Proceedings of the British Academy, **88**, 251–268

The Emergence of Cultures among Wild Chimpanzees

CHRISTOPHE BOESCH
Institute of Zoology, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

Keywords: chimpanzees; culture; imitation; social learning; social norms.

Summary. Culture has been granted by primatologists to the chimpanzee, on the base of the many population-specific behaviour patterns they possess. Psychologists tend to disagree arguing that individual learning constrained by ecological factors could produce the same results. After setting up some rigorous criteria to differentiate between these two opposite positions, I show that social canalization, including imitation, is important in explaining the acquisition of nut-cracking behaviour in wild chimpanzees. Then, I argue that a culture requires not only a social learning process to produce a faithful transmission of information, but also a mechanism that guarantees the permanence of the information between transmission events. Leaf-clipping, leaf-grooming, knuckle-knocking and a symbolic drumming communication system are proposed to be examples of behaviour patterns fixed within chimpanzee populations by social norms. The stringent criteria that have to be fulfilled to grant a behaviour cultural properties in an animal species strongly limit the possible candidates. Despite these restrictions, the repertoire of the wild chimpanzee includes many cultural behaviour patterns.

IS CULTURE UNIQUE TO MAN?

THE DEBATE ABOUT WHAT DISTINGUISHES MAN from the other animal species goes on for centuries. And the fact that Darwin proposed in his theory of evolution that human beings had a common ancestor with other primates did not ease the quest for what constitutes our uniqueness. In parallel with the progress of our understanding of the evolutionary processes, paleoanthropologists have discovered an impressive series of early human species showing that hominization was a gradual evolution from very chimp-like ancestors. Therefore, there has been an increasing tendency to search for clear-cut differences between human and other primates in the behavioural domain: tool use and tool making, food sharing and co-operation among others have been proposed to characterize man (Isaac 1978; Johansen & Edey 1981; Leakey 1980; Washburn 1978). But recent observations revealed that wild chimpanzees possess these behaviour patterns too (Boesch & Boesch 1990; Goodall 1986; Nishida 1987), showing that they are not exclusively part of the hominization process (Boesch-Achermann & Boesch 1994). As a consequence, culture and some cognitive abilities underlying it have been proposed to be uniquely human (Galef 1990; Tomasello 1990; Tomasello *et al.* 1993a; Visalberghi & Fragaszy 1990).

Biologists are also interested in culture as it is one of the mechanisms in nature allowing the transmission of information between individuals (Bonner 1980; Maynard-Smith & Szathmary 1995). Contrary to the more common genetical transmission of information, cultural transmission is not genetic. Potentially this non-genetical mechanism could be much quicker than genetic transmission, first because transmission is not dependent upon the reproductive events but could occur at any moment in the lifetime of an individual, and second, because innovation is not dependent upon a rare event such as mutation, and can occur much more often. It is this rapidity that has been proposed to be responsible for the high human social and behavioural diversity (Tomasello *et al.* 1993a; Segall *et al.* 1990).

The chimpanzee challenge

Chimpanzees have been proposed to possess culture (Boesch & Boesch 1990; Goodall 1973, 1986; McGrew 1992; Nishida 1987). The argument of the primatologists is based on the abundant evidence of population-specific behaviour patterns that have been observed. Comparing Figure 1 with Table 1 shows that the distribution of many proposed cultural behaviours in chimpanzees do not follow any obvious ecological differences. For example, the nut-cracking behaviour has been observed in only the western most forest chimpanzee populations in West Africa, whereas those living in forests some 30 km east of the Sassandra river in Côte d'Ivoire or further away do not crack these nuts (Boesch *et al.* 1994). In all the forests where investigations were done for presence or absence of the nut-cracking behaviour, nuts are available as well as the potential hammers and roots to

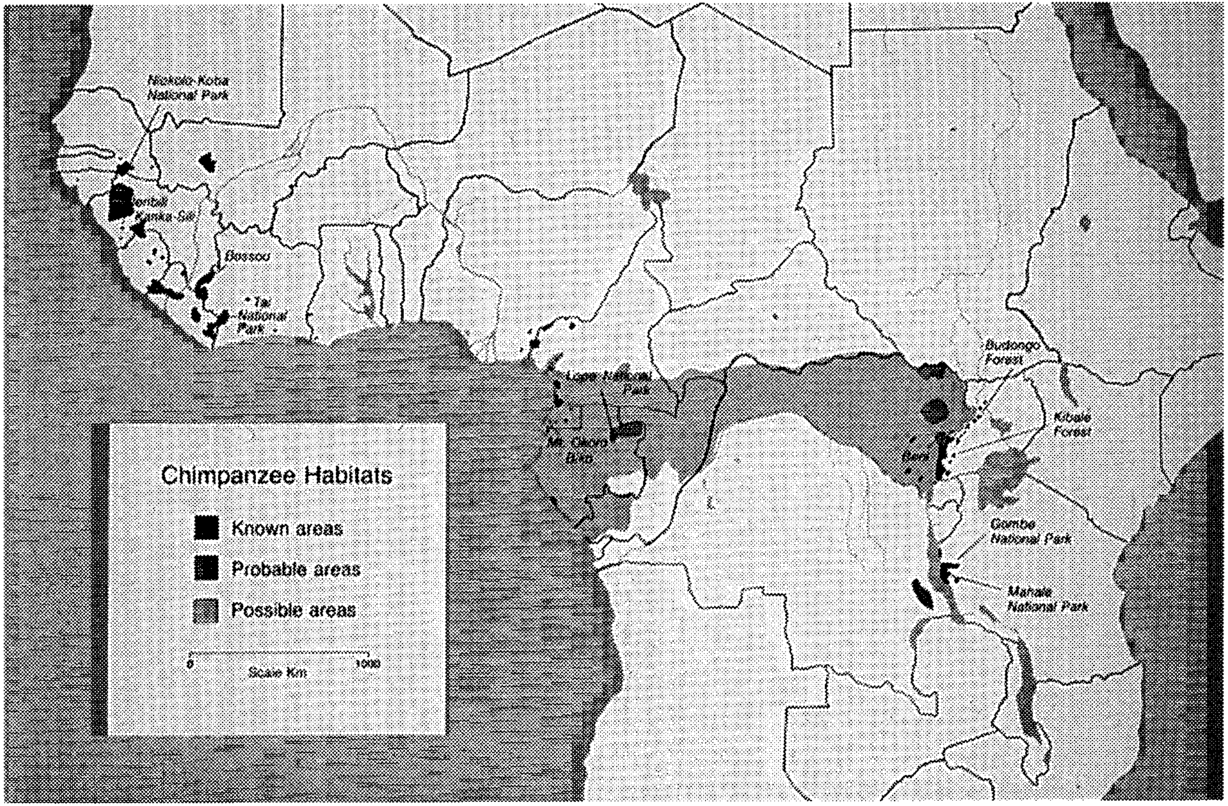

Figure 1. Present distribution (known, probable and possible) of chimpanzees (*Pan troglodytes*) throughout Africa (from Goodall 1986).

Table 1. List of behaviour patterns that have been proposed to be cultural and their distribution within populations of wild chimpanzees. To exclude the most obvious bias (length of the study period), positive and negative results are presented for long-term studies (more than 8 years) in which chimpanzees were directly observed, but only positive observations for shorter studies. [Assirik is located in Senegal (West Africa) and Kibale in Uganda (East Africa).]

	West Africa		Other sites	East Africa	
Pattern	Bossou	Taï		Gombe	Mahale
Ant-dip	+	+	Assirik	+	−
Fly-whisk	+	+		+	−
Leaf-sponge	+	+		+	−
Leaf-clip	+	+		−	+
Nut-crack	+	+		−	−
Play-start	−	+		+	+
Honey-dip	−	+		+	−
Hand-clasp	−	+	Kibale	−	+
Marrow-pick	−	+		−	−
Leaf-groom	−	−	Assirik	+	+
Termite-fish	−	−	Kibale	+	−
Leaf-napkin	−	−		+	−
Self-tickle	−	−		+	−

Bossou: Sugiyama 1981; Sugiyama & Koman 1979
Taï: Boesch & Boesch 1990
Gombe: Goodall 1986; McGrew 1992
Mahale: Nishida 1973; 1987; McGrew 1992
Assirik (Senegal): McGrew *et al.* 1979
Kibale (Uganda): Wrangham & Isabirye-Busata in McGrew 1992

use as anvils (Boesch *et al.* 1994). Similarly, the leaf-clipping behaviour has been observed in both West and East African chimpanzees but not in all populations (Boesch 1995; Nishida 1987). It is this seeming independence of cultural behaviour from ecological factors in chimpanzees that have led the primatologists to claim culture in chimpanzees.

Recently, psychologists have challenged this proposition by suggesting a more parsimonious explanation; what we observe in chimpanzees is merely the result of individual learning processes that are constrained by the ecological limitations in which the individuals are learning the task (Galef 1988; Heyes 1993; Tomasello 1990). To take one example, a youngster learning to crack nuts on its own in the Taï forest may end up using the same behaviour as other group members, because the technical and ecological limitation within the forest allows him to solve the problem in only one way. Under such a scheme, we would obviously not grant the chimpanzee cultural abilities. The distinction made by the psychologists is between individual learning and social learning processes and only the second ones could lead to a culture.

ARE CHIMPANZEES CAPABLE OF SOCIAL LEARNING?

What are the social learning processes?

Many different mechanisms have been recognized by different authors (in their review Whiten & Ham 1992 listed 27 of them). It seems relevant to differentiate the part of the task that is copied in the model. At the lowest level, 'local enhancement' is the process in which the naive observer uses an already acquired behaviour in a *new context* used by the model (Thorpe 1956). By 'stimulus enhancement', the observer's attention is drawn to a *stimulus* in the model's performance (Thorpe 1956). For example, if the model is cracking nuts, the observer will use the tool more frequently. In 'emulation', the observer attempts to reproduce or reach the *goal* that the model is pursuing (Tomasello 1990). Finally, in 'imitation', the observer is attempting to copy the *behaviour* of the model and this behaviour was not part of the repertoire of the observer previously (Piaget 1935; Thorpe 1956).

Recently, experiments done with captive primates showed that social transmission of knowledge is less easy for primates than was previously assumed (Galef 1988; Visalberghi & Fragaszy 1990). Even captive chimpanzees were thought to only emulate aspects of the sand-throwing or food-raking behaviour (Tomasello *et al.* 1987). This has strengthened the point of view of some that advocate that imitation is unique to man (Galef 1988; Tomasello 1990). However, other studies working with animals under enriched captive conditions showed that imitation was possible in chimpanzees (Custance & Bard 1994; Tomasello *et al.* 1993b) and in orang-utans (Russon & Galdikas 1995).

How to prove that chimpanzees are capable of social learning?

The bone of contention is to know if what we observe within a given population is the product of individual learning processes constrained by ecological factors or the result of a social learning process. Are termite-fishing, leaf-clipping, ant-dipping or nut-cracking in chimpanzees cultural sets of behaviour as proposed by primatologists working on these populations or are they the product of individual learning as championed by many psychologists?

The key aspect to settle such a point is to show that during the learning process young chimpanzees do not try all the possibilities they have, within the physical and psychological limits of their species, in order to achieve a task, but that they try only a subset of those and that the subset they try is influenced by what they see in social models. Therefore, we need to know *from the chimpanzees themselves* how they would learn a task when not affected by a model and what would be different if they were affected by a model. We, as members of another species with other physical and psychological limits, cannot decide what are these differences. If no difference is expected in the learning of a task, whether it is through individual learning or through social learning, we will not be in a position to differentiate between the two learning processes and we will not be able to test the social learning hypothesis. In other words, we have to use a very limited criterion to test our two alternatives on the learning process and this will, by definition, strongly limit the possible candidates for cultural transmission.

A last criterion has to be fulfilled in the sense that we need this information from a behaviour that has been proposed to be culturally transmitted. Tomasello and his collegues (1987) have shown that captive chimpanzees do not imitate sand-throwing behaviour. Despite the interest of this result, nobody has ever claimed sand-throwing to be a cultural behaviour in chimpanzees. In addition, the absence of imitation in sand-throwing does not say anything about the presence or absence of imitation in the learning processes of ant-dipping, leaf-clipping or nut-cracking behaviour in wild chimpanzees.

To conclude, to test the two alternatives about the learning process of a task, three criteria have to be fulfilled. First, the behaviour under consideration has to be a candidate of a cultural behaviour, which at the present stage mainly means that it is a population-specific behaviour not directly influenced by ecological factors (Boesch, in press). Second, the different ways the behaviour could be acquired or the final form once acquired should differ if learned by individual or social processes. Third, we need to gather the information on the second point from the chimpanzees themselves: What are the individual learning possibilities and what are the socially limited possibilities?

Nut-cracking might be a good candidate as it fulfils the three criteria; it has been proposed to be a cultural behaviour in chimpanzees (Boesch & Boesch 1990; Goodall 1986; McGrew 1992) and an attempt has been made to introduce it to a group of naive chimpanzees in Zürich zoo (Funk 1985), and this allows us to answer the second and third criteria. The chimpanzees in Zürich were offered nuts and hammers, and were observed for two weeks as they manipulated the objects, trying to open the nuts. None of them succeeded, and no reinforcement from other group members operated. If we compare the methods used by the Zürich and the Taï chimpanzees, we see that Taï chimpanzees tried definitively fewer different methods; of the 14 methods used by the Zürich chimpanzees, only 7 were seen in Taï chimpanzees (Table 2). This is intriguing because some of these rarely or unused methods were actually observed in Taï chimpanzees but in other contexts. Stabbing with a stick was observed against a leopard, and rubbing is observed regularly when feeding on other kinds of fruit. Thus, in

Table 2. Social canalization in the learning of nut-cracking behaviour in chimpanzees: list of all methods used to attempt to open nuts by two populations of chimpanzees. The study on the captive chimpanzees of the Zürich zoo was performed by Martina Funk (1985). A + indicates that the method was used in the population, whereas a – indicates that it was never observed.

Method	Zürich chimpanzee	Taï chimpanzee
Hit with a hammer	+	often
Bite the nut	+	often
Pound the nut against hard surface[1]	+	regular
Hit with hand the nut	+	regular
Hit with an object[3]	+	rare
Rub the nut against hard surface[1]	+	rare
Throw the hammer on nut	–	regular
Throw the nut against hard surface[1]	+	–
Hit with other body part[2]	+	–
Shake the nut	+	–
Press nut against teeth[4]	+	–
Sit on nut	+	–
Scratch the nut with fingers	+	–
Press on the nut	+	–
Stab with a stick	+	–

[1] Chimpanzees can rub, pound or throw the nut directly with the hand against the ground, a stone, a tree trunk or a root.

[2] By other body parts is understood the back of the hand or the elbow.

[3] By object, I understand material that could not make a hammer such as a piece of cloth, small twigs or in the Taï forest another nut, a piece of termite mound or a hard-shelled fruit.

[4] Chimpanzees pressed the nut with the hand against the teeth with the mouth kept open.

comparison to the Zürich chimpanzees, a social canalization of the individual learning potentialities is at work in Taï youngsters and this is strongly influenced by the behaviour observed in the model: 5 of the 7 methods used include behavioural movements commonly observed in adults cracking nuts (Boesch, in press). The object used by the models is less of a guidance, since young Taï chimpanzees used as hammers large hard-shelled fruits, pieces of termite mounds and rotten branches. In nut-cracking behaviour, social canalization through imitation is at work and it confines the individual learning possibilities to the different types of objects that could be used to pound the nuts.

WHAT MECHANISM IS NEEDED TO PRODUCE CULTURE?

There are three possible mechanisms:

1 Imitation, teaching or co-operative learning are the only processes able to produce culture (Galef 1988; Tomasello *et al.* 1993b).

2 All social learning processes (imitation, teaching plus emulation, local enhancement...) produce culture (Whiten & Ham 1992; Russon & Galdikas 1995).

3 Social canalization is the criterion independently of which process produces it (Heyes 1993).

In my opinion, it seems rather arbitrary to single out one process of information transmission as the only one able to produce culture. First, individuals should use all sources of information that could help them to solve a task and information most probably will come from individual experiences and from social partners. For example, in some tasks, some kinds of information cannot be learned through imitation (e.g. non visual properties of tools such as hardness, weight), and without a combination of information from different sources the task will not be acquired. Second, it seems difficult to imagine that an individual imitates a behaviour without being at the same time influenced by the goal to be reached and the object to use, and vice versa. Therefore, I will adhere to the view that social learning processes in general, and not just imitative learning, contribute to cultural transmission. In support of this opinion are the studies showing that in some human populations learning through imitation is rare and sometimes absent (like in the 'Kung bushmen) (Olson & Astington 1993; Rogoff *et al.* 1993). This shows that in humans culture can develop without much reliance on imitation.

Social transmission of information is necessary to produce culture but is not enough. To use an analogy, in genetical transmission the mechanism itself is not so important and many different kinds are observed, i.e. isogamy or anisogamy, sexual or asexual transmission. However, evolution over generations is only possible because of inheritance that maintains the quality of the genetical information stable over time (heritability of a character has to be high for evolution to take place) (Maynard-Smith 1989). Similarly, culture is only possible if we have a mechanism that guarantees information stability between transmission events, e.g. during the retention period between acquisition and re-transmission. If the information is altered under the influence of individual and ecological factors during this retention period, we will never observe a culture (Heyes 1993). Permanence of the information in cultural transmission requires fidelity during transmission *and* a mechanism to guarantee fidelity between transmissions. In other words, social canalisation should be at work all the time.

Thus, the key to culture is not so much the precise transmission mechanisms, as we saw that many of them could be at work, but a permanence-guaranteeing mechanism. At present, the discussion about culture in animals has been restricted to the transmission mechanisms, and this important aspect of the problem has been forgotten. I shall devote some time to this aspect of culture in chimpanzees.

HOW CAN PERMANENCE OF THE INFORMATION BE GUARANTEED?

Two mechanisms have been proposed (Heyes 1993):

1 The information could be stored in object or language supports. This could include all extrasomatic artefacts, i.e. technological objects, books, myths and fairy tales about traditions and the past.

2 Social norms (or social conventions) limit variations in the information, as not all possibles will be socially acceptable.

Logically, we think that these two processes would be likely to operate in conjunction with a symbolic or instructional process of learning, as seen in our own species. However, this might only be an assumption and I think that in the case of the second mechanism, this assumption might be wrong, since this mechanism applies also to animals.

How can we evaluate this point with animals?

Social norms will exist when a strong social canalisation exists in an animal population, that prevents or discourages individuals from modifying the socially acquired information through individual learning and from testing it against all possibilities allowed within a given ecological context. As we can see, such a situation could provide us with a solution to our problem. The lack of testing all possibilities in an ecological context might lead to non-adaptive solutions being retained or to arbitrary solutions being used. I shall review the evidence for the two mechanisms in wild chimpanzees.

Cultural behavioural patterns are maladaptive

The three criteria proposed above still apply, as we need a behaviour that has been proposed to be cultural and we need two different solutions possible from the chimpanzees' point of view. Now, if the solution used by all group members is also the best possible of the two alternatives, we will not be able to differentiate whether what we observed is the result of modifications through individual learning or the result of rigidity resulting from a social norm. This is because we expect individuals to test the possibilities and choose the best ecological solution they find. But if, of the two solutions possible, the group members use the one we know not to be the best one, we could exclude the individual learning alternative. Therefore, for the present test, we need to exclude cases where the animals use the best ecological alternative to a given problem. Please note that such situations might be rare, as we expect in wild populations natural selection to be at work, and there will be a cost related to the selection of non-adaptive behaviours.

The *ant-dipping behaviour* is to my knowledge the best example of such a culturally non-adaptive behaviour of which the maintenance can be explained by different social norms prevailing in different social groups. The ant-dipping behaviour has not been observed in all chimpanzee populations (Table 1), but, more important, the chimpanzees found two different techniques to dip for the ants (Boesch & Boesch 1990; Goodall 1986). Both Gombe and Taï chimpanzees use sticks that they dip into the nest entrance of the driver ants of the species *Dorylus nigricans*, so as to eat them. In Gombe, chimpanzees use one hand to hold the stick among the soldier ants guarding the nest entrance and, once they have swarmed about halfway up the tool, withdraw the stick and sweep it through the closed fingers of the free hand; the mass of insects is then rapidly transferred to the mouth (McGrew 1974). Gombe tools are in average 66 cm long and the dipping is performed 2.6 times per minute. McGrew (1974) estimates that they take 292 ants per dipping movement. In Taï, the chimpanzees hold the stick with one hand among the soldier ants guarding the nest entrance until they have swarmed about 10 cm up the tool. Then, they withdraw it, twist the hand holding it and directly sweep off the ants with the lips. Taï chimpanzees use short sticks of about 24 cm long and perform the dipping movement about 12 times per minute (Boesch & Boesch 1990). We estimate, from our own trials, that they obtain 15 ants per dipping movement. In Gombe, the Taï dipping movement has been observed only sometimes with two individuals, McGregor and Pom (McGrew 1974).

So ants can be dipped by two different techniques, but each of them is seen in only one chimpanzee population. I have tested the two techniques in the two sites and found no ecological factor that would prevent the use of either of them in both sites. The Gombe technique is four times more efficient than the one used in Taï (Gombe, 760 ants/minute; Taï, 180 ants/minute; Boesch & Boesch 1990). Here, Taï chimpanzees restrict themselves to an ecologically sub-optimal solution that must be maintained by a social norm preventing the individuals from testing all possibilities.

Arbitrariness of behaviour is socially dependent

With the same line of argument, the solution selected by group members might have no connection to an ecological solution but be purely socially determined. Such a solution would then be independent of ecological factors and would not present the cost that we expect for non-adaptive behaviours. Therefore, we should expect them to be more frequent.

Leaf-clipping among wild chimpanzees. This behaviour was first described in the Mahale chimpanzees in Tanzania: 'A chimpanzee picks one to five stiff leaves, grasps the petiole between the thumb and the index finger, repeatedly pulls it from side to side while removing the leaf blade with the incisors, and thus bites the leaf to pieces. In removing the leaf blades, a ripping sound is conspicuously and distinctly produced. When only the midrib with tiny pieces of the leaf blade remains, it is dropped and another sequence of ripping a new leaf is often repeated' (Nishida 1987: 466). Note that nothing of the leaves is eaten. This behaviour has also been seen regularly at Bossou (Sugiyama 1981) and Taï (Boesch 1995) but only twice at Gombe (Goodall, personal communication cited in Nishida 1987). The fact that this behaviour is present in three chimpanzee populations but absent in a fourth one could be explained by an ecological difference, although we do not know yet what difference might produce such an irregular distribution of that behaviour.

When present, the function of this behaviour seems arbitrary. In Mahale, the chimpanzees most often use it as a herding or courtship display in sexual contexts (23 of 41 observations; Nishida 1987). Young adult males and adult oestrous females apparently perform it to attract the attention of group members of the other sex (Huffman, personal communication). In Bossou, it occurs mostly in apparent frustration or in play (41 of 44 observations; Sugiyama 1981, personal communication). During the habituation period, individuals surprised in trees would leaf clip while looking at the observer. Once habituation was more advanced, this form of leaf clipping disappeared and is seen now only in youngsters at play. In Taï, leaf-clipping is mainly part of the drumming sequence of the adult males (249 of 319 observations; Boesch 1995) and is seldom seen during a resting period (32 cases) or in frustration situations (34 cases) (Table 3). It seems very difficult to propose ecological reasons to account for the fact that each chimpanzee populations uses leaf clipping in a different context. The arbitrariness in the context of use observed in three chimpanzee populations suggests that leaf clipping is a cultural behaviour whose context of use is locally determined by a social norm fixed among group members.

Conventional behaviour patterns in chimpanzees. Such social norms seem to have influenced other behaviours as well (Table 3). For example, in Mahale young males use leaf clipping to attract the attention of oestrous females (Nishida 1987). This is less conspicuous than the dominant males' way, who routinely shake saplings for the same purpose. Intriguingly, Taï

Table 3. Behavioural variants following population specific norms in wild chimpanzee populations (see text for more explanations).

	Bossou	Gombe	Mahale	Taï
BEHAVIOUR	FUNCTION			
Leaf-clip	Play	–	Courtship	Drumming + Resting
FUNCTION	BEHAVIOUR			
Courtship	–	–	Leaf clip	Knuckle knock
Squash ectoparasite	–	Leaf groom	–	Index hit

low-ranking males also use a less conspicuous way to attract the attention of oestrous females than sapling-shaking behaviour and that is by knocking with their knuckles on the trunks of small saplings (Table 3). Here, we have a class of individuals that have a social problem to solve, 'attract the attention of an oestrus female', and that solve it in two different ways (our criteria 2 and 3). And a different solution is used in each population. Why chimpanzees in Mahale do not knock to attract the attention of females seems to be arbitrarily fixed and determined by a social norm that group members acquire by social learning processes.

Similarly, Gombe chimpanzees have recently started to use leaf grooming in order to squash ectoparasites that they find while grooming somebody else or themselves (Boesch 1995). This has been observed in most members of the group. In Taï, chimpanzees also squash ectoparasites they find during grooming sessions in order to eat them, but they do it in a different way to the Gombe chimpanzees; they place the parasite on one forearm and hit it with the tip of the forefinger until it is squashed, and then eat it. Here, again, we have two different solutions to the same problem, of which only one is used in each population (Table 3). The arbitrariness of the solutions retained as well as of the decision of which one is to be used in one population seems also to indicate that a social norm is at work and that group members acquire it through social learning processes.

Symbolic drumming code in Taï chimpanzees. The last example I want to give of an arbitrary behaviour concerns a case of symbolic communication in forest chimpanzees (Boesch 1991a). Chimpanzees forage typically in ever-fluctuating parties of 7–12 individuals, remaining permanently in auditory contact with the majority (75%) of the community (of 80 chimpanzees), and follow for hours a constant direction even if totally silent. Normally the community splits in at least three major parties that may communicate with one another by vocalizing and drumming. Buttressed trees are abundant in this forest and adult males, after loudly pant-hooting, hit these buttresses powerfully and rapidly with their hands, feet or both. Drumming is a way for males to communicate their position to other group members and it may inform them about the direction in which the drummer progresses, and thus contains information about the group's progression.

However, we suspected that these drummings were more than just an indication of an individual's position, because we tended to lose contact with them just after some drummings were heard. It seemed that the whole chimpanzee community had abruptly and often silently changed direction following these drummings. It took many months to unravel this communicative system. During this time, I learned to differentiate the pant-hootings of the individual adult males. In early 1982, three years after we had initiated the study of the Taï chimpanzees, I began to realize that it was only after Brutus, the alpha male, drummed that the community reacted by abruptly changing the direction of travel. On some occasions, Brutus's drumming sequence appeared to transmit a specific message. There was no audible difference between sequences that did or did not have such a message; rather this message was indicated by the spatial and numerical combination of the sequences. During a 16 month period (January 1983 to May 1984), I studied the information conveyed in Brutus's drummings and was able to identify three messages in Brutus's emissions (Table 4).

1 Change in the travel direction. Brutus, by drumming twice at two different trees, indicated to other community members the direction he was proposing. The direction followed by Brutus when moving between the two drummed trees was used by other group members as indicating the new travel direction he was proposing. In addition, such drummings always occured within a time interval not exceeding two minutes. Individuals that were not part of Brutus's party apparently inferred the direction proposal by mentally visualizing Brutus's displacement between the two trees and then transposed it to their travel direction. Table 4 summarizes the number of occurrences in which I could identify the transfer of information about directions.

2 Indication about resting periods. On other occasions, Brutus seemed to propose a resting period of a specific duration that the community would follow: this was communicated by drumming twice at the same tree within 2 minutes. I was able to identify this message from Brutus in 14 cases (see Table 4) when the community activity stopped for an average of 60 minutes ($N = 12$, range = 55 to 65 minutes). Community activity was judged to be resting by the absence of movement and vocalization of parties not observed

Table 4. Symbolic communication in Taï chimpanzees: Brutus's communication system with the frequency of emissions in which communication about travel direction and resting duration could be identified. The number of cases heard correspond to the number of response of the group members in aggreement with my prediction of their response to Brutus's message, except for one case of 1 hour rest, in which Brutus himself canceled his message by drumming farther away 7 minutes later.

Number of drumming	Location of emission	Group response	Number of cases heard
2	same	1 hour rest	8
2	different	Change of direction	8
3	same	–	–
3	different	1 hour rest + change of direction	6
4	same	2 hours rest	1
4	different	–	–

as well as by the behaviour of the party under observation. After this rest, parties sometimes indicated vocally that they had begun to move. A chimpanzees' resting bout in the wild corresponds to an hour and Brutus proposed probably such a resting bout rather than the duration of one hour.

3 Direction and resting time combined. By combining both messages, Brutus could propose both a change of direction and an hour's rest; in such a case he would drum once at a tree on the movement axis and then twice at another tree in the direction he was proposing (see Table 4) within a short period of time. Alternatively, Brutus could drum twice on the axis and then once further in the proposed direction. In all cases, the information about time had an immediate effect, whereas that about the direction applied only later. It is worthwhile noting that if Brutus were simply adding information about direction and time, he would have drummed four times (twice for each kind of information). In fact, he really combined them and drummed only three times; thus, one of the drummings contained information on both direction and time.

Brutus stopped using this code rather abruptly, when several of the prime males suddenly disappeared from the community, probably through poaching, and as a consequence the number of travel parties diminished (Boesch 1991a). This mode of symbolic communication has only been observed in the Taï chimpanzees and in this community its use was also limited in time. This is clearly emphasizing the arbitrariness of this form of communication.

In conclusion, the examples given in this section show clearly that social norms exist in wild chimpanzee populations and that they do limit the variation that might be introduced by individual learning. Social norms are thought to bring social advantages that could compensate for the possible costs related to adopting the norm. This is obvious for communicative gestures: if one leaf clips in another context than the one generally used, the risk of being misunderstood exists. Therefore, social norms in the communicative gesture domain are not a surprise. However, this does not seem to apply to domains that represent solutions to ecological problems, like ant dipping or parasite squashing. Why do Taï chimpanzees never dip for ants using the Gombe technique that is so much more efficient? Similarly, why squash parasites only on the forearm, when other methods seem as efficient? It has been argued in humans that one effect of culture is to allow a better identification with a social entity and that part of what we observe merely functions to differentiate individuals from different groups (Segall *et al.* 1990). Would this apply to chimpanzees?

The two mechanisms required to allow a culture have been found in wild chimpanzees: first social learning processes that guarantee the fidelity of the information transfer between individuals, and second, social norms that guarantee the fidelity of the information once it has been acquired by an individual.

IS CULTURE RARE IN ANIMALS?

When studying culture in animals, it is generally required that the behaviour is independent of ecological factors (Bonner 1980; Tomasello 1990). Here, I adopted rigorous criteria to identify the presence of cultural behaviours in chimpanzees. To prove both the existence of social learning processes and of social norms, we need tasks that can be solved in more than one way by the species under consideration, and the individual learning results should differ from the social ones. This excludes many behaviour patterns from the analysis, such as termite fishing or leaf sponging, because we have observed these to be done in only one way by wild chimpanzees. In addition, if individual learning with ecological constraints and social learning give the same result for the same task, we would deny the second explanation on grounds of parsimony. Under such criteria, the appropriate tasks will be difficult to identify and possibly rare. Thus, culture in animals will be rare by definition. If we would apply the same criteria to human cultural behaviours, the list would also be much shorter. Similarly, if we lift the ecological independence criteria for the chimpanzees, culture in this species would then be present in many more aspects of their life (such as hunting or food sharing behaviours).

Nevertheless, we described clear examples of cultures in wild chimpanzees. Does it mean that cultures in chimpanzees and humans are identical and that they could not be used as a criteria to distinguish the two species? I would like first to sound a cautionary note: compared to man, the most studied species on earth, we know impressively little about wild chimpanzees which have been studied for only 30 years in at most 200 different individuals. Any conclusion when comparing the two species has to be tentative. Having said this it seems far-fetched to pretend that human cultures are similar to chimpanzee cultures. But are they qualitatively or only quantitatively different? The comparisons we made showed that the basic mechanisms required to produce culture in humans are present in chimpanzees, whether it be social learning including imitation, teaching and instructional learning (Boesch 1991b), as well as the social norms. Why then is culture not observed in many more aspects of the chimpanzees' behaviour? This brings us to the basic question about the function of culture, which seems to be the possibility for much more rapid adaptation than genetical evolution allows. I would suggest that wild chimpanzees with their suspected limited migratory potentials (Morin *et al.* 1994) live in stable ecological and social environments and that the need for rapid adaptation is limited. This also seemed to be the case for our early ancestors as is observed in the incredibly stable and rudimentary cultural products for most of the history of *Homo habilis*, *Homo erectus* and for early *Homo sapiens* (Davidson & Noble 1993; Toth & Schick 1993). Only when the number and the products of the cultural behaviours reached a certain threshold did they become part of the environment and require much quicker evolution, thus sparking off the 'human revolution' (Mellars & Stringer 1989).

Note. I thank the 'Ministère de la Recherche Scientifique', the 'Ministère de l'Agriculture et des Ressources Animales' of Côte d'Ivoire, the Tanzania Commission for Science and Technology, the Serengeti Wildlife Research Institute as well as the Tanzania National Parks for permitting this study, and the Swiss National Foundation, the L.S.B. Leakey Foundation and the Jane Goodall Institute for financing it. In Côte d'Ivoire, this project is integrated in the UNESCO project Taï-MAB under the supervision of Dr. Henri Dosso. I am most grateful to A. Aeschlimann, F. Bourlière, J. Goodall, S. Stearns and H. Kummer for their constant encouragement. I thank H. Boesch-Achermann for commenting upon and correcting the manuscript. Figure 1 is reproduced from Goodall (1986) by kind permission of Harvard University Press.

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