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Is nut cracking in wild chimpanzees a cultural behaviour?

Nut-cracking behaviour, once thought to be typical for most West African chimpanzees, is in reality restricted to a very small area within the evergreen forest perimeter. In Côte d'Ivoire, the N'Zo-Sassandra river is the eastern limit of its distribution. Neither the chimpanzee density, the density of nut-producing tree, anvils and hammers, nor the type of forest can explain this clear-cut limit. From two cases of chimpanzee populations less than 50 km apart on either side of the river we can conclude that this limit is most probably cultural. This result completes the image of cultural behaviour in wild chimpanzees having irregular and unpredictable distribution patterns similar to those of human culture.

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Introduction

Is nut cracking in wild chimpanzees a cultural behaviour? Such a question is controversial as it is still commonly assumed by anthropologists that culture is an exclusively human characteristic. During the last 30 years, long-term studies on wild chimpanzees have led to a wealth of data and a striking picture has emerged with local populations presenting many differences in their behaviour that suggest cultural differences (Goodall, 1973, 1986; Nishida, 1987; Boesch & Boesch, 1989, 1990; Sugiyama, 1990; McGrew, 1992). However, to grant culture in an animal species, the criteria are more stringent than just showing a patchy distribution in the occurrences of a given behaviour. The question can be approached from two different points of view. The first approach concentrates on the transmission mechanisms that allow the propagation of the behaviour between individuals. The current assumption is that a behaviour is cultural only if it is learned through imitation or teaching from other group members (Galef, 1988; Tomasello *et al.*, 1993). In recent reviews on studies dealing with the evidence of cognition in primates any such ability tends to be denied to monkeys and apes (Galef, 1988; Whiten, 1989; Visalberghi & Fragaszy, 1990), but the debate is still open as new interpretations of patterns of behaviour and new examples of imitation and teaching are reported (Hauser, 1988; Boesch, 1991, 1993a; Tomasello *et al.*, in press). It is also probable that

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not all so-called cultural sets of behaviour in humans are learned only by imitation or teaching (Whiten & Ham, 1992; Boesch, 1993*b*). The second approach takes into account the ecology of the behaviour. In this approach, a behaviour is considered as cultural only if differences in its distribution between populations are independent of any environmental or genetic factors (Goodall, 1973; Nishida *et al.*, 1983; McGrew, 1992). It is in this respect that some of the local differences in chimpanzee behaviour are puzzling: Why do Bossou chimpanzees eat the pulp of the oil palm nuts and crack them in order to eat the kernel, whereas Gombe chimpanzees eat only the pulp (Goodall, 1986; Sugiyama, 1990)? Why do Gombe chimpanzees dip for ants with long tools, while Tai chimpanzees dip the same ant species with much shorter tools (McGrew, 1974; Goodall, 1986; Boesch & Boesch, 1990)? Excluding any genetic differences for populations living thousands of kilometers apart is difficult. Similarly, the environmental conditions are sometimes very different between such sites and it remains delicate to completely exclude this factor (see Tomasello, 1990).

Much care should be taken in interpreting behavioural differences between wild chimpanzee populations; it took us 8 years of study to observe ant dipping in Tai chimpanzees, because the shy females, the main performers of this tool use, did not easily accept being observed at close range (Boesch & Boesch, 1990). Without direct observations, it would have been speculative to attribute functions to sticks found near an ant nest, as they are usually either shifted from the nest entrance or covered with earth by the ants within minutes of use. Much care is required when discussing the absence of tool use within a given population if the duration of observation is not comparable to long-term studies which provide positive observations. For example, ant dipping should not be considered as absent in a population before complete habituation of the females.

Nut-cracking behaviour is a promising exception for its existence can be ascertained without observing the chimpanzees, due to the presence of the anvils (horizontal roots or rocks with wear traces due to nut pounding) with nut remains lying around them and sometimes with a hammer (a log or a stone) on top or nearby, that remain visible for years to an experienced observer (Beatty, 1951; Rahm, 1971; Struhsaker & Hunkeler, 1971; Anderson *et al.*, 1983; Boesch & Boesch, 1983). Based on the presence of such traces, nut-cracking behaviour seems restricted to the forest chimpanzees of West Africa, with its presence positively confirmed in Ivory Coast, Guinea, Liberia and Sierra Leone (see Figure 1) (Savage & Wynam, 1843/44; Sugiyama & Koman, 1979; Sugiyama, 1981; Boesch & Boesch, 1983; Kortlandt & Holzhaus, 1987; Whitesides, 1985). It is reported to be absent from the forest inhabited by chimpanzees in Cameroon (Sugiyama, 1985) and Gabon (Tutin & Fernandez, 1983), forests where, however, some of the same nut species occur. This excludes any obvious ecological differences and, thus, many authors have proposed nut-cracking behaviour in chimpanzees to be cultural (Boesch & Boesch, 1983; Goodall, 1986; Sugiyama, 1990; McGrew, 1992). However, we see from Table 1 that not all populations crack the same species of nuts nor use the same kind of tools, indicating that environmental factors are somehow involved. In addition, more subtle ecological differences that could affect the benefit of nut cracking, such as too low an availability of potential tools, too low a density of the nut producing trees as well as an over-abundance of other food types, have not been studied so far (see Sugiyama, 1985).

We present here the results of a survey done in Côte d'Ivoire to search for the limits of the nut-cracking behaviour, as some information (C. Martin, pers. comm.) indicates that chimpanzees in Ghana do not crack nuts. The limit of the behaviour might thus be within Côte d'Ivoire. We collected detailed data on ecological factors which might have affected the nut-cracking behaviour of different populations.

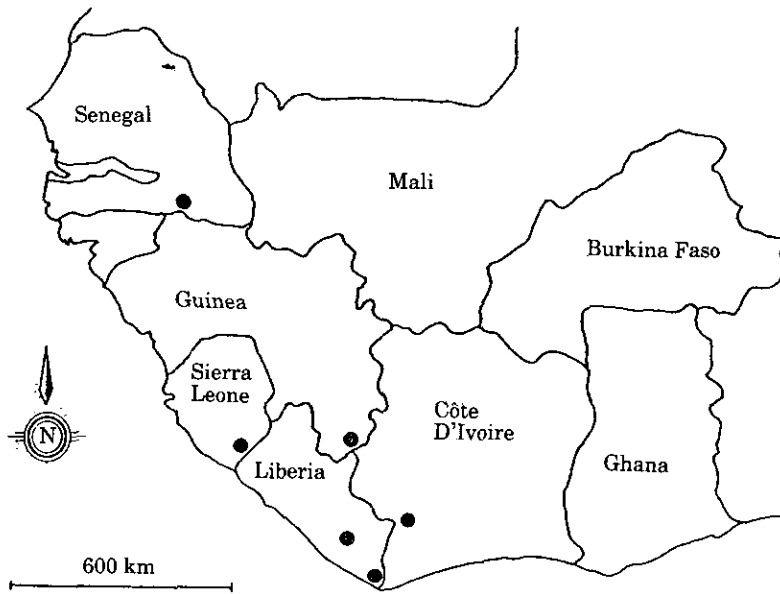


Figure 1. Confirmed nut cracking sites (●) of chimpanzees in West Africa.

Table 1 Nut species cracked and tools used by chimpanzees in different regions of West Africa

	Nut species										Tools						
	Coula		Detarium		Elaeis		Panda		Parinari		Sacoglottis		Wood		Stone		
	P	C	P	C	P	C	P	C	P	C	P	C	H	A	H	A	
Sierra Leone																	
Tiwai Island	1	+	-	+	+	-	-	-	-	+	-	?	-	+	+	?	?
Liberia																	
Sud-West	2	+	+	?	?	+	-	?	?	+	-	?	?	-	-	+	+
Unknown	3	?	?	?	?	+	+	?	?	?	?	?	?	-	-	+	+
Sapo N.P.	4	+	+	-	-	+	-	+	+	+	+	+	+	-	+	+	+
Guinea																	
Bossou	5	?	-	?	-	+	+	-	-	+	-	-	-	-	-	+	+
Cote D'Ivoire																	
Tai N.P.	6	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+

P: tree present, C: tree present and nut cracking confirmed, H: hammer, A: anvil, +: yes, -: no, ?: not known. Literature sources: 1, Whitesides (1985); 2, Savage & Wyman (1843/44); 3, Beatty (1951); 4, Anderson *et al.* (1983); 5, Sugiyama & Koman (1979); 6, Boesch & Boesch (1983).

Methods

As many locations as possible throughout Côte d'Ivoire were visited and the presence or absence of nut-cracking traces recorded. Local people eat the very abundant and tasty nuts of *Coula edulis*, but as a rule open them with a bushknife, occasionally with a stone in the village. They rarely crack them in the forest and if so, only in small quantities so that human activity

can be excluded in most cases (Boesch & Boesch, 1983). They usually carry them back to the village to dry and store them for later consumption.

To control for the effect of ecological factors on nut-cracking behaviour, we collected data on the nut-cracking sites as well as on the distribution and the densities of nut-producing trees, potential hammers and anvils at some locations with confirmed chimpanzee presence. The procedure was the following: Using a compass, a hipchain and bushknife, we marked line transects of 9 to 15 km long, 20 m wide, and in the form of a T or a cross (Marchesi *et al.*, in press). The following data were collected within these transects.

(a) Presence and production of the *nut-producing trees*: all trees were marked, the trunk diameter measured, and the presence of fruits, nut-cracking sites (or *ateliers*, see: Boesch & Boesch, 1983) within the "nut-falling zone" (the area on the ground directly under the tree crown) were recorded;

(b) The *availability of material*, i.e. roots, wooden clubs and stones potentially usable by the chimpanzees as anvils and hammers were counted and measured (size and weight) within rectangles of 60 m² (20 m × 3 m) distributed every 100 m on a 3 km transect distance. For anvils, the availability was measured in length of potential roots or stones divided by the total area surveyed (cm/m²), whereas for hammers it was measured as the number of potential tools divided by the area surveyed (nb/100 m²);

(c) The specific *availability of material under the nut-producing tree* with ateliers, including the availability of potential and used tools within the nut-falling zone were registered. In some sites the availability under trees without ateliers was also recorded for comparison.

Operational definition of tools

Our study of nut cracking in Taï (Boesch & Boesch, 1983) showed that not all stones or branches can be used by the chimpanzees. Thus, to make a sound comparison, we used clear-cut criteria to differentiate between stones or branches lying on the forest floor that would never be used by the chimpanzees, that could be used ("potential tools") or that had been used ("used tools"):

(a) *Potential tools*: Potential anvil: Root or stone (seldom liana or bent tree) whose hardness and shape (≥ 10 cm wide, > 10 cm long) allows it to crack nuts. Hardness was measured by pounding a 9 cm long nail into the anvil by the force of five falls of a 2 kg stone from 1 m height. The hardness of the root is ranked following a scale of hardness units (HU) from 1 (softest) to 9 (hardest). We excluded roots with a hardness equal or below 3, because they were too soft for pounding nuts.

Potential hammer: stones or clubs hard enough to crack nuts (operational criteria: it should not break when banged vigorously against a hard surface, weight between 0.6 kg to 20 kg and a diameter between 5 to 20 cm).

(b) *Used tools*: Used anvil: The part of a root or a stone which shows traces of wear due to nut cracking (either the stone surface attacked or the bark removed and the wood underneath attacked by the hits).

Used hammer: stones or clubs which show evident wear due to nut cracking.

The nuts

Five species of nuts are cracked by chimpanzees in Côte d'Ivoire (see also Boesch & Boesch, 1983). Oil palm nuts (*Eleais guinensis*) are not included in this list because only the Bossou chimpanzees (Guinea) are known to crack them (Sugiyama & Koman, 1979).

(a) *Coula edulis* (Olacaceae) is a round soft nut of about 3 cm diameter, also known as African walnut. It is present in most of the ombrophile sector of the Guinean belt and in the lower parts of the Mont Nimba region. It is common in the humid evergreen forest of Taï, the N'Zo reserve and in Yapo.

(b) *Panda oleosa* (Pandaceae) is a very hard 5 cm long nut, absent from the Soudanian belt and always less abundant than *Coula*. It grows often in the low and wet lands.

(c) *Parinari excelsa* (Rosaceae) is a hard, slightly smaller nut than *Panda*, only present in the Guinean belt and most common in the wettest forest. It is the characteristic tree species of the forest above 1000 m altitude in the Nimba and Dan mountainous regions (Aubréville, 1959).

(d) *Sacoglottis gabonensis* (Humiriaceae) is a small soft nut characteristic of the wettest evergreen forests (Aubréville, 1959). It is most common in Taï forest.

(e) *Detarium senegalense* (Caesalpiniaceae) is a flat, coin-like 5 cm-large soft nut, most common in the semi-deciduous forest of Marahoué national park but present throughout the evergreen forests.

All observers taking part in this project spent a 2-month period in the long-term study site at Taï in order to become acquainted with the methodology and with the traces left by the chimpanzees. B. Fruth and F. Jouliau collected the data on the North-Western part of the nut-cracking zone (including Mont Nimba), B. Fruth and P. and N. Marchesi collected the data in Taï Nipla and Mont Kopé, and P. and N. Marchesi collected data of all other sites.

Results

We visited 35 locations in Côte d'Ivoire, most of them situated within the Guinean belt (area covering about 110 000 km² in the southern part of the country and comprising the evergreen and semi-deciduous forests) (Figure 2). The presence of chimpanzees was confirmed in 24 of these locations, whereas nut-cracking sites were found only in seven of them. Figure 2 shows that these seven locations are all situated in the southwestern part of the country. In Côte d'Ivoire, the N'Zo-Sassandra river constitutes the eastern limit of this nut-cracking behaviour as, in spite of a careful search, no nut-cracking site has been found on the eastern side of these rivers. After intensive prospecting in the Mont Nimba and Mont Dan regions (points 1 to 6 of Figure 2), only two *Coula*-cracking sites have been found in Mont Nimba. But, as they were along a trail with remains of cigarette paper laying around, along with the fact that local inhabitants (tribes of Manon and Yacouba) confirmed to us that they do crack *Coula* and oil palm nuts (*Elaeis guinensis*) the same way as chimpanzees, we cannot exclude the possibility that these two cracking sites were human work. However, Sugiyama (pers. comm.) recently saw some *Coula* nut-cracking sites in the higher part of the Guinean side of Mont Nimba, which, he believes, were most probably made by chimpanzees, suggesting that chimpanzees may crack nuts on this mountain, but at a very low frequency.

What are the ecological factors that might explain such a limited distribution?

(a) Chimpanzee density

As part of the survey, we made a census of the chimpanzee populations in Côte d'Ivoire (see Marchesi *et al.*, in press). We tested the most commonly used census techniques on the known chimpanzee community of the Taï National Park and found that the best density estimates were obtained by counting all groups of nests found within the surface of the transects in each site and by correcting for the real forest cover within each region as chimpanzees make nests only in forested regions (see Marchesi *et al.*, in press for more details). Chimpanzee densities are



Figure 2. Geographic distribution of the visited sites in Côte d'Ivoire. (●) sites with nut cracking; (○) sites without nut cracking; (*) sites without indications of chimpanzees presence; (*) two other sites where chimpanzees have been mentioned recently by credible observers; (-) northern limit of the guinean belt; (I) guinean belt; (II) soudanian belt; (NP) National Park; (CF) Classified Forest.

- | | | |
|---------------------------|---------------------------------|--------------------------------|
| 1. Mt Nimba NP (MN) | 14. Nzo reserve | 27. Mopri CF |
| 2. Gbapleu (Tiapleu CF) | 15. Taï NP -Audrenisrou (TA) | 28. G6 CF (GO) |
| 3. Tiapleu CF | 16. Taï NP -Nipla (TN) | 29. Azagny NP |
| 4. Mt Nieton CF | 17. Mt Kourabahi CF | 30. Irobo CF |
| 5. Blépleu (Sangouiné CF) | 18. Mt Kopé (MK) | 31. Agnéby |
| 6. Mt Tonkoui CF | 19. Haute Dodo CF | 32. Yapo CF |
| 7. Mt Sangbé NP | 20. Monogaga CF (MO) | 33. Songan CF |
| 8. Tyonlé CF | 21. Marahoué NP (MA) | 34. Bossematié CF (BO) |
| 9. Mt Péko NP | 22. Nizoro CF (Ni) | 35. Comoé NP -Gansé |
| 10. Goulaleu CF | 23. Guiniadou (Nieggré CF) | 36. Comoé NP -Amaradougou (CO) |
| 11. Mt Bérou CF | 24. Davo | 37. Comoé NP -Kolonkoko (CO) |
| 12. Mt Zoa (Scio CF) | 25. Kouadiokro (Niegre CF) | |
| 13. Duékoué CF (DU) | 26. Dagbégo (Dassiékro CF) (DA) | |

influenced both by habitat type and human impact and not by geographical locations (Marchesi *et al.*, in press). Nut-cracking populations west of the Sassandra river have densities ranging from 1.72 ind/km² in Taï to 0.45 ind/km² in Monogaga ($n=4$, $\bar{x}=1.28$ ind/km²), while non nut-cracking populations east of the Sassandra river have densities ranging from 6.39 ind/km² in Marahoué to 1.02 ind/km² in Dagbégo and 0.51 ind/km² in Bossematié ($n=6$, $\bar{x}=1.49$ ind/km²) (Wilcoxon-Mann-Whitney test: $Wx=25$, $P=0.76$) (Marchesi *et al.*, in press). Thus, chimpanzee densities in these sites cannot explain the presence or absence of nut-cracking behaviour.

(b) *Density of nut tree species*

Table 2 shows the presence and the density of nut-producing trees in 19 of the visited sites with confirmed chimpanzee populations. The density of nut trees, especially for Coula, tends to be greater in Taï than in the other places. But there are no differences between Mont Kopé or Monogaga and the regions where nuts are not cracked (for all sites with density measures, Wilcoxon-Mann-Whitney test: Coula; $Wx=25$, $n_1=4$, $n_2=6$, $p=0.76$, Panda; $Wx=28$, $n_1=3$, $n_2=10$, $p>0.7$, Parinari; $Wx=38$, $n_1=4$, $n_2=10$, $p>0.7$). Although we could not find any chimpanzee populations in Yapo managed forest (presumably recently extinct through poaching pressure), this site figures in Table 2 because it shows that all the nut species are present in this region, and at densities close to that of Taï. In conclusion, sites without nut cracking show no difference from sites where nut-cracking behaviour occurs in the densities of the nut-producing trees. Thus this factor cannot explain the absence of the behaviour.

(c) *Availability of potential hammers and potential anvils*

The availability of potential tools calculated on transect samples is given for 10 sites in Table 3. No difference in the availability of potential hammers (Mann-Whitney U test: $U=12$, $n_1=5$, $n_2=5$, $P>0.05$) and potential anvils (Mann-Whitney U test: $U=7$, $n_1=5$, $n_2=5$, $P>0.05$) exists between sites within or outside the nut-cracking region. The availability of potential hammers is even lower in the two sites of the Taï forest, where nuts are regularly cracked. For these two sites and for Dagbégo and Duékoué most of the potential tools are of wood, whereas stones predominate in the other sites. Thus, the absence of nut-cracking behaviour cannot be explained by differences in the tool availabilities between these sites.

(d) *Floristic description*

All the cracking sites are localized in the Guinean evergreen forest as defined by Guillaumet (1967). But this is also the case for the Niégré and Dagbégo regions situated east of the Sassandra river. In Table 4, we have separated sites with and without nut cracking using the precise floristic divisions used by Guillaumet & Adjanooun (1971), in order to point out that, apart from Mont Zoa, there is always at least one site *without* nut cracking in the same floristic zone as sites *with* nut cracking. Thus, the absence of nut cracking cannot be explained by differences among sites in the forest type and its general availability of food.

Discussion

A very precise limit of the distribution of nut-cracking behaviour was found in Côte d'Ivoire. The analyses of the different sites shows that none of the ecological parameters

Table 2 Density of nut-producing trees (per km²) for the five nut-cracking regions (left columns in table) and for the 14 non nut-cracking regions

	Tai		Mont		Mont		Mont		Comoé		Mont		Gô		Songan		Yapo		
	Audr	Nipla	Kopé	Mont	Mongaga	Béto	Nimba	Dagbôgo	Duékoué	Marahoué	Amar	Niégré	Péko	Azagny	Bossemanié	Nizoro	Blépleu	Songan	Yapo
KM	6.4	15.0	9.0	9.0	9.0		10.9	9.0	12.0	15.0	12.0	6.0	12.4	10.0	12.0	2.0	7.1	8.8	2.6
CO	17.7	38.8	2.7	2.8	(+)		2.4	1.0			6.2				0.8	0.8	1.6	0.5	0.5
PI	1.3	1.5	0.7	0.7			1.5	0.4			1.3			1.1	0.5	0.2	0.4	0.6	2.7
PA	0.5	1.1	(+)	0.6	+		0.2	0.4			0.5		2.3		0.3	0.5	0.7	0.8	0.4
SC	6.3	(1.2)	(+)	(0.2)			0.3	1.0			+				0.6				0.4
DE	0.2	0.1					4.3		0.6	0.6	0.3	8.0	+		0.8	1.5	1.1		+
TOT	26.0	42.9	3.3	4.2			4.3	1.7	1.4	0.6	0.3	8.0	2.3	1.1	1.3	1.5	1.1	3.0	14.0

CO: Coula; PI: Parinari; PA: Panda; SC: Sacoglottis; DE: Detarium.

+ : Presence observed but outside of the transect or of the prospecting counting.

() : Nut species for which no nut-cracking ateliers were found but the site is within the nut-cracking regions.

For Tai, the values are given both for the habituated chimpanzee community (Tai Audrénsirou) and from the southern adjacent one yet not habituated (Tai Nipla). The measurements in Niégré, Azagny, Blépleu, Songan and Yapo have not been done along transects but along the path followed during prospecting walks. The general length recorded is given for each site in kilometers (KM). If no value is given this means the tree species was not found.

Table 3 Potential anvil and hammer densities on randomised sampled surfaces along transects (site availability) in five nut-cracking regions (left columns in table) and five non nut-cracking regions (right columns in table). The proportions of stone tools compared to wooden ones is given

	Tai Audr	Tai Nipla	Mt Kopé	Monogaga	Mt Bétro	Mt Nimba	Dagbégo	Duékoué	Niégré	Blépleu
Surface (m ²)	1860	1860	1260	1800	469	902	1020	1800	1200	780
Potential hammers										
Density per 100 m ²	0.6	1.1	27.4	3.3	16.8	37.1	0.8	0.4	18.1	6.9
% stone	8.3	25.1	98.2	96.0	93.0	68.0	50.0	57.1	98.0	98.0
n	12	20	344	60	79	335	8	7	217	54
Potential anvils										
Density per cm/m ²	2.5	3.6	3.0	0.4	4.1	6.5	0.2	0.1	1.0	2.1
% stone	3.6	0.6	59.0	43.6	86.3	89.8	7.9	14.9	81.0	100

Table 4 Distribution of the studied sites in the natural vegetation belts described by Guillaumet & Adjanooun (1971); under the different forest types are given the species that characterise them

	Guinean belt				Soudanian belt	
	Ombrophile sector		Mesophile sector		Sub-soudanian sector	
Evergreen forest	Evergreen forest	Semi-deciduous forest	Evergreen forest of medium altitude	Semi-deciduous forest	Dry forest	
<i>Diospyros</i> spp	<i>Eremospatha macrocarpa</i>	<i>Celtis</i> spp	<i>Tarrieta utilis</i>	<i>Aubrevillea kerslingii</i>	<i>Anogeissus leiocarpa</i>	
<i>Mapania</i> spp	<i>Diospyros mannii</i>	<i>Triplochiton scleroxylon</i>	<i>Chrysophyllum perpulchrum</i>	<i>Kaya grandifolia</i>	Savanna woodland	
Taï Audrenistrou	N'Zo reserve				<i>Panicum phragmitoides</i>	
Taï Nipla	Mont Bétro					
(Mont Kopé)	Monogaga					
Gó	Dagbégo	Duékoué	Mont Nimba	Marahoué	Comoé	
Yapo	Niégré (23)	Mont Péko	Gbapleu		Amaradougou	
	Niégré (25)	Nizoro	Blépleu		C. Kolonkoko	
	Azagny	Marahoué			Haut Bandama	
	Songan	Bossématié				
		Mopri				

Sites belonging to non nut-cracking regions are listed in the lower part of the table.

considered can explain the presence or absence of this behaviour. In addition, all the different populations belong to *Pan troglodytes verus* allowing us to exclude major genetical differences as an explanation for the observed behavioural differences. We are aware that ecological differences are very difficult to exclude completely but the present level of deforestation in the Côte d'Ivoire prevented us from selecting sites exactly contiguous on both sides of the Sassandra river. However, the Taï and the Niégré forests are at most 50 km apart on both sides of this river within the same floristic division, with the same latitude (5°30'N) and a similar altitude (about 100 m above sea level). The same applies for Monogaga and Dabégo forests situated on both sides of the Sassandra river, both being coastal forests at most 30 km apart. These two examples that we investigated with special care convinced us that ecological differences cannot explain the behavioural differences between the two chimpanzee populations.

Nut cracking is thus a cultural behaviour and we propose that its present distribution may be related to historical factors: During the Pleistocene (about 17 000 years ago), a big drought occurred and the desert reached the sea cutting West Africa into two forest refuges, one west from the Sassandra to Liberia, the other east from the Sassandra in Ghana (Hamilton, 1982). We may speculate that the nut-cracking behaviour appeared during this period on the western side of the Sassandra River. Once all West Africa was forested again, the size of the Sassandra river in the south prevented the chimpanzees from crossing it. This river represents also the geographic limit for five rainforest monkey sub-species (Haltcnorth & Diller, 1977). Further north, near Duékoué, it is possible to cross the river as is shown by the many hybrids of those monkeys whose distribution is restricted in the southern part of the Sassandra river (Booth, 1958). However, as this northern region is within the semi-deciduous forest zone, which is poorer in nut-producing trees (see Table 4), the propagation of the nut-cracking behaviour to the forests east of the Nzo-Sassandra rivers might have been prevented.

The presence of a strip of 50 to 100 km of semi-deciduous forest between the northern part of the nut-cracking distribution (point 11 and 12 of Figure 2) and the Mont Nimba–Mont Dan regions might explain the absence of the behaviour in these mountains. The tropical rainforest belt is, however, continuous between these two regions further west in the Nimba County in Liberia and it is in this zone that some sites with nut-cracking traces were found (Kortlandt & Holzhaus, 1987). As mentioned previously, on the Guinea side of the Mont Nimba, chimpanzees appear to crack *Coula* nuts on the higher parts of the mountain (Sugiyama, pers. comm.), whereas on the Ivorian side the *Coula* trees are restricted to the lowest part of the forest (maximum 400 m above sea level) and chimpanzees seem not to crack them there. As mentioned previously, cracking of the oil-palm nut seems to be limited to the chimpanzees of the Bossou region in Guinea (Sugiyama, 1981; Table 1) and might be a second more recent innovation.

The hypothesis of the invention of the nut-cracking behaviour in the forests of the south-west Côte d'Ivoire/south-east Liberia followed by propagation only to evergreen forests may explain this distribution. The Cavally is a smaller river than the Sassandra and was probably not a barrier south from the Mont Betto (point 11 of Figure 2). Under this scenario nut cracking in chimpanzees would be at least 10 000 years old, as it appeared within the ivorian forest refuge during the last big Pleistocene drought. This implies that no other invention of nut cracking occurs in the forest regions east of the Sassandra river. For forests farther east, the invention of nut cracking could establish itself only in very rich forest types, as we observed that the acquisition of nut-cracking skills requires 4 years of practice before the

Table 5 Behavioural differences that are proposed to be cultural and their distribution within populations of chimpanzees

Pattern	West Africa		East Africa		Other sites
	Bossou	Taï	Gombe	Mahale	
Ant-dip	+	+	+	-	Assirik
Honey-dip	-	+	+	-	/
Leaf-clip	+	+	-	+	/
Leaf-groom	-	-	+	+	/
Leaf-napkin	-	-	+	-	Kibale
Leaf-sponge	+	+	+	-	/
Marrow-pick	-	+	-	-	/
Nut-crack	+	+	-	-	Figure 1/2
Play-start	-	+	+	+	/
Self-tickle	-	-	+	-	/
Termite-fish	-	-	+	+	Assirik
Hand-clasp	-	+	-	+	Kibale
Fly-whisk	+	+	+	-	/

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

To exclude the most obvious bias (length of the study period, see Introduction), we restrict the list to long-term studies in which chimpanzees could be directly observed (more than 8 years). Under other sites, we present only the positive observations of shorter studies.

first net benefits are achieved and inventors would have to compensate for these extra costs during this practice period (Boesch & Boesch, 1990). Thus, for these further regions (such as Central Africa) we cannot exclude the possibility that nut cracking might have been invented at some time but has never become established.

In this context, it is worthwhile noting that some cultural sets of behaviour in chimpanzees are not the most adaptive solution to a given task, in the sense that they are not designed to achieve an optimal use of the environment. The length of the sticks selected by Taï chimpanzees to dip for ants, which we propose to be a cultural difference between populations, makes them four times less efficient at capturing ants than Gombe chimpanzees (Boesch & Boesch, 1990). Similarly, cracking nuts in Niégré, which is very close to Taï, would probably be beneficial but is absent. The poorly adaptive aspect of some of these cultural differences emphasises their independence from environmental parameters and the predominance of social parameters (for these cases, the rule would be "do what others do" and not "search for the best solution").

We are conscious that one positive result will not settle the problem of the presence of culture in animals, but should give more ground to it. The presented data indicate that the view of large cultural regional differences that coincide with the limits of the three sub-species of chimpanzees [i.e. the nut-crackers of West Africa versus the termite-fisher of Central and East Africa (Nishida, 1987; Struhsaker & Hunkeller, 1971; Sugiyama, 1985), the termite fishers of East Africa and the termite-diggers or termite-probers of Central Africa (Teleki, 1974; McGrew, 1992)] is not supported by more recent observations. Table 5 reviews the present evidence on the distribution of some behaviour patterns proposed to be culturally distributed. Of the 13 behaviour patterns considered, none has a large regional distribution; one,

leaf-grooming, is limited to the Tanzanian chimpanzees and two, marrow-pick and self-tickle, are limited to one population (Taï and Gombe respectively). The others present local and irregular distributions and might occur within populations that are less than 30 km apart, a pattern very similar to that of human populations (Leakey & Lewin, 1977; Tomasello, 1990).

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