



VOLUME 5

HANDBOOK OF ADVANCES IN

CULTURE
&
PSYCHOLOGY

EDITED BY
MICHELE J. GELFAND
CHI-YUE CHIU
YING-YI HONG

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Handbook of Advances in Culture and Psychology

Advances in Culture and Psychology

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Volume Five

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Handbook of Advances in Culture and Psychology

Similarities Between Chimpanzee and Human Culture

CHRISTOPHE BOESCH

Abstract

Originally the concept of culture was proposed only for humans, stressing the importance of social influences on its dynamics and development. Although there is no question that all human groups have different diverse, complex, and rich cultures, a debate begun in the early 1950s raised the issue of animal culture and what it may mean for the uniqueness of human culture. This chapter argues that data from captive studies that difficult to use in this regard owing to the artificiality of the “social dimension” in captive groups and the absence of a species-specific ecological environment—issues that have obscured progress toward a better understanding of human culture. Two major attributes of human culture—cumulative cultural evolution and symbolic culture—arise in adopting an ethnographic approach to the study of differences between wild chimpanzee populations. Culture is observed among both humans and chimpanzees; therefore further work should be aimed at uncovering the specifics of culture in each of these species.

Keywords: captive studies, chimpanzees, cumulative cultural evolution, social influences, symbolic culture

I. INTRODUCTION

Because of the flourishing fieldwork that has been done in studying different populations of a single animal species, the reality of animal culture has been continuously confirmed by new observations. This has directly led to the question of what is uniquely human in the cultural abilities of *Homo sapiens*.

Alongside came a reactivation of the discussion of nature and/or culture and a questioning of the pertinence of using captive animals for studying culture. The socioecological dimension of culture is often absent or very limited in captive groups. In this discussion one main contentious aspect is how much ecological influence should be ascribed to primate and other animal species in the development of their sociocultural abilities.

In the second part of this chapter, I illustrate some of the most striking examples of cultural diversity seen in wild chimpanzee populations; I then concentrate on two specific cultural abilities that have been claimed to be uniquely human, based on captive comparative results, for which new and important field evidence has recently been provided. First, the cumulative cultural evolution that is producing, among other things, computers and airplanes, is hugely important for the production of modern human cultural products. Detailed observations of many chimpanzee populations across the African continent have now revealed that such a process is at work in our closest living relative, the chimpanzee; this has also been confirmed in a broad nested structure analysis. Second, the symbolic culture that developed so largely with human language has now been observed in some communicative signals used by different wild chimpanzee populations.

To be able to progress in the understanding of the uniqueness of human culture will require from researchers a better inclusion of the ecological and social dimensions as well as an open consideration of the specific limitations of captive studies in addressing questions regarding the cultural abilities of animals. Animal cultures emerged in wild populations exposed to all the challenges of survival, and that is where we need to study them if we want to progress in our understanding of their cultural abilities and potential species uniqueness in that domain.

II. HOW WE THINK ABOUT NATURE AND CULTURE

The nature/culture debate was originally about nature *or* culture. Many scholars saw human beings as the only cultured animal, while all other animals were nature-driven—in other words, driven by instinct and fixed genetic programs. This distinction was already proposed by the ancient Greek philosophers with, on one side, the Stoics, those proposing continuity between animals and humans, and, on the other, Aristotle and his

followers, arguing for a strong dichotomy, with humans clearly separated from other animals. Such a dichotomy has often been impregnated with subjective ideological considerations about how to position humans in relation to all other living beings. Naturalists classically challenged the strong dichotomy between humans and animals proposed by many in the human sciences, and the surge in wild animal studies from the mid-1960s onward has led to a broad reevaluation of the abilities of nonhuman animals, providing a new impetus for cross-species comparisons (Allen, 2004; Boesch, 2012; Wise, 2000).

Alongside these developments and more recently, a better understanding of how gene expression works has led to a progressive shift away from the *nature-or-culture* debate to a debate about the interactions between *nature and culture*. In essence any phenotype is the result of the many interactions between the genotype of the individual with the environment in which that individual has grown up and lives. Even in insects, like fruit flies, numerous studies have documented how importantly environmental influences affect body size, life span, and even flight behavior (Stearns & Hoekstra, 2000). Therefore the open question is to understand how species-specific such environmental influences are and how much they affect social and cultural behavior. Today, therefore, the main divergences of opinion concern the relative contribution to the phenotype of the social and material environment versus genetic factors.

Here there has been a lack of general agreement among scholars, partly because data measuring precisely those respective contributions are hard to collect and require long-term longitudinal studies. This gives room to a large diversity of opinion, sometimes sustained by individual subjective preferences. The recent acceptance of experimental studies, with captive individuals considered as fully representative of an entire species, is based on the assumption that socioecological factors play a minimal role in the development of the cognitive and cultural abilities of the individual (Boesch, 2007). Therefore, independent of the specifics of the captive conditions under which an individual has grown up, such an individual can be considered to be fully representative of its whole species (e.g., Penn et al., 2008; Povinelli, 2000; Silk et al., 2005; Tomasello & Call, 1997, 2008). Others, on the contrary, recognize that the development of full cognitive and cultural abilities requires the typical species-specific physical and social environmental challenges and that much care must be taken in using results obtained from individuals

that have been placed in non-species specific socioenvironmental conditions and have grown up in them (e.g., Barrett et al., 2007; Boesch, 2007; de Waal, 2001; de Waal et al., 2008; Laland & Janik, 2006; Whiten et al., 1999). Because of today's increased understanding of the important interactions between genotype and environment, it seems essential to be aware of the potentially important negative impacts of captivity on the development of cognitive and cultural abilities in individuals living in such situations.

III. THE IMPORTANCE OF SOCIAL ENVIRONMENT IN CULTURE

The social environment is essential for the expression of social and cultural skills; thus removing individuals from their socioecological environment can be directly detrimental to the development of such skills. The pivotal role of social influence in the development of human cognitive and cultural performance has been amply documented in numerous studies (Chen et al., 2011, 2012; Corriveau & Harris, 2009a,b; Harris & Corriveau, 2011; Henrich & Broesch, 2011; Over & Carpenter, 2009, 2012, 2013). Human infants, for example, are subject to a complex set of social influences, and

the complexity of children's imitation can only be fully understood by considering the social context in which it is produced. Three critical factors in determining what is copied are children's own (learning and/or social) goals in the situation, children's identification with the model and with the social group in general, and the social pressures which children experience within the imitative situation. (Over & Carpenter, 2012)

Helping other individuals or imitation can be up to three times more frequent when infants are placed in a social-friendly context than otherwise (Over & Carpenter, 2013). Because the evidence is so convincing, the conclusion was that trust is needed for children to develop sociocultural skills, and children trust long-term familiar individuals.

Is this different in our closest living species? Does it make any evolutionary sense to expect that in chimpanzees the situation would be totally different from that in humans and that social factors have no effect on chimpanzees' social cognition and cultural abilities? Can the socioecological environment be totally ignored when we study the ontogeny of sociocultural abilities? All these questions have been answered with a yes when only captive individuals are used to study sociocultural abilities. This strong Cartesian

attitude is predominant in some circles of experimental psychology (Boesch, 2007, 2010) and explains the popularity of captive studies of cognition and cultural abilities in chimpanzees and other primates. However, we must first question the validity of this answer, and three lines of evidence should make everyone careful about it.

IV. PRIOR EXPERIENCE AFFECTS SOCIOCULTURAL COGNITION

First, the majority of captive individuals have experienced serious deprivation and even trauma. Harlow and his team already produced convincing evidence of the terrible detrimental effects on the cognitive and social development of young primates who had been kept in isolation (e.g., Davenport & Rogers, 1970; Harlow & Harlow 1962). Some may argue that Harlow studied primates kept under extremely bad captive conditions and that present-day captive conditions are much more adequate (e.g., Tomasello & Call, 2008). It may be true that captive conditions have improved since the 1950s, but present-day captive conditions remain extremely depriving for chimpanzees. Over 54% of captive individuals from six accredited zoological institutions have been found to present stereotypical behaviors (Birkett & Newton-Fisher, 2011). A similar negative link between early social deprivation (e.g., the absence of the mother) and the development of socially attuned behavior has been observed in chimpanzees (Leeuwen et al., 2013) and bonobos (Clay & de Waal, 2013), whereby social play turns into aggression much more frequently among individuals raised without their mothers. Even today, most captive chimpanzees are still being human-raised after having been rejected by their mothers (e.g., Tempelmann et al., 2011).

The situation is similarly worrying for orphan chimpanzees growing up in sanctuaries in Africa, which are now being used more and more frequently for psychological experimental studies (e.g., Herrmann et al., 2007; Melis et al., 2009, 2011, 2013).¹ However, we should not forget that the chimpanzees in sanctuaries are all orphaned as a result of the bushmeat trade, observed in many countries in Africa; such orphans have all been forcefully separated from their mother and kept chained or in boxes in isolated African villagers

1. To increase access to a larger number of individuals and limit some of the negative impacts of totally artificial captive conditions, some research groups have started to work with orphan chimpanzees living in captive sanctuaries with access to large natural enclosures in Africa (e.g., Herrmann et al., 2007; Melis et al., 2009).

before being confiscated. Once they have been taken in by sanctuaries, they go through a resocialization and medical care program that can last many months, since they are badly damaged by the traumatic events of their young lives (see Claudine Andree at www.lolayabonobo.com and Arlette Jamart at www.helpcongo.org). Within a sanctuary, the orphans' recovery is still traumatic; despite the often formidable dedication of their caretakers, some 15% of them, owing to their earlier deprivation, die within the first months of being rescued. Furthermore, a detailed study has revealed that 58% of 168 chimpanzees in African and US sanctuaries have presented clear signs of depression and 44% had posttraumatic stress disorder, while only 3% and 0.5%, respectively, of 196 wild chimpanzees showed the same disorders (Ferdowsian et al., 2011, 2013). Since sanctuary chimpanzees' psychological health has been shown to be very similar to that of zoo chimpanzees (Wobber & Hare, 2011), this questions the validity of using captive chimpanzees to elucidate the cognitive and cultural abilities of the chimpanzee species.

Captive individuals are not only confined to enclosures of varying types and sizes but also facing very different social and ecological conditions. When these conditions are deliberately improved, with the presentation from an early age of a richer social environment—including extended interactions with humans and conspecifics of different ages as well as diverse possibilities to explore and manipulate artifacts, materials, and other aspects of their physical environment—an improvement in the cognitive performance of such captive chimpanzees is noted (see Bania et al., 2009; Bulloch et al., 2008; Furlong et al., 2008; Yocom & Boysen, 2011). For example, whereas deprived captive chimpanzees failed to understand the importance of the connectivity and intactness of a raking tool that could enable them to reach food (Herrmann et al., 2008; Penn & Povinelli, 2007; Povinelli, 2000), captive chimpanzees provided with enriched social and object-rich living conditions succeeded in the very same tests (Bania et al., 2009; Furlong et al., 2008).

Indeed, a direct comparison of the cognitive performance of wild and captive animal species exposed to exactly the same task has hardly ever been made, and captive studies have only sometimes attempted to replicate tasks observed in the wild. In one of those rare studies, capuchin monkeys' understanding of the physical properties of hammers with which to crack open nuts has been directly compared, and the wild capuchins clearly outperformed the captive ones in the number of physical properties of the tools they could consider in selecting such hammers (Visalberghi et al., 2009). Two of three

captive capuchin individuals failed to consider weight in selecting a hammer with which to crack open hard nuts (Schrauf et al., 2008), while all eight wild individuals considered the weight in addition to the material of the hammer with which they could crack the nuts efficiently (Visalberghi et al., 2009).

These observations confirm that the social and ecological environment plays an essential role and that when individuals are removed from such an environment, there are widespread consequences for the development of these animals' behavior and social cognition.

The social is defined both "within and between groups," and it is this notion that cannot be reconstructed among captive animals. Sure, captive individuals are today mostly kept in groups. However, those human-made associations do not correspond to a "social group." A social group among humans and among animals is not only a long-lasting association of individuals but also a stable network of kin of different levels of relatedness that have grown up together and are constantly facing "outsider" groups. It is through this confrontation with outsiders that individuals within the same social group develop the sense of "belonging" that is so important to their cultural identity. It is this sense of group belonging that is at the core of cultural transmission mechanisms, such as imitation, teaching, and social norms (see Harris & Corriveau, 2011; Over & Carpenter, 2012, 2013). These mechanisms have been identified by some psychologists, anthropologists, and philosophers as essential for the development of culture (e.g., Boesch & Tomasello, 1998; Laland & Janik, 2006). However, without this sense of group belonging, cultural transmission loses its significance, and we should not expect it to be prevalent or preferred to other learning mechanisms.

V. CAPTIVE LIVING CONDITIONS DIFFER

A second aspect of captive studies that renders them problematic for the elucidation of cultural abilities is that they have yielded many conflicting conclusions. Table 1-1 shows that with regard to most cognitive abilities suggested to contribute to the acquisition and transmission of culture—such as tool use, imitation, altruism, and understanding of others—captive studies reach conflicting conclusions. As a consequence, many scientists have been confused by the contradictions prevailing in the animal culture debate between the different sorts of knowledge gained from captive experiments as opposed to natural observations. For example, it is difficult to draw conclusions from the fact that groups of wild chimpanzees in the Tai Forest use

TABLE 1-1: Comparisons of Cognitive Performance in Chimpanzees Under Different Experimental Paradigms Where Internal and External Validity Has Been Evaluated

Test type	Cognitive ability tested	Results	References	Validity		Problems with validity	Results with more validity	References
				Internal	External			
Tool selection ¹	Causality	Failed	Povinelli et al., 2000 Povinelli, 2000	Yes	None ^b	Absence of prior	Success	Furlong et al., 2008 Bania et al., 2009
Trap-tube test ²	Causality	Failed	Limongelli et al., 1995 Visalberghi et al., 1995 Povinelli, 2000 Martin-Ordas et al., 2008 Horner & Whiten, 2007	Limited	None ^a	Many factors considered ²	Not done	Silva et al., 2005 Silva & Silva, 2006
Sharing test ³	Altruism	Failed	Silk et al., 2005 Jensen et al., 2007 Vonk et al., 2008	None	Limited	Complex apparatus/ time delay	Success	Horner et al., 2011 Smith & Silberberg, 2010
Artificial fruit test ⁴	Imitation	Failed	Whiten et al., 1996 Tennie et al., 2006	Limited	Yes	Many factors considered	Not done	Horowitz, 2003
Visual attention ⁵	Understanding of others	Failed	Povinelli & Eddy, 1996 Povinelli, 1999 Penn & Povinelli, 2007	Yes	None ^b	Absence of prior social experience	Success	Bulloch et al., 2008 Thomas et al., 2008

Pointing test ⁶	Understanding of others	Failed	Barth et al., 2005 Tomasello et al., 1997 Brauer et al., 2006	Yes	None ^b	Absence of prior social experience	Success	Lyn et al., 2010
Number pointing ⁷	Working memory	Chimpanzee > human	Inoue & Matsuzawa, 2007	None	None ^a	Absence of prior experience	Chimpanzee = Human	Silberberg & Kearns, 2009

Source: Boesch (2012). Wild cultures: a comparison of chimpanzee and human cultures (p. 211). Cambridge, UK: Cambridge University Press. Note that many studies listed in column 4 have been used to substantiate claims of "human uniqueness."

Internal validity: Yes, data have shown that the focus of the test was ambiguous or not natural. Limited, when adult human subjects considered many factors although the experimenter had designed the test considering only one factor. None, when the test apparatus was too complex to be understood by the subject.

External validity: None^a, when no equivalent of the test is found in real life, None^b, when the subjects had no prior knowledge/experience owing to impoverished living conditions.

¹ Tool selection: The test was about selecting between two different tools to gain access to food. Typically one tool was either a stick on which the food was placed while the other tool was either placed near the food or had the food on it but was broken in the middle so that only one of the tools could be used to obtain the food. However, in the studies on the left; the chimpanzees chose at random, while; in the studies on the right; they selected the functional tool significantly more frequently.

² Trap-tube test: In the classical version of the test, a food reward was placed in a transparent tube and a stick was provided to be used to push the food out of the tube for the subject to eat. The test resulted from the fact that a trap was present in the tube, and if the food was pushed toward the trap, it would fall into it and no food could be obtained. Tests done with humans, studies on the right, showed that contrary to the assumptions of the experimenters on the left, the test was ambiguous. It was not clear to adult humans what they were expected to do and which aspects of the test were relevant; thus they were just as unsuccessful as the chimpanzees.

³ Sharing test: Subjects could obtain a food reward when they pulled a handle toward them. However, they had a choice of two handles, one that made food accessible to them only and a second that would also provide the same amount of food to a second animal in a nearby cage. Since this implied no cost to the subject, it was suggested that this test would reveal prosocial tendencies in the tested individual. The studies on the right showed that additional factors, such as the complexity of the food delivery machine or the time to access the food directly, affected the prosocial tendencies of the chimpanzee individuals.

⁴ Artificial fruit test: A food was hidden in a box that could be opened in two different but equally efficient ways. A demonstrator showed only one of two ways to open it, and the subject's tendency to follow the demonstrator's example was measured. The study on the right, done with adult humans, revealed that it was not clear to the subjects what exactly in the test should be copied, and they performed at the same level as chimpanzees tested in the left.

⁵ Visual attention: In this classic experiment, two human observers were present when a piece of food was hidden, and the chimpanzee subject could beg it from them. However, one of the observers could not have seen the act of hiding as he either had a bucket over his head, a blindfold on his eyes, or was facing the opposite way. The chimpanzee subjects tested in the studies of the left begged equally often to both human observers. By opposition, in the studies on the right, the chimpanzees gestured significantly more often toward the one that had seen the hiding.

⁶ Pointing: In another classical experiment, the chimpanzee subject sees the food and then an experimenter points to a place where the food had been placed behind one or more visual obstacles. In the experiments on the left, the chimpanzees had difficulties in prolonging the information coming from the pointing across such obstacles. Here again the study on the right showed that chimpanzees from another captive group could solve the problem and found the food.

⁷ Number remembering: On a computer screen the numbers 1 to 9 are presented in a random position for a few seconds; once they disappear, the subject is asked to point to all of them in increasing order. One young chimpanzee was more efficient than adult humans in the study, cited on the left, while in the one on the right, which gave more experience with the tests to humans, it was found that humans performed equally well.

complex cooperative tactics in hunting for arboreal monkeys (Boesch 2002, 2012; Boesch & Boesch, 1989), yet captive chimpanzees in the Leipzig zoo or in Japan have difficulties in jointly pulling a rope to access out-of-reach food (Hirata & Fuwa, 2007; Melis et al., 2006). Table 1-1 provides more examples of such contradictory conclusions reached by various studies working with captive chimpanzees.

An illustrative example of the dominant confusion can be seen in the following citation: “The proposal here is that nonhuman primate (and other animal) culture is essentially individualistic, or maybe even exploitative.... In contrast, human culture and cultural transmission are fundamentally cooperative” (Tomasello, 2011, p. 5). In truth, Tomasello should have said “*captive* nonhuman primate culture,” as his complete work and his references concentrate on individuals that have lived for years in captivity. Therefore Tomasello’s hypothesis may have much less value because it is contradicted by the many observations of frequent cooperation among wild chimpanzees, either when hunting in coordinated groups to capture a single arboreal prey (Boesch, 2002, 2012) or in defending their territory against intrusions by very aggressive neighboring groups (Mitani et al., 2002). In an attempt to convince his readers of the stronger explanatory power of captive studies over wild observations, Tomasello (2011) explains that if Tāi chimpanzees hunt in a group, they do not do so with a joint goal, as humans would do. He continues by saying:

This interpretation of chimpanzee hunting is supported by what happens after the kill. When a group of chimpanzees captures a monkey, the participants in the hunt typically all get meat—more than late-arriving chimpanzees who did not participate in the hunt. However, recent research by Gilby (2006) elucidates the basically individualistic mechanisms involved in this “sharing.” Gilby notes, first of all, that chimpanzees who possess meat after the kill often attempt to avoid others by stealing away from the kill site, by climbing to the end of a branch to restrict the access of other chimpanzees, or by chasing beggars away. (Tomasello, 2011, p. 8)

Regarding the first part of this quotation, it is not true that only hunters are present during the hunt and just after the capture; many chimpanzee observers are present during the hunt. It is the rules of meat sharing that favor good hunters over average hunters, and those, in turn, are favored over passive observers of the hunt (Boesch, 1994, 2002). In the second part of the quotation, Tomasello confuses observations of Gombe chimpanzees

(Tanzania, East Africa), which are known to be mainly solitary hunters and do not share meat according to their contributions during the hunt, as do the Taï chimpanzees in Côte d'Ivoire, West Africa (see Boesch, 2002, 2012; Boesch & Boesch, 1989). Social groups that live in different ecological environments adopt solutions that are group-specific, and this has been amply documented in the case of chimpanzees (Boesch, 2003, 2012; Whiten et al., 1999).

Thus a large part of the presence of animal culture revolves around the importance of the “social” on one side and the “ecology” on the other. From tradition and training, biologists and ethologists emphasize these two notions (Boesch, 2012), while classical experimental psychologists, instead, concentrate on the design of the experimental procedures and neglect the social and ecological aspects. Being a biologist myself, in the rest of this chapter I highlight some aspects of the culture of wild chimpanzees (see Table 1-1).

In the following I first review some of illustrative evidence for culture among wild chimpanzees and then provide more details on newly acquired observations of both cumulative cultural traits and symbolic culture.

VI. EXPERIENCING CULTURE IN NATURE

Culture is defined by many scholars as a set of social behavioral traits that are learned from and shared with group members—traits that set them apart from members of other social groups (e.g., Barnard, 2000; Boesch, 1996; Kuper, 1999; Whiten et al., 1999). The preeminence of the social group in the concept of culture has always been stressed by anthropologists and is at the core of the concept in human sciences. It is similar for animal culture, and to understand this we must realize that our knowledge of chimpanzee populations is still extremely fragmented; we have direct observations from only a very small subset of all chimpanzee populations that have existed or still exist in Africa (Figure 1-1).

For culture to develop, the socioecological environment is essential. “All cultural learning takes place within the specific learning environment that prevails in that culture” (Boesch, 2012). In Taï chimpanzee culture, *Coula* nuts are seen as food and wooden and stone materials found in the forest as potential tools. In looking for a hammer, for instance, a Taï chimpanzee can “mentally transform” a branch lying on the ground into a good hammer, independent of its real shape (Boesch, 2012). This *subjective reality* is at the base of flexible tool use, which infants must learn before starting to practice—in this case, nut cracking (Boesch, 2012). This inducement of mental transformations from objective perception is driven by the mother and other group

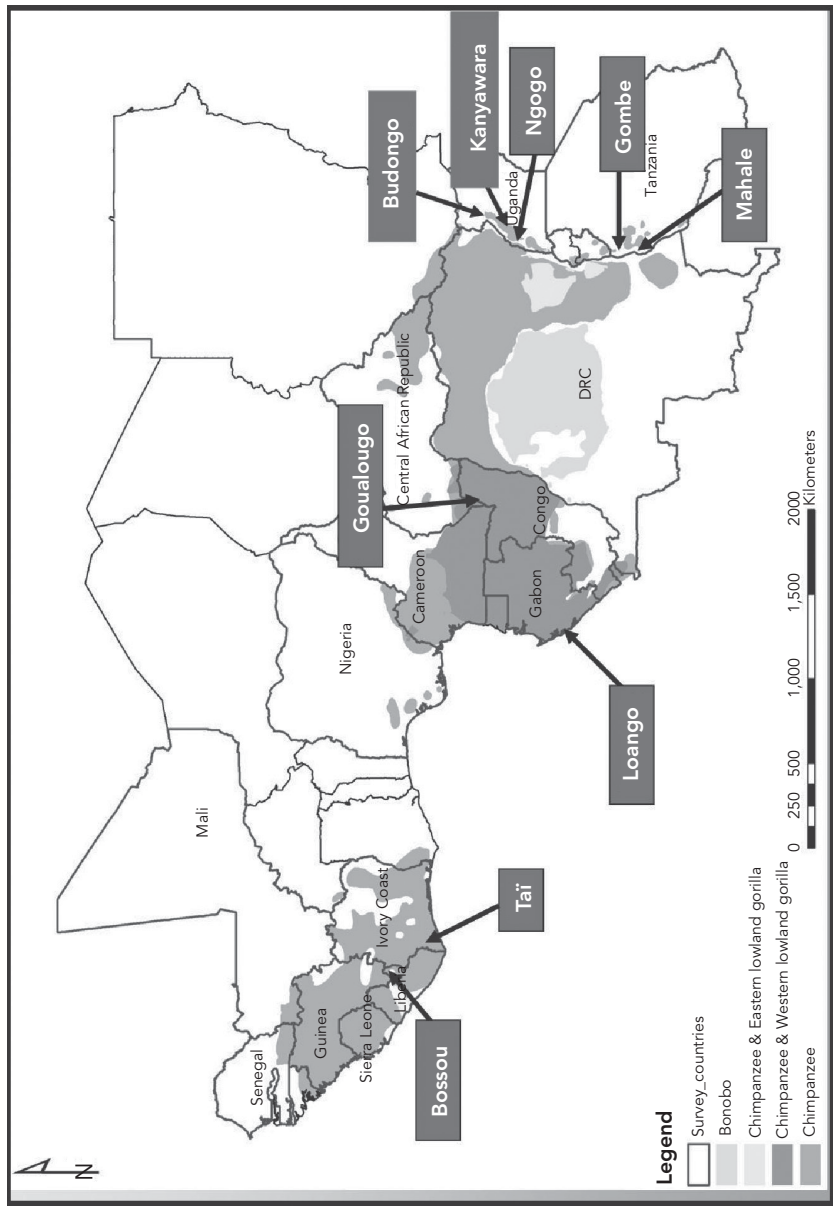


FIGURE 1-1: Culture in chimpanzees: distribution range of chimpanzees in tropical Africa with the main long-term study sites and their names (see text for examples of cultural behavior in those populations). Wild chimpanzees are found only in Africa, and although they are badly threatened by human activities, they are still found in 14 African countries ranging from dry savannahs, as in Senegal and Mali, to high-altitude regions, as in Rwanda, to the deep rainforest in Côte d'Ivoire, Gabon, Congo, and the Democratic Republic of the Congo.

members; infants are constantly exposed to the various ways in which objects are used. They will then begin to manipulate branches according to the subjective reality they have acquired from their passive but intense observations (Boesch, 2012). As I have argued, “Copying the effect on objects, like the breaking of a nutshell when it is pounded by hard hammers, and using the same objects—that is, the stone or wooden hammers—will be important guides for the faithful reproduction of material skills with specific technical constraints” (Boesch, 2012). Gombe infant chimpanzees, in Tanzania, have never seen their mothers or other group members use a stone or a thick branch as a hammer, as nut cracking is absent in their natural behavior repertoire; it is therefore difficult for them to develop a subjective reality that would allow them to see stones as potential hammers.

Such cultural influences have nicely been illustrated in a field experiment performed to see how chimpanzees would access honey in a hole if they needed to use a tool (Gruber et al., 2009). Budongo chimpanzees in Uganda used only leaves to access the honey, while the Kanyawara chimpanzees used sticks to do so. The most obvious explanation was that individuals resorted to solutions according to their group-specific cultural habits: Budongo chimpanzees have never been seen to use sticks as tools, but only leaves, whereas Kanyawara chimpanzees select both leaves and sticks to be used as tools. Thus the subjective reality of tools and prior experience is group-specific, and this directly affects the solution adopted by individuals trying to access honey.

One of the most decisive discoveries about culture among chimpanzees was the large variability in the way individuals from different social groups performed different daily actions, for which no genetic or ecological explanation could be found (e.g., Boesch, 1996, 2003, 2012; Whiten et al., 1999, 2001). Below I give some examples to illustrate the arbitrariness and social normative dimension of the behavior.

VII. HOW DO CHIMPANZEES CRACK NUTS?

In 1970, two reports suggested that chimpanzees in the Taï forest of Côte d’Ivoire could crack wild nuts by using natural hammers (Rahm, 1971; Struhsaker & Hunkeler, 1971), reinforcing a suspicion raised from a first report relating a direct observation of a chimpanzee using a hammer to crack oil palm nuts in Liberia (Beatty, 1951). Some 10 years later, I and my wife, Hedwige Boesch, arrived in the Taï forest, Côte d’Ivoire, in order to confirm the presence of this complex tool-using behavior. We also intended to test how this fitted with ideas prevalent in some

circles that it is an adaptation to a savanna environment, which forced our ancestors to adopt “human-like” behavior patterns, such as tool use, tool making, and cooperation. We started by habituating the chimpanzees to our presence while at the same time making first observations about this, to the scientific world, still unknown chimpanzee behavior. Because chimpanzees are hunted for meat by humans all over Africa, any research projects must first invest in overcoming these animals’ natural fear of humans and, with time and patience, gaining their trust (the “habituation” process). Over the years, we habituated four neighboring chimpanzee communities within the Taï study site (Boesch, 2009, 2012). We started our study with the North group in 1979 and, in an attempt to understand intergroup interactions as well as the dispersal of individuals, we then habituated their neighbors to the south in 1995. However, it turned out that we had actually habituated two communities there, the Middle group and the South group. With a continuing decline in the number of chimpanzees in the North group, we then started, in 2005, to habituate the East group, neighboring the South group. All of these groups are neighbors and have regular intergroup encounters (see Boesch, 2009, 2012).

We were quickly able to confirm that chimpanzees in the Taï National Park crack five different species of nuts on a daily basis for a minimum of eight months per year (Boesch & Boesch, 1981, 1983, 1984). This tool technique is extremely beneficial, as a chimpanzee can gain over 3,000 calories per day from nut cracking (Günther & Boesch, 1993). In order to understand the distribution of nut-cracking behavior among the chimpanzees of Côte d’Ivoire, we performed a national survey and controlled 35 locations for the availability of the nuts, the tools, and nut-cracking sites (Boesch et al., 1994). What we found strongly supported a cultural explanation: all chimpanzee populations living west of the Sassandra River, running north to south in the western part of the country, cracked the same species of nuts as did chimpanzees in Taï forest and with the same kinds of tools, whereas all chimpanzee populations living east of the Sassandra River did not crack these nuts, despite the fact that all the nuts were available, as were the potential tools (Boesch et al., 1994). If nut cracking had been a purely adaptive response to ecological conditions, we would have expected chimpanzees on both sides of the Sassandra River to be cracking these highly nutritional nuts. This was not the case, which therefore supports a cultural explanation.

The story turned out to be even more complex in that, even within the nut-cracking regions, cultural variations were observed. At the beginning of the *Coula* nut season, when the nuts are hardest, the chimpanzees in our three study groups cracked the nuts mainly with small stone hammers. As the season progressed and the nuts became easier to crack, the chimpanzees in the North and East groups more often selected wooden hammers, which are more abundant in the forest, while the South group continued to select stone hammers, although they had the same access to wooden and stone hammers as the two other groups (Luncz et al., 2012). Surprisingly, females, which disperse among groups just before maturity—at which point they are already skillful nut crackers—adopted the tool preference of their new groups within a few weeks after migration.

This tendency for neighboring groups to adopt different cultural sets of behavior has been seen repeatedly among the Taï chimpanzees (see Figure 1-2) (Boesch, 2003, 2012). I detected many differences among the three communities we followed. For example, a member of the North group would push a whole arm into a termites' nest to extract some handfuls of grubs, while a member of the South group would push only a forearm into a nest and extract a single handful at most. Similarly, only the South group chimpanzees would eat the pith of the herbal plants found in swamps throughout the Taï forest, and only members of the North group would eat the abundant *Thoracotermes* termites. In addition, members of the South group would eat the *Strychnos* fruits only when they were fresh, while those of the North group ate them only when they were decayed. More differences like these are now emerging with the habituation of the East group, which seems to also have its own subculture within the Taï forest. For example, they use wooden clubs as hammers, like the North group, but they select much longer wooden clubs than those used by the North group. They also knuckle-knock in a courtship behavior, like the North group but unlike the South group (Luncz et al., 2012, Luncz & Boesch, 2014).

Our observations confirmed that among chimpanzees, cultural differences persist between neighboring communities in the Taï forest despite the regular transfer of females. In large communities with many adult males, which are attractive to young females, we observed the immigration of a new young female about once or twice per year. The more recent observations of differences within a cultural trait—the nut-cracking behavior—led to the question of whether this is a specific instance of a complex tool-using behavior or whether it is also seen among other cultural traits in chimpanzee

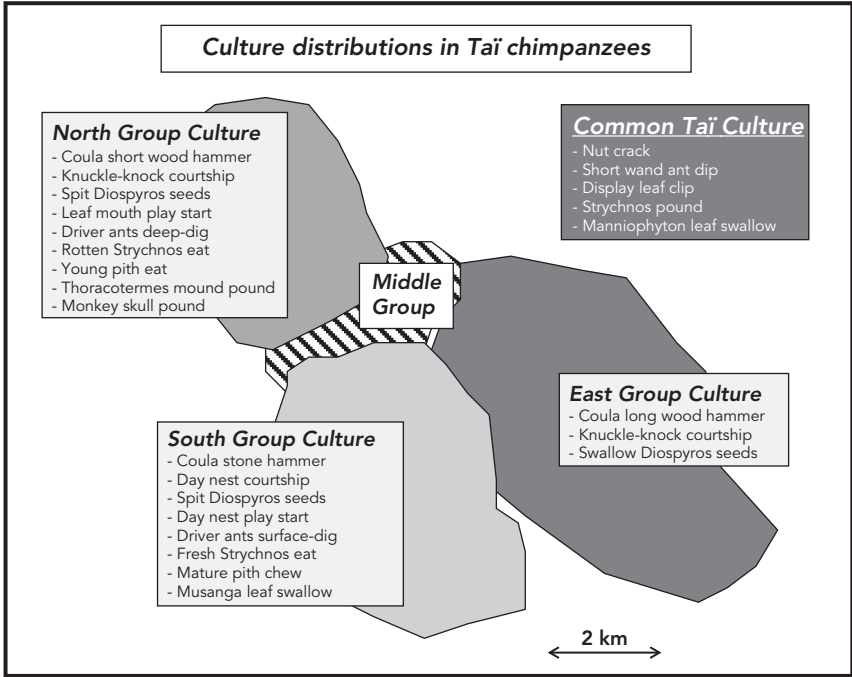


FIGURE 1-2: Distribution of cultural differences between three neighboring communities in the Tāi forest (Boesch, 2012) including a list of some cultural traits shared by all three communities. The territories of the communities are represented with different gray patterns, with lists of specific cultural traits that distinguish them from one another. The Middle group remained exceptionally small during the entire observation period and we have only limited observations on it.

groups and is therefore a more general ability. I now turn to ant consumption to illustrate this.

VIII. HOW DO CHIMPANZEES EAT ANTS?

In Gombe, all chimpanzees have been seen to use sticks 66 cm long on average. When a chimpanzee places one end of such a stick in the entrance of an ants' nest, the soldier ants bite the stick and climb onto it. When about 30 cm of the stick remains outside the nest, the chimpanzee rapidly turns it upside down, seizes it strongly with the other hand placed in a fist below the ants, and sweep the stick through the fist, collecting all the ants in a heap. The mass of furious ants is then transferred into the chimpanzee's mouth, there to be chewed vigorously (Goodall, 1986; McGrew, 1974). The chimpanzees of the Tai Forest eat driver ants by using sticks that are 24 cm long on average,

and once the ants are about 10 cm up the stick, the chimpanzee places the extremity with the ants directly into its mouth, then also chewing them vigorously; but only one hand is used in this maneuver (Boesch & Boesch, 1990). In this case we are in the presence of one particular predator, the chimpanzee, eating one particular prey, driver ants, using tools of different lengths and two different hand techniques. This is a case of cultural traits having different forms (Boesch 1996).

Two points must be added to this discussion. First, both the Gombe and Taï ant-harvesting techniques work well; I tested them myself at both sites (Boesch & Boesch, 1990). Taking a thin wooden stick, as chimpanzees do, I inserted it into the entrance of ants' nest. Trying both the Gombe and the Taï techniques, I noticed that the ants' nest structure was similar enough at both sites to allow the efficient use of both techniques. Because the nest structures and the ants' nests are similar at both sites, we can exclude ecological explanations for the differences in the techniques used by the Gombe and Taï chimpanzees. Second, the Gombe technique is about four times as efficient as the Taï technique (Boesch & Boesch, 1990); thus if ant dipping were only an adaptation to an ecological problem, we should expect all chimpanzees, over time, to adopt the Gombe technique. However, the chimpanzees of both groups strictly followed the group-specific techniques they had seen for decades, thus supporting the concept of a cultural habit that the group members had adopted (Boesch, 1996, 2012).

Later, a study of the Bossou chimpanzees in Guinea showed that individuals there would select sticks of different lengths as a function of the lifestyle of the driver ants they dip for; longer wands for dipping at the nests and shorter ones for dipping them along roads (Humble & Matsuzawa, 2002). Could it be that the lifestyle of the ants was driving the length of the tools used by all chimpanzee populations and that, therefore, it had nothing to do with a cultural habit? To address this question, we developed a collaborative project for the Bossou and Taï chimpanzees, and we could clearly show that within Bossou, the aggressiveness and speed of the ants played a clear role in explaining the length of the tools selected by the chimpanzees. However, none of the differences seen between Bossou and Taï chimpanzees could be explained by the ant-nest structure or behavioral differences of the ants, thus supporting the cultural explanation (Möbius et al., 2008).

As illustrated in the case of nut cracking and ant dipping, cultural differences in chimpanzees go much beyond the mere presence or absence of a trait but directly affect the form and context of the use of such traits, for

which, moreover, we observed a very high level of fidelity in the performance within each group (Luncz & Boesch, 2014). Now I want to turn to two cultural aspects recently considered to be two of the domains in which human cultural abilities were clearly different from those of the apes: cumulative cultural evolution and symbolic culture. These two domains of culture have recently been especially debated. Both are obvious traits of human culture and are predominant in all human cultures around the world (Ford, 1962; O'Brien et al., 2003, 2010; Shennan, 2000). They have been suggested to be absent in chimpanzees and other animal species (Boyd & Richerson, 1996; Richerson & Boyd, 2005; Tomasello et al., 1993); but with new studies being done with new chimpanzee populations, we have gained new evidence suggesting that a similar process of cultural evolution occurs among chimpanzees. Similarly, detailed comparisons of chimpanzee populations suggest the presence of symbolic culture, previously suggested to be unique to humans, because it was thought to require language.

IX. CUMULATIVE CULTURAL EVOLUTION AMONG CHIMPANZEES

Many human cultural artifacts seem too complex to have been invented at one time by one individual; therefore many cultural products are thought to result from a cumulative evolutionary process (Boyd & Richerson, 1985). Cumulative cultural evolution, by which one individual improves on a socially acquired cultural trait and this new innovation is then transmitted to other group members who might, at a later time, improve on it further, has gained special status, since it was proposed to be at the base of the cultural complexity we see in many human cultural products (Ford, 1962; O'Brien et al., 2001). It is the successive accumulation of changes by different individuals that characterizes this cumulative process.

In humans this process has been suggested to have led to many observed cultural changes, such as changes in the shape and size of pottery, carpet weaving, basketry, and projectile points (e.g., Beaune, 2004; Ford, 1962; Jordan & Shennan, 2003; O'Brien et al., 2001; Shennan, 2000; Tehrani & Collard, 2002). Psychologists, who sometimes call this process the "ratchet effect," have argued that only humans attain enough faithfulness in their copying of others' innovations to make such a process evolutionarily beneficial (e.g., Boyd & Richerson, 1996; Galef, 1992; Tennie et al., 2009; Tomasello, 1999).

Although archeologists have very nicely shown evidence for the accumulation of cultural changes, the definition of a cultural trait remains

mainly descriptive and is often stated without any direct connection to the functionality of such changes. Therefore it is difficult to understand why two similar pots, one with a 2-cm neck and another with a 3-cm neck, should be regarded as two distinct cultural traits (e.g., Ford, 1962). To circumvent this issue, I suggest that we consider only changes that result in a measurable improvement in efficiency or a change in function. To clarify, below are five suggested criteria that I believe must be considered before cumulative cultural evolution can be claimed in any animal species, including humans:

1. *Heritable continuity*: Accumulation of changes within one technical chain or lineage (technical, as most archeological work uses artifacts to infer cultural changes).
2. *Functional efficiency*: Each level within the technical chain should represent a technical improvement in completing the task.
3. *Temporal increment*: Accumulation of changes should happen over a time period that excludes successive improvements by the same individual.

Furthermore, when no archeological data are available:

4. *Nested distribution*: The distribution range of the more complex technical level should be more restrictive than that of the simpler one.
5. *Concomitant use*: Different technical levels should be observed concurrently.

I am fully aware that, as seen in humans, the accumulation of changes could also lead to the simplification of a task, or that successful levels could spread more widely and therefore contradict the nested distribution criteria. But for comparative purposes, we need criteria that can be compared between species, including those for which no archeological data are available. The best example of such a cumulative cultural process in animals comes from New Caledonian crows, which, over large areas of the island of Grande Terre, use a stepped tool made of a *Pandanus* leaf to extract grubs from branches. But in a smaller area in the southernmost part of the island, the crows were seen to fashion tools with more different shapes (Hunt & Gray, 2003).

In our own research on tool use among chimpanzees (Boesch et al., 2009; Sanz et al., 2004; Sanz & Morgan, 2007), a cumulative cultural

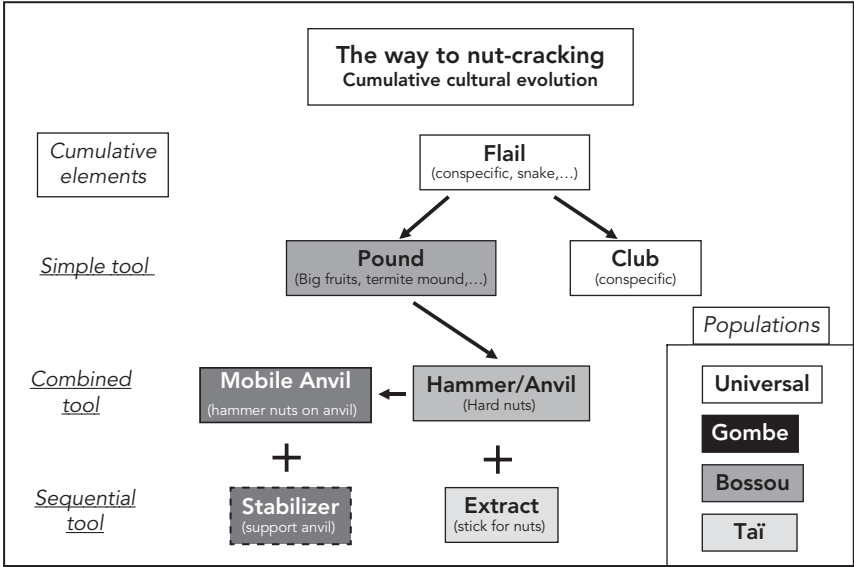


FIGURE 1-3: Cumulative cultural evolution leading to the nut-cracking technique (Boesch, 2012). Here a behavior seen in all chimpanzee populations, flailing, is elaborated through the successive addition of new elements. First, a simple tool is integrated into the pounding movements, as seen in the Gombe, Bossou, and Taï chimpanzees (see the simple tool line). Then the introduction of a second tool led to the invention of combined tool use, as seen in the Taï and Bossou chimpanzees (see the combined tool line). Combined tool use occurs when at least two tools are used at the same time (e.g., an anvil is selected and used at the same time as a hammer). For each step of the accumulation process seen in a given population, the different resources gained or involved are listed. The stabilizer box is dashed, as it has been observed only twice so far in the Bossou chimpanzees.

evolutionary process can be observed in some technological chains, as illustrated in Figures 1-3 and 1-4 (see also Boesch 1993, 2003; Boesch & Tomasello, 1998; Matsuzawa, 2001). In accounting for all the field observations made among different chimpanzee populations, it seems likely that nut cracking resulted from an accumulation of progressive changes, as illustrated in Figure 1-3 (see Boesch, 2012, for a more complete explanation). These improvements center on the increased complexity of objects included in the hitting movements. First, flailing of insects, conspecifics, or snakes with leafy branches still attached to a sapling has been reported among all chimpanzee populations, as has the clubbing of playmates or social competitors with wooden sticks (see white boxes in Figure 1-3). One innovation was added to this universal behavior of hitting with attached leaves by the Gombe and Taï chimpanzees, who pound hard fruit directly against tree

trunks or roots to break them open. This is similar to clubbing, but in this case the fruit is held in the hand and serves a different purpose, namely to access food inside the hard exterior (see Figure 1-3). A second innovation was seen in West Africa, where it is now a hammer that serves to pound the hard fruit, which is first placed on a hard surface. From this last innovation, two parallel additions can be distinguished, both examples of sequential tool use: the Taï chimpanzees added a stick in order to extract nut remains embedded in cracked shells, and the Bossou chimpanzees added mobile anvils on which they placed the nuts. A final innovation, which has been observed a few times among the Bossou chimpanzees, was the placement of a stone under the mobile anvil to stabilize it before the nut was hit with the hammer (see Figure 1-3). For each step in the cumulative process, the tool technique improved access to a given food resource and was used effectively in at least one chimpanzee population, but it was later elaborated for a new food source. Thus, for nut cracking, the observation is compatible with a

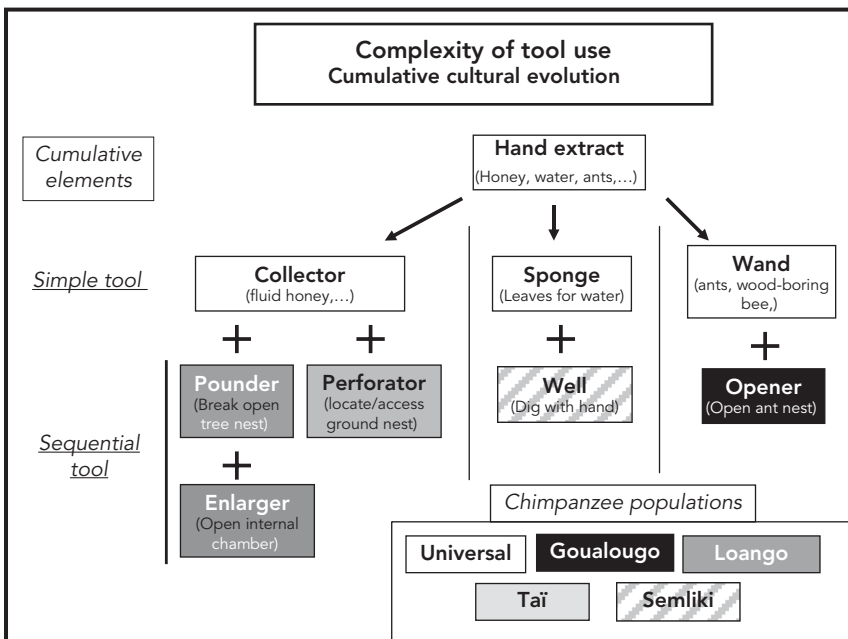


FIGURE 1-4: Cumulative cultural evolution in chimpanzees leading to sequential tool use (Boesch, 2012). All chimpanzee groups have been seen to extract different objects or food types from holes with their hands (called here "universal" in white). From this, a cumulative cultural process is developing and leading to more complex techniques in three different kinds of technical chains in wild chimpanzees, each of which is seen in one or more different chimpanzee populations.

cumulative cultural process developing from a universal, simple technique (Boesch, 2012).

Another tool-use technique also suggests a cumulative cultural process—that is, the sequential use of tools in order to extract honey extraction, which has been described among different populations of chimpanzees in Central Africa (Boesch et al., 2009; Sanz & Morgan, 2009). Reconstructing past behaviors is always challenging because behavior does not leave fossil remains. All chimpanzee populations have been seen to extract different types of food from within holes with their hands, but only a few populations have added a level of complexity to this simple behavior by using a tool to access food in such holes where access is difficult (see left side of Figure 1-4); see Boesch, 2012, for further explanation). This is the case for the Tai, Loango, and Goualougo chimpanzees, who all extract honey from beehives with one type of stick (see second box from the top in Figure 1-4).² From observations of the Tai chimpanzees, we know this is most successful with beehives in fallen trees, enabling easy access to the honey. To access honey from thickly protected beehive species, we found that a thick branch was incorporated into the behavioral sequence to make a hole by pounding strongly on the protective barrier surrounding the intact nest's entrances. We have seen this in Goualougo and Loango, where the chimpanzees use heavy pounders to break open nests before beginning to use the thinner extraction tools. Finally, for the deeper and more structured nests of the large stingless bees commonly found in Central African forests, chimpanzees add a third tool type to their tool set to open chambers within the nests. Alternatively, for underground hives of stingless bees, the Loango chimpanzees did not include a pounder in the sequence but instead incorporated a stick to perforate the ground while searching to locate the nest. This was also seen among the Goualougo chimpanzees, not in attacking beehives but to locate underground termites' nests (left side of Figure 1-4) (Sanz et al., 2004). Hence a cumulative process of cultural technical improvement is strongly suggested by the comparison of tool use among different chimpanzee populations (Boesch, 2012).

2. For the honey extraction technique, I mention only the Loango and Goualougo chimpanzees here, since we have directly observed the behavior in these groups. We should not forget that tool remains found in association with beehives have suggested sequential tool use among different populations of chimpanzees throughout the central African range of the species.

Further, we see in Figure 1-4 that beginning with the universal behavior of accessing food in holes directly with the hand, all chimpanzee populations have, as far as we can tell, gone on to add leaves to make a “sponge” in order to extract water from such holes (central part of Figure 1-4). But only in Semliki, Uganda, were chimpanzees seen to first dig a well from which they could then extract water with the help of the sponge. In a parallel process to honey extraction, some chimpanzee populations have added different types of tools to the universal technique of dipping for ants (see right part of Figure 1-4), while only the Goualougo chimpanzees have been seen to first use a second tool to open the nest of the driver ants before dipping for them with the wand.

Thus, although we found convincing evidence of a cumulative process in some chimpanzee cultural products, cumulative cultural evolution has recently been proposed by some psychologists to be a central element in distinguishing humans from other animal species (Galef, 1992; Heyes, 1994; Tennie et al., 2009; Tomasello et al., 1993). Their argument is that this process can work only when the actions are copied in the most faithful way, and since only humans are capable of imitation and teaching, it is suggested that cumulative culture is seen only in humans. As a result, these psychologists will probably greet the scenarios I have presented in Figures 1-3 and 1-4 with some skepticism. However, the ethnographic comparison of the techniques used among different chimpanzee populations leaves no doubt that a recurrent increase in the complexity of cultural traits based on the addition of new behavioral elements exists. Obviously, the alternative explanation would be that each step has been invented totally independently from any other. However, that would not explain the fact that within each technical lineage, the simpler form has a much wider distribution range than the more complex one, suggesting that the latter originated from the former. Furthermore, each of these steps has been seen to increase the performance of the previous steps under the conditions in which it is performed (see Figure 1-4). For example, a perforator improves the technique of using a collector in searching for underground beehives; it also allows for cleaner drinking water than would the use of only a sponge in the rivulet water. Finally, a stick enables its user to extract more of a nut kernel after the nut has been cracked with a hammer than could be had by eating only the bits made accessible by the pounding.

The predisposition of humans to innovate and cumulate changes might indeed be much more important than in any other species, as is so evidently