hammer. Thus, for nut-cracking behavior, social learning prevails as an important part of the learning process.

Because youngsters were so attentive to what their mothers did, we might also expect mothers to guide their offspring's attempts. In humans, such actions by parents or older group members is proposed to be of central importance for the transfer of knowledge and skills between generations that is necessary for cultural transmission.41-43 Such different pedagogical actions are often presented as a "scaffolding process"44 whereby the teacher's selective interventions provide support to learners, extending their skills to allow the successful accomplishment of a task not otherwise possible. This allows a learner to produce new skill components that are often understood but yet not performed. This includes not just teaching but all the ways parents use to stimulate and facilitate their offspring's attempts at a given task. Teaching is considered to be the most elaborate form of pedagogy, but is often less frequently used in humans for learning a task than attention-fixing or motivating.<sup>45,46</sup>

At Taï, chimpanzee mothers rely on many forms of pedagogy to help their offspring's acquisition of the nutcracking technique.<sup>40</sup> We observed three different ways by which mothers assist their infants' acquisition of the task. First, mothers stimulated their offsprings' attempts at nut cracking by leaving their hammers and some intact nuts behind on the anvil while they searched for more nuts under the trees. Only mothers with young infants were seen to do so, as good hammers are rare in the forest and leaving one behind increases the risks of losing it to another chimpanzee. In this way, the mothers provide their offspring with the opportunity to learn what a good nut and a good hammer look like, and give them the chance to practice. Stimulations were performed most frequently for threeyear olds that had started to use a hammer, occurring seven times per hour (Fig. 1). Second, facilitation was seen for offspring trying on their own to open nuts. In this case, mothers provided better hammers or intact nuts they had collected. Facilitation,

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like stimulation, was more frequently performed for infants that had acquired some of the technique. While stimulations occurred most frequently for three-year old infants, facilitations started with four- to fiveyear olds and occurred on average once every seven minutes, with a peak at more than one instance per minute for eight-year old individuals (Fig. 1). The mothers' acts were adjusted to the level of skill attained by their infants. The offspring always used the hammers left, and their nut-cracking performance always improved, sometimes greatly.<sup>40</sup>

Finally, by active teaching, mothers helped offspring solve technical difficulties that they were unable to overcome on their own. In two instances, mothers noticed the offspring's specific technical problems and were seen to make a clear demonstration of how to solve them. Both were performed with offspring that had already successfully opened nuts but, in these cases, either did not notice the problem or could not find a solution.<sup>40</sup>

When I first published these examples of teaching, the main criticism was that such cases were too rare, given that chimpanzees have the ability to teach.43,47 This critique assumes that active teaching is the best way to acquire a cultural behavior, and therefore should be used frequently. Is this assumption correct? The few studies that have examined the acquisition of cultural behaviors in human societies show that many transmission mechanisms are at work. For example, observational learning is the primary mechanism used by apprentices to learn skilled and complex weaving techniques in different South American, African, and Arabic societies.45,48,49 Observational learning is supplemented by facilitation and stimulation from an expert during the later phases of the acquisition process. The same is true when students are learning to become sushi masters in Japanese cuisine.<sup>50</sup> For some tasks, the type of learning mechanism used depends in part on the desired result. In weaving, for example, learning by observation and shaping by scaffolding prevail when maintenance of traditional methods is important. However, when innovation is valued, learning by trial and error dominates.49 Therefore, in the case of human cultural traditions, active teaching seems less essential for learning some cultural techniques than often is assumed.

In the case of nut cracking, cultural learning is based on both social learning by the infants and pedagogical interventions by the mothers. These pedagogic interventions are frequent (on average twelve times per hour for nut cracking) and result in specific aspects of this technique being brought to the attention of the offspring. Consequently, the learning of cultural bechimpanzees.

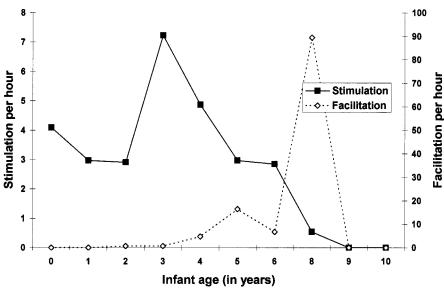


Figure 1. Maternal scaffolding actions in relation to the infant age when nut cracking in Taï

havior in chimpanzees is surprisingly similar to human learning of some cultural tasks. In both species, observational learning is the base; experts supplement it with such methods as attention-fixing and facilitation. What seems specific to cultural learning is both the social canalization, which results in having naïve individuals practice only what they see in models, and the scaffolding, through stimulation and facilitation, that assists naïve individuals in mastering specific aspects of the task with fewer difficulties. Both chimpanzee and human "teachers" appear to understand the skill level reached by naïve individuals and to react properly to it. Care should be taken before drawing definite conclusions on the use of such mechanisms, as more observations are needed about the mechanisms used in learning a variety of cultural techniques in both species.

#### CULTURAL MEANING

In anthropology, culture is commonly viewed as a matter of ideas and values, a collective cast of mind.<sup>10</sup> In other words, cultural behaviors have a shared meaning within each social group, and it is this aspect that has been described as being unique to human culture.

However, chimpanzees also possess some cultural behaviors that have not only a form but also a meaning that is shared between members of the same group and is unique to the group. Take the example of "leaf clip," a behavior whereby chimpanzees bite a leaf into pieces to produce a ripping sound without eating any of the leaf. In forty years of observation, leaf clip has never been seen in any of the Gombe chimpanzees. However, three populations of chimpanzees regularly leaf-clip. All males in the Taï forest regularly leaf-clip before drumming. Among Bossou chimpanzees, leaf clip is performed in the context of playing, as a means to enlist a playmate,<sup>51</sup> while Mahale chimpanzees leaf clip as a way to court estrous females.52 Taï chimpanzees have never been observed to leaf-clip in the context of playing nor in courtship. Similarly, Mahale chimpanzees have never been seen to leaf-clip in the context of playing nor when drumming (Table 1).

While the leaf-clipping sound attracts the attention of others in all communities, group members respond differently according to its meaning within a particular community. Sexually active females will present to a leaf-clipper in Mahale, whereas in Bossou youngsters will attack or pursue the leaf-clipper with a play face. Individuals in Mahale have never been observed to answer with a play face to a leaf clip. Similarly, a female from Taï has never responded sexually to leaf clipping. Rather, voung males from Taï attract females by knuckle-knocking discreetly and repeatedly on a small tree trunk (Table 1). Females respond to this behavior by sexual presentation. It can even happen that another female may present to the knuckle-knocker. despite the fact that he was not looking toward her. Even sexually immature youngsters may react by sexually presenting to the knuckle-knocker, demonstrating that they have understood the meaning. In other words, the meaning of the behavior is clear by itself and independent of the sexual state of the receiver or the gaze of the emitter.

The meanings of some cultural behavior rely on arbitrary conventions. Nothing in the form of the behavior or in the noise produced by the leaf clipping indicates that it could mean play rather than courtship. The meaning is adopted collectively and rests on an arbitrary convention shared by group members. Thus, shared meaning and symbolism go together at this level of cultural complexity observed in chimpanzees.

Another example of a socially shared meaning concerns the fascination directed by all chimpanzees towards ectoparasites like ticks and lice. When a chimpanzee finds one, either on itself or while grooming a group member, he first manipulates it and then eats it. However, the way he manipulates it is population-specific. At Gombe, chimpanzees tear a bunch of four or five leaves from a small branch, carefully pile one leaf on top of the other, and

TABLE 1. Cultural Meaning of Different Behaviors Within Different Chimpanzee Populations

|                       | Bossou    | Gombe | Mahale    | Ταϊ                       |
|-----------------------|-----------|-------|-----------|---------------------------|
| Behavior<br>Leaf-clip | Plav      | _     | Courtship | Drum + Rest               |
| Meaning               | Tidy      | _     |           |                           |
| Courtship             | _         | —     | Leaf clip | Knuckle-knock             |
| Play                  | Leaf-clip | —     | —         | Ground nest (South Group) |

place the parasite on top of the leaves. Then, with the nails of both thumbs, they squash it and eat it. This behavior pattern has been labeled as leaf groom.53 At Mahale, chimpanzees were thought to have a similar way of handling parasite. However, when I visited Mahale in 1999, I compared this behavior to that seen in Gombe and found it quite different. Mahale chimpanzees take one single leaf, place the parasite on it, carefully fold the leaf lengthwise to cover the parasite, then cut the leaf with the nail of one thumb so as to expose it again. Finally, they take it with their lips and chew it. They may replace the parasite on the same leaf and repeat the procedure a few times. I labeled this behavior sequence "leaf fold" to distinguish from the Gombe leaf groom. At Taï, an ectoparasite is placed on the forearm and hit with the tip of the forefinger until it is smashed. One male repeated this behavior 350 times! The communicative function of this behavior is more limited than that of leaf clipping, but others obviously understood the function of the behavior, as each time it occurred they reacted by hurrying over to look intently at what was happening.

Thus, in chimpanzees, some cultural variants function as signals that have acquired collective shared meanings based on a behavior independent from any external factors. Interestingly, in the case of leaf clipping, the relationship between the form of the behavior and its meaning is totally arbitrary and based on a group convention. Thus, a particular behavior can acquire different meanings in different populations. Conversely, the same meaning may be conveyed with different behaviors.

#### CULTURAL FIDELITY

Often human cultural habits allow close social groups to differentiate themselves from their neighbors. This is possible only because individuals transferring between groups, for example after a marriage, adopt the new cultural tradition of the groups into which they immigrate. The bulk of our knowledge about chimpanzee cultures comes from comparing social groups that are hundreds of kilometers apart. We wonder: Are there cultural differences between nearby chimpanzee groups that have individuals transferring between them?

Because of the lengthy investment required to habituate wild chimpanzees to human observers, each project has concentrated on a single community at a time. Recent developments in the Taï chimpanzee project have led to three neighboring communities being observed concurrently.<sup>54</sup> To my surprise, I noticed some behavior patterns that differ between the three communities, and several of them were not directly related to ecological differences. Map 1 shows the position of the three groups within the forest

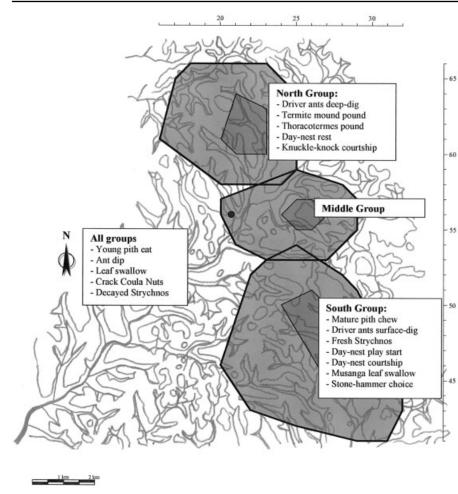
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and lists the cultural behaviors that distinguish the North from the South group. Within a three-year interval, I documented twelve behavior patterns that distinguished the two groups. All three communities share the typical traits of the Taï culture, including cracking five species of nuts with hammers, dipping for ants with short sticks, pounding hard food on tree trunks, leaf clipping in a drumming context, performing a slow and silent rain dance as rain approaches, and squashing parasites with the finger on the forearm. The map shows that in addition subcultures are present in

the North and South groups that distinguish group members by their behavioral repertoire. Seven behavioral traits were observed only among South group members and any plausible ecological differences were excluded. Similarly, five behavioral traits distinguished the north group members from the south.

Let me illustrate some of these differences. First, feeding on young Haloplegia leaves has been observed in all three groups, but the chewing of mature leaf stems is seen only in the South group. Second, South group chimpanzees use a different technique from the North group to feed on grubs extracted by hand from driverant nests. Whereas North individuals introduce their arm into the nest multiple times and almost to the shoulder, South individuals introduce their arm only once and rarely deeper than the elbow. Consequently, the Southgroup chimpanzees eat many fewer grubs. Third, they differ in how they eat the hard-shelled Strychnos ac*uleata* fruits. The South chimpanzees eat the flesh only when it is fresh and white, while the North chimpanzees wait for the flesh to be totally decomposed and eat only the embedded kernels. Finally, the North chimpanzees eat large amounts of the winged form of Thoracotermes termites as they gather on the aerial part of the mounds; South group members totally neglected them even though they are present at the same time of the year.

Differences between populations were also found in communication. The North group members regularly build nests on the ground when resting.30 In contrast, South group members build ground nests for totally different purposes. Youngsters build ground nests as signal to play. Often, before or during a pause in a play session, I observed a youngster build a ground nest, after which another jumped on him, trying to destroy the nest while the first protected it; each showed a wide play face. This behavior has never been observed in the North group. Remember that Bossou chimpanzees use leaf clipping as a play-start signal, whereas the same goal is reached in the Taï South group with building of a ground nest (Table 1). In addition, South chimpanzees were seen to build a coarse ground



Map 1: Cultural differences between three neighboring chimpanzee communities in the Taï forest.

nest as a signal to attract sexually active females. This was seen only once in twenty years the North group. In the North, knuckle-knock is used to attract sexually active females. Thus, subcultures between communities within a single area do exist in chimpanzees and, like more regional cultures, incorporate traits based on shared meaning.

Subcultures between neighboring chimpanzee communities persist despite a regular exchange of individuals. New immigrant individuals adopt the new subculture they encounter and seem to lose that of their natal group. It is puzzling that a female should switch from an efficient technique for feeding on ants to a less efficient one. Conformity might be an aspect that plays a role in chimpanzee sociality. We have not yet been able to follow the transfer of one individual between two of those communities, but we know that exchanges have occurred in the recent past. In the North group, transfer of individual females happened more than once per year during a fifteen-year period.<sup>28</sup> We do not know how this melting into the local subculture is achieved. It could be either that new immigrant females actively try to fit into their new culture or that resident members impose it.<sup>25,55</sup> The fact that we saw foreign cultural patterns so rarely in each community suggests that this process takes place very rapidly.

Thus, subcultures were present that distinguish chimpanzee communities within the Taï forest. This group-related variation illustrates the complexity and flexibility of chimpanzee cultural behavior, which helps increase the freedom chimpanzees gain from environment constraints. Both between- and within-region cultures show a tendency for communicatory behavioral traits to be more flexible and based on arbitrary shared social meanings.

### CULTURAL HISTORY

Archeology classically has been defined as the science documenting human cultural artifacts. We recently attempted to use the same methodology to investigate nut cracking, the only chimpanzee cultural trait to leave a lasting record. We found that this behavior has existed for at least 900 years.<sup>56,57</sup> Further excavations will allow us to document the exact age of this behavior, but our early data clearly suggest that chimpanzee cultural traits could be quite old.

Was a cumulative cultural evolution process at work during this long period of time? By cultural evolution I am referring to a process under which a cultural behavior pattern is elaborated by further invention within the group followed by dissemination, a process similar to what has occurred with, for example, hammers in human cultures.15,25,58 We cannot yet respond directly to this question. One indirect indicator of such a process is the complexity of certain cultural sets of behavior, as it is unlikely that such behaviors would have been invented in their full complexity by a single individual. Is there any indication of a similar process in chimpanzees? Three cultural variants in chimpanzees might well be the outcome of a cumulative cultural evolutionary process.

The first candidate is nut-cracking behavior. Many chimpanzee populations open large hard-shelled fruits by hitting them directly with the hand against tree trunks or roots. This ancestral behavior pattern seems to have been further developed in West African populations by incorporating a hammer to hit the fruits, thereby making it possible to break harder and smaller fruits. Among Bossou chimpanzees, two additional developments occurred, the use of loose stones as anvils and then the use of a second stone to increase the stability of the anvil.59

A similar scenario might be suggested with the second candidate, parasite manipulation. As mentioned earlier, all known chimpanzees show a fascination for ectoparasites and eat them after manipulation. Most chimpanzee populations in East Africa have been observed using leaves to remove parasites and some populations (at Budongo, Mahale, and Gombe) place the parasites on a leaf to inspect and squash them before consuming or discarding them.<sup>2</sup> This looks like the ancestral behavior. Two parallel complexities have been incorporated. As discussed earlier, Mahale chimpanzees not only place the parasite on a leaf, but then fold the leaf and cut it with the nail of a thumb. Alternatively, Gombe chimpanzees place parasites on many leaves previously carefully piled one on the other.

A last candidate is well-digging behavior. Chimpanzees living in waterpoor habitats (Uganda,60 Senegal61) have been seen to dig the soil in dried water beds to gain access to water. This behavioral pattern could be the ancestral form, which was then further developed to incorporate well digging during wetter periods, either near running water or near algaechoked water, perhaps to filter parasites or dirt. A final development in this behavior is the incorporation of leaf-sponges to extract water from deeper wells by chimpanzees in Semliki, Uganda.<sup>60</sup> A third of the wells had sponges that chimpanzees used, drinking the water from the little holes. Gombe chimpanzees have frequently been observed to leaf-sponge water directly from streams.<sup>2</sup>

These three examples illustrate how cumulative cultural evolution could work. Combined with the creativity observed in chimpanzees, it suggests that cultural evolution might exist in this species. One paradox of cultural evolution is that it potentially is very rapid, yet seems to be rather slow in traditional societies.<sup>25,55</sup> As long as social and ecological conditions remain stable, cultural evolution might remain very slow because there is little need to alter the environment. This seems to be the case in the chimpanzee populations that have been studied.

# CHIMPANZEE AND HUMAN CULTURES

What we observe in different chimpanzee groups nicely matches our definition of culture as a set of behaviors learned from group members and not genetically transmitted, mainly independent from ecological conditions, and shared between members of some specific groups. In addition, the flexibility of the chimpanzees' culture allows them to shape their environment to gain access to important new food sources, develop arbitrary signs that have shared meaning, and develop subcultures that distinguish individual groups from their neighbors. In a sense, this all sounds disappointingly similar to what we observe in humans. This coincidence might reflect the fact that cultures fulfill a special niche in the world and therefore develop in rather similar ways when they develop at all.

The proposition that human culture is the only one to rely on one specific social learning mechanism<sup>43</sup> is contradicted by the fact that in chimpanzees social learning strongly affects

... the flexibility of the chimpanzees' culture allows them to shape their environment to gain access to important new food sources, develop arbitrary signs that have shared meaning, and develop subcultures that distinguish individual groups from their neighbors.

the acquisition of nut-cracking behavior. Teaching seems to be more common in some human societies than in others<sup>45</sup>; such variability has not vet been found in chimpanzees. However, it might be relevant to consider what is being learned and in what social context. When the tasks can be observed and practiced, simpler forms of scaffolding are observed in human societies,49,62 as is the case in chimpanzees. When innovation is valued, trialand-error learning dominates, while when maintenance of traditional ways is important, learning by observation, shaping, and especially scaffolding prevails in humans.48,49 Maintenance of traditional methods may rarely be

important in chimpanzee societies. Therefore it should not be so surprising that teaching has, up to now, been observed only in the context of nut cracking, one of the most complex tool-use techniques seen in chimpanzees. Language seems to introduce a new dimension to cultural transmission mechanisms, as pedagogical intervention can be performed with individuals one has not seen and demonstrations can be performed out of context.

Material culture seems to be another similarity between humans and chimpanzees, as both species are the only ones in which all known populations commonly use different and multiple tools.28 It is in this domain more than in any other that anthropologists have claimed that human culture frees us from Mother Nature. However, this benefit functions in chimpanzee societies as well as human ones. The invention of nut-cracking behavior transforms a forest habitat into a green paradise for months, with energetic food now available in large supply. In both species, considerable benefits can be attained with limited and simple tools.24,63 In humans, however, the more adverse the environment is, the more important material culture becomes. All wellstudied chimpanzee populations live in tropical forested habitats, where the ecological conditions provide them with a warm climate and good feeding conditions, conditions that do not require a large material culture.

If we look at what has been proposed as culture in other animal species, one striking fact emerges. In most species, very few cultural behavior patterns have been described. For example, the Californian sea-otter population differs from other populations only by using stones to open ovsters.<sup>17</sup> In sperm-whale populations, cultural differences are limited to click sounds that distinguish maternal groups from each other and remain stable over generations in spite of changes within the group. Killerwhale populations living near land possess different feeding habits and click calls than do those living in the open sea.<sup>5</sup> While increased data might demonstrate greater cultural traditions in a variety of species, it remains true that at the current time the presence of a large repertoire of different

behavior variants is apparent only in great apes. In the orangutan, the number of possible cultural behavioral patterns has recently been reported to increase.<sup>26</sup> In this species, the use of tools to extract Neesia kernels looks extremely similar to what is observed for the nut-cracking behavior in chimpanzees, including the fact that a river represents the boundary of the cultural behavior.<sup>4</sup> This suggests the possibility of a broad great-ape foundation for culture. Similarly, data from studies of capuchin monkeys indicate multiple behavioral variations.64 The discussion about animal culture is quite recent and more information is needed on the species concerned before we can understand the entire range of their cultural behavior. Nevertheless, human cultural products have in recent times led to an inflation of artifacts that is unequalled in the animal kingdom. It remains to be seen whether our acquisition mechanisms are qualitatively different from those of, for example, chimpanzees.

The implications of this emerging picture go far beyond chimpanzees alone. Characteristics that chimpanzees share with humans support strong inferences about the way of life of our common ancestor five million years ago. An exciting prospect arises to gain insights into the ancient foundations of our extraordinary human capacity for culture. The present overview of what we know about chimpanzee cultures shows that it goes a long way beyond being simply a set of behaviors not explained by genetic or ecological factors. The similarities with what we observe in human groups are striking. At this stage, I want to propose that these aspects are common attributes of human and chimpanzee culture and that they probably were part of the repertoire of our common ancestor. This means that they could be as old as five million years. Much later, language would have opened a wide new window, facilitating the development of cultural traits in the communicative and the shared reflective domain, and paving the way for all our cultural beliefs and rituals.

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