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Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments

Abstract Chimpanzees (*Pan troglodytes*) are the most proficient and versatile users of tools in the wild. How such skills become integrated into the behavioural repertoire of wild chimpanzee communities is investigated here by drawing together evidence from three complementary approaches in a group of oil-palm nut- (*Elaeis guineensis*) cracking chimpanzees at Bossou, Guinea. First, extensive surveys of communities adjacent to Bossou have shown that population-specific details of tool use, such as the selection of species of nuts as targets for cracking, cannot be explained purely on the basis of ecological differences. Second, a 16-year longitudinal record tracing the development of nut-cracking in individual chimpanzees has highlighted the importance of a critical period for learning (3–5 years of age), while the similar learning contexts experienced by siblings have been found to result in near-perfect (13 out of 14 dyads) inter-sibling correspondence in laterality. Third, novel data from field experiments involving the introduction of unfamiliar species of nuts to the Bossou group illuminates key aspects of both cultural innovation and transmission. We show that responses of individuals toward the novel items differ markedly with age, with juveniles being the most likely to explore. Furthermore, subjects are highly specific in their selection of conspecifics as models for observation, attending to the nut-cracking activities of individuals in the same age group or older, but not younger than themselves. Together with the phenomenon of inter-community migration, these results demonstrate a mechanism for the emergence of culture in wild chimpanzees.

Keywords Chimpanzees (*Pan troglodytes verus*) · Tool use · Social transmission · Culture

Introduction

Over the decades that followed the discovery of termite-fishing at Gombe (Goodall 1964), examples of tool-use reported in wild chimpanzee populations have steadily increased in number. Long-term research at various sites around Africa has highlighted considerable variation among communities in the nature of objects that chimpanzees use as tools as well as the items in the environment that serve as targets toward which the tools are directed (Boesch and Boesch-Achermann 2000; Nishida 1990; Goodall 1986). Patterns in the presence or absence of distinctive tool using traditions at particular sites are now seen as defining features of unique chimpanzee cultures (McGrew 1992; Whiten et al. 1999; Yamakoshi 2001). A recent survey of geographic variation in orangutans' (*Pongo pygmaeus*) tool use and social signals has identified a corresponding pattern (van Schaik et al. 2003), and mountain gorillas (*Gorilla gorilla beringei*) are also known to exhibit not only individual but also regional variation in food processing skills (Byrne and Byrne 1993). However, the basis upon which such site-to-site differences are maintained is still a controversial issue (Tomasello 1994). While ecological factors are likely to account for at least some of the variation observed (Baldwin et al. 1981), the question remains whether population-specific traditions are maintained through inter-population genetic differences or some form of post-natal learning. Furthermore, if individual learning is involved, is it reliant upon information being passed from one member of a group to another in a social context, or is the skill acquired independently by every individual during ontogenesis (Kummer 1971)? So far, answers to questions probing the potential for transmission of traditions among wild populations of chimpanzees have only been available through inference from the geographical distribution of particular tool-using behaviours (Boesch et al. 1994; McGrew et al. 1997; Whiten et al. 1999). Studies which trace the appearance of a novel tradition and its subsequent spread within a community have been extremely rare (Boesch 1995). Here we present the first attempt at drawing together evidence from a variety of different sources to construct a model for the establishment and maintenance of cultural traditions unique to particular wild chimpanzee communities. Our conclusions are based on data collected from three complementary sources: (1) extensive field surveys charting the regional distribution of a specific tool-using behaviour, (2) long-term records tracking the developmental course of individual acquisition of the skill, and (3) a field experiment demonstrating aspects of innovation and transmission through observational learning.

Methods

Study sites and populations

The long-term study of chimpanzees at Bossou (7°39′N, 8°30′W), Guinea, West Africa began in 1976 (Sugiyama 1981, 1984), since which time the size of the community has remained relatively stable, currently numbering 19 individuals (lowest: 16, highest: 23), of whom 12 are females and 7 are males. The core area of the community's range encompasses 5–6 km^2 composed of primary and secondary forest, surrounded on all sides by dry savannah which the chimpanzees have never been seen to traverse.

Neighbouring groups inhabit the Nimba Mountains to the south-east: the nearest community so far identified occupies the forest bordering the village of Seringbara, only 6 km away. The study of chimpanzees at another Nimba site, near the village of Yeale (Cote d'Ivoire; 12 km to the south-east of Bossou), is now also underway (Yamakoshi and Matsuzawa 1993; Humle and Matsuzawa 2001). In addition, the presence of chimpanzees at Diecke forest, at a distance of 50 km to the west, has recently been confirmed (Matsuzawa et al. 1999). It is suspected that immigration between Bossou and Nimba has been possible until the recent past (with the last recorded immigration to Bossou, with high probability from Nimba, having occurred in 1982; Sugiyama 1984), whereas that between Bossou and Diecke has been prevented by the lack of continuous vegetation for decades (at least 50 years).

Data collection

Evidence of nut-cracking was collected at all four sites, either through direct observation or by locating traces of the behaviour such as broken shells scattered near pairs of stones. In the case of trace evidence, strict criteria (e.g. the presence of chimpanzee knuckle or footprints no more than 5 m from the site of nut-cracking) were applied before assigning the findings to chimpanzee activity (Humle and Matsuzawa 2001). The species of nuts cracked was determined in each case. The vegetation was surveyed and local guides questioned as to the availability of hard-shelled nuts in each community's home range.

Intensive study of nut-cracking was conducted at Bossou, beginning in 1988. Observations were carried out in a small clearing in the forest ("outdoor laboratory"; Matsuzawa 1994) located on the summit of Mont Gban, south of the village of Bossou. The clearing was roughly rectangular, 7 × 20 m, with dense forest on three sides, and a wall on the fourth constructed from branches and leaves behind which the experimenters hid, out of view of the chimpanzees. Several paths used regularly by the chimpanzees to traverse Mont Gban converged in this clearing, such that parties of chimpanzees visited the outdoor laboratory regularly, on average once a day. When stones and nuts were made available by the experimenters, the chimpanzees stopped to crack in the majority of cases.

Through the years we recorded nut-cracking ability (or lack thereof) in every member of the community along with the identity of the hand used to hold the hammer stone while performing the behaviour. Data were collected in the dry season, December to February, over a total of 20–30 h of observation each year.

Introduction of novel nuts

Along with the familiar piles of stones and oil-palm nuts (*Elaeis guineensis*), we provided the group at Bossou with exposure to hitherto unfamiliar coula (*Coula edulis*) and panda (*Panda oleosa*) nuts (Fig. 1) in the outdoor laboratory. The novel nuts were presented on a daily basis over a 2-week period during the regular field season (see above). Coula nuts were provided in 4 years: 1993, 1996, 2000, and 2002. Panda nuts were presented in 2000.

All the materials necessary for nut-cracking at the outdoor laboratory were provided by the experimenters. A total of 48 individually numbered stones were used, the largest weighing 5 kg, the smallest 0.2 kg (mean 1.2 kg, SD 1.0). These were collected from various locations around Bossou, and care was taken to ensure that no other hard objects were available at the site. Oil-palm nuts were provided in 12 small piles of 40–50 nuts each (approx. 500 g per pile), scattered around the clearing. Piles were replenished following each visit by the chimpanzees to the outdoor laboratory (between once and twice a day, on average). Panda nuts were first presented 3 at a time, arranged in a row 10 cm apart, then in a pile of 10 in a conspicuous location near the centre of the clearing. Coula nuts were provided in two piles of 30 nuts each (containing approximately equal proportions of both ripe and unripe exemplars), resembling in size the piles formed by the other two kinds of nuts. As neither panda nor coula nuts are naturally available at Bossou, they were instead collected at and brought from Diecke forest and the Nimba mountains, respectively. Nuts continued to be presented daily, until all members of the community had visited the outdoor laboratory and thus had access to the novel nuts over at least four sessions in each year that the experiments were conducted.

From behind the man-made wall of vegetation at one end of the outdoor laboratory (at a distance of approximately 20 m from the cracking site), we were able to note the responses of individuals to the unfamiliar nuts. Besides live observation, all visits by the

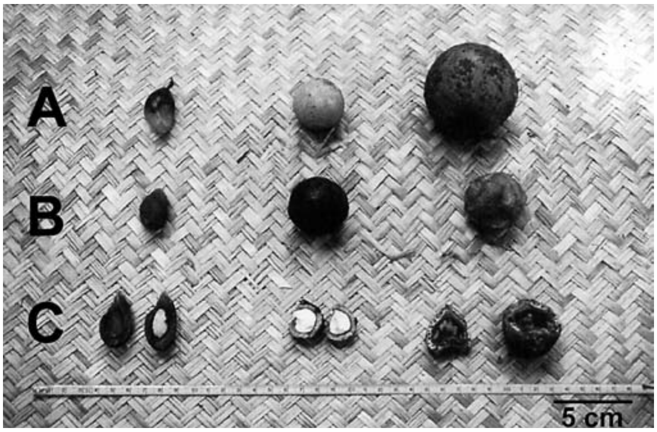

Fig. 1 Photograph showing the three species of hard-shelled nut used in the study. *From left to right*: oil-palm nuts (*Elaeis guineensis*), coula nuts (*Coula edulis*), and panda nuts (*Panda oleosa*). For each species, three stages are shown: *A* fruit, *B* hard-shelled contents of fruit before cracking, and *C* after cracking, with edible kernels visible

Table 1 Species of nuts cracked by wild chimpanzees at Bossou, Seringbara, Yeale, and Diecke. – indicates that the target nut species is not available at the site, while *No* indicates that no evidence of cracking by the chimpanzees has so far been found even though the nuts are available

Site	Distance from Bossou	Species of nut		
		Oil-palm (*Elaeis guineensis*)	Coula (*Coula edulis*)	Panda (*Panda oleosa*)
Bossou 7°39′N 8°30′W	–	Yes	–	–
Seringbara 7°38′N 8°25′W	6 km	No	–	–
Yeale 7°32′N 8°25′W	12 km	Yes	Yes	No
Diecke 7°38′N 8°55′W	50 km	No	Yes	Yes

chimpanzees to the outdoor laboratory were videotaped from different angles by two or three video cameras simultaneously (Sony Digital Handicam, DCR-VX1000).

Results

Survey of neighbouring communities

Chimpanzee communities at three of the four sites examined (Bossou, Yeale, and Diecke) were found to include individuals who used a pair of stones as hammer and anvil to crack open hard-shelled nuts (Humle and Matsuzawa 2001). However, as Table 1 shows, the range of target nut

Table 2 Longitudinal record of stone-tool use by chimpanzees at Bossou, Guinea. Individuals are sorted according to matrilinial kinship. Oil-palm nut-cracking ability (or lack thereof) and hand used to hold hammer stone recorded for all individuals since 1988 (*L* Always uses left hand for hammer; *R* always uses right hand for hammer; *A* ambidextrous use of hammer; *l* uses left hand to pound nut without a hammer; *r* uses right hand to pound nut without a hammer; *X* no successful hammer use but eating nuts cracked by others; *?* data unavailable due to lack of observation; - data unavailable as subject had not yet been born, had disappeared, or died; *N.A.* not available; *age* represents estimate as of January 2003; *figures in brackets* represent age at which individual died)

Name	Sex	Age	Mother	Year observed													
				88	90	91	92	93	94	95	96	97	98	99	00	02	03
Tua	M	Adult	N.A.	?	L	L	L	L	L	L	L	L	L	L	L	L	L
Kai	F	Adult	N.A.	?	R	R	R	R	R	R	R	R	R	R	R	R	R
Kie[a]	F	27	Kai	?	R	R	–	–	–	–	–	–	–	–	–	–	–
Kakuru[a]	F	16	Kie	?	A	R	–	–	–	–	–	–	–	–	–	–	–
Nina	F	Adult	N.A.	?	X	X	X	X	X	X	X	X	X	X	X	X	X
Na[a]	M	17	Nina	?	R	R	R	R	R	R	–	–	–	–	–	–	–
Nto[a]	F	9.5	Nina	–	–	–	–	–	X	X	X	R	R	R	R	–	–
Fana	F	Adult	N.A.	?	L	L	L	L	L	L	R	R	R	R	R	R	R
Foaf	M	22	Fana	?	R	R	R	R	R	R	R	R	R	R	R	R	R
Fotayu	F	11	Fana	–	–	–	X	X	X	AR	R	R	R	R	R	R	R
Fokaiye	M	1.5	Fotayu	–	–	–	–	–	–	–	–	–	–	–	–	X	X
Fanle	F	5.5	Fana	–	–	–	–	–	–	–	–	–	X	X	X	R	R
Jire	F	Adult	N.A.	?	L	L	L	L	L	L	L	L	L	L	L	L	L
Ja[a]	F	19	Jire	?	R	R	R	R	–	–	–	–	–	–	–	–	–
Jokro[b]	F	(3)	Jire	–	X	X	X	–	–	–	–	–	–	–	–	–	–
Julu[a]	F	9	Jire	–	–	–	–	–	X	X	X	X	r	r	r	–	–
Jeje	M	5	Jire	–	–	–	–	–	–	–	–	–	X	X	X	X	X
Jimatou	M	0.5	Jire	–	–	–	–	–	–	–	–	–	–	–	–	–	X
Velu	F	Adult	N.A.	?	R	R	R	R	R	R	R	R	R	R	R	R	R
Vube[a]	F	20	Velu	?	L	–	–	–	–	–	–	–	–	–	–	–	–
Vui[a]	M	16	Velu	?	X	X	L	L	L	L	L	L	L	L	–	–	–
Vuavua	F	11	Velu	–	–	–	X	X	X	AL	L	L	L	L	L	L	L
Veve	F	1.5	Vuavua	–	–	–	–	–	–	–	–	–	–	–	–	X	X
Yo	F	Adult	N.A.	?	L	L	L	L	L	L	L	L	L	L	L	L	L
Yunro[a]	F	18	Yo	?	X	X	X	l	–	–	–	–	–	–	–	–	–
Yela[b]	M	(0.5)	Yo	–	X	–	–	–	–	–	–	–	–	–	–	–	–
Yoro[a]	M	11	Yo	–	–	–	X	X	X	X	L	L	L	L	L	L	L
Pama	F	Adult	N.A.	?	X	X	X	X	X	X	X	X	X	X	X	X	X
Puru[a]	M	22	Pama	R	R	R	–	–	–	–	–	–	–	–	–	–	–
Pili[a]	F	15.5	Pama	?	X	R	R	R	R	R	R	R	R	R	R	–	–
Pokru[a]	M	6.5	Pili	–	–	–	–	–	–	–	–	X	X	X	X	–	–
Poni	M	10	Pama	–	–	–	–	X	X	X	R	R	R	R	R	R	R
Peley	F	4.5	Pama	–	–	–	–	–	–	–	–	–	–	X	X	AL	L

[a] Individual disappeared prior to January 2003

[b] Individual confirmed dead

species for the behaviour is unique in each community. Raw materials necessary for oil-palm nut-cracking – dried nuts and stones – are available at Bossou, Seringbara, and Yeale (density of oil-palm trees at the three sites: 7.2/km^2, 1.0/km^2, 4.2/km^2, respectively; Humle 2003), however, only the chimpanzees of Bossou and Yeale are known to perform the behaviour. In addition, the panda nut is available at Yeale and Diecke (rare in Yeale and 5/200 trees in Diecke; T Humle, H Takemoto, personal communication), yet only at the latter site have traces of cracking been found (Matsuzawa et al. 1999). Meanwhile, the coula nut is available at the same pair of sites (at a density of 5.0/km^2 in Yeale, and in clumped patches near the edge of the forest in Diecke), and is cracked at both.

Longitudinal record of skill acquisition

Table 2 presents a summary of data gathered for individual nut-cracking activity for all the chimpanzees sighted at Bossou over a period of 16 years. Such a long-term record has allowed us to highlight aspects of the skill on the individual level. We have identified a sensitive period in acquisition between the ages of 3 and 5 years (Matsuzawa 1994; Inoue-Nakamura and Matsuzawa 1997). During this time the infant remains in close proximity of the mother, who in turn serves as the primary model for the infant's observation of nut-cracking activity performed by conspecifics, particularly in the early stages of acquisition. If not learnt by the end of this period, the skill will not be acquired and individuals instead become habitual scroungers of others' abandoned half-cracked nuts. Between the ages of 8 and 14 years, performance gradually reaches an asymptote, with highly skilled individuals often requiring no more than a couple of blows of the hammer to extract the edible kernels (Fig. 2). Besides the necessity to co-ordinate three objects in a specific spatial and temporal order (Matsuzawa 1996), several other characteristics of stone-tool use obey general rules, such as the tendency to select anvils heavier than hammers (average weights 2.6 kg and 1.0 kg, respectively). However, individuals have also demonstrated considerable flexibility in the selection of tools (Sakura and Matsuzawa 1991), such as the use of a metatool, or tool-for-another-tool, where a third stone is used as a prop for a slanted anvil (Matsuzawa 1991). Taken together, these features make oil-palm nut-cracking using a pair of stones one of the most complex forms of tool use observed in the wild.

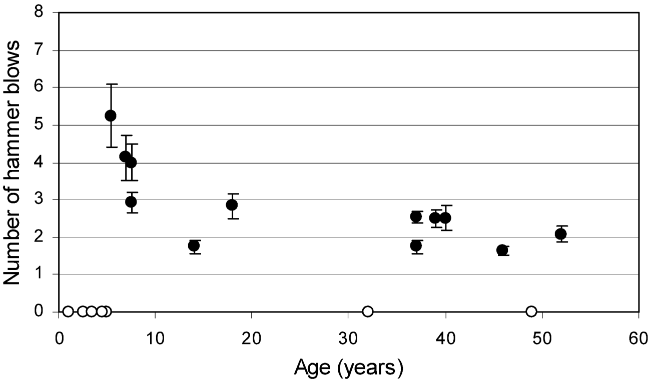

Fig. 2 Average number of hammer blows required to crack a single oil-palm nut as a function of age. Data collected in 1999 by D.B. and T.M. *Filled circles* represent the performance of individual chimpanzees who were able to crack nuts, while *open circles* show age distribution of individuals who were never seen to succeed at cracking. *Error bars* are standard errors of the mean

Once acquired, the behaviour takes on a highly stereotyped appearance (Fig. 3). Bossou chimpanzees demonstrate perfect laterality in nut-cracking, with all individuals using either the left or the right hand on every occasion (Sugiyama et al. 1993; the only exception being Fana who, in 1996, switched from left-handed to right-handed cracking, following the onset of paralysis of the left arm). Of the ten mother-offspring relationships where the cracking hand of both the mother and the offspring was known, in only four cases did we find correspondence in laterality (binomial test: P =0.205). In contrast, the degree of inter-sibling agreement in laterality is striking (Matsuzawa 1999). Currently, 13 of 14 comparisons of siblings where two or more offspring of the same mother survived to acquire nut-cracking skills demonstrate correspondence in laterality: a statistically significant departure from randomness (binomial test: P >0.001). Only a single individual (Peley) has developed divergent preferences in the identity of the cracking hand from that of his siblings, all of whom are descended from a non-nut-cracking mother (Pama).

Introduction of novel panda and coula nuts

Cracking of novel nuts

Individuals who comprised the group at the time of the study each year were divided into three age groups for the purposes of analysis: adults (based on the earliest age at which first parturition has been observed at Bossou: 9 years and above), juveniles (5–8 years), and infants (based on age at weaning: 0–4 years). Chimpanzees' responses to the unfamiliar nuts were classified into one of three general categories. First, "ignore" described individuals who displayed no visible signs of interest towards the nuts: they neither approached them, nor looked at or handled them in any way. Second, "explore" comprised the behaviour of individuals who looked at closely, handled, sniffed, mouthed, or bit into nuts. Finally, "crack" included all attempts when a nut was placed on an anvil stone and when a hammer was used to deliver blows in the manner used for oil-palm nuts, whether or not the cracking efforts were eventually successful. Table 3 shows the proportions of group members exhibiting the three different types of responses in each year when the experiments were conducted.

In the case of coula nuts, the behaviour of one individual was of particular interest: an adult female named Yo (estimated age in 2002: 40 years) who, from the very first presentation of coula proceeded to crack the nuts with all the signs of familiarity – that is without any form of exploratory behaviour (Matsuzawa and Yamakoshi 1996). The hard shell of coula nuts is covered by a thin layer of dried fruit and there is no obvious indication that an edible part is concealed below both of these layers. Nevertheless, Yo never tried to bite or chew the outer layer; instead she cracked to extract the kernel. Furthermore, she showed a clear preference for dark-coloured, ripe coula nuts (which are customarily cracked at other sites) over green, unripe ones, carefully removing all of the former from the mixed piles, and cracking them all before moving on to the latter. All other individuals who eventually went on to crack coula nuts did so after extensive sniffing and handling.

While in the initial series of presentation adult members of the group, with the notable exception of Yo, did not crack coula nuts – and of the remaining adults only half showed any interest in the novel items – all of the juveniles proceeded to either crack or explore them. Through the years of repeated presentation, such high levels of interest were sustained in this age group (at least 60% of juveniles cracking in each of the following years), while the percentage of adults attempting to crack coula gradually rose from 11% in 1993 to 33% in 1996, 40% in 2000, and 67% in 2002. This was partly due to juveniles who had already cracked in previous years growing up to adulthood, and partly to adults who had shown only exploratory behaviours in the first year or two eventually moving on to cracking (among the nine individuals who were already in the adult category in 1993, this was a significant increase: Cochran's Q =9.75, *df* =3, *P* =0.021). By the years 2000 and 2002, coula nuts had become popular targets for cracking, so much so that several individuals altogether abandoned oil-palm nut-cracking in the outdoor laboratory, focusing instead on the limited number of available coula nuts.

Results from the panda nut experiment presented a contrast to the above. Of the 13 individuals who were able to crack oil-palm nuts in 2000, only four attempted to crack the hitherto unfamiliar nuts. Two (including Yo) were adult females and two were juveniles. All four displayed exploratory behaviours of sniffing and mouthing before cracking, and after succeeding to crush the shell, the kernel was again sniffed then cautiously chewed. The only other three individuals who showed any interest in panda nuts were youngsters (two juveniles and one infant), two of whom were unable to crack nuts by themselves; they sniffed and held panda nuts in their hands before dropping and abandoning them. The remaining 13 chimpanzees

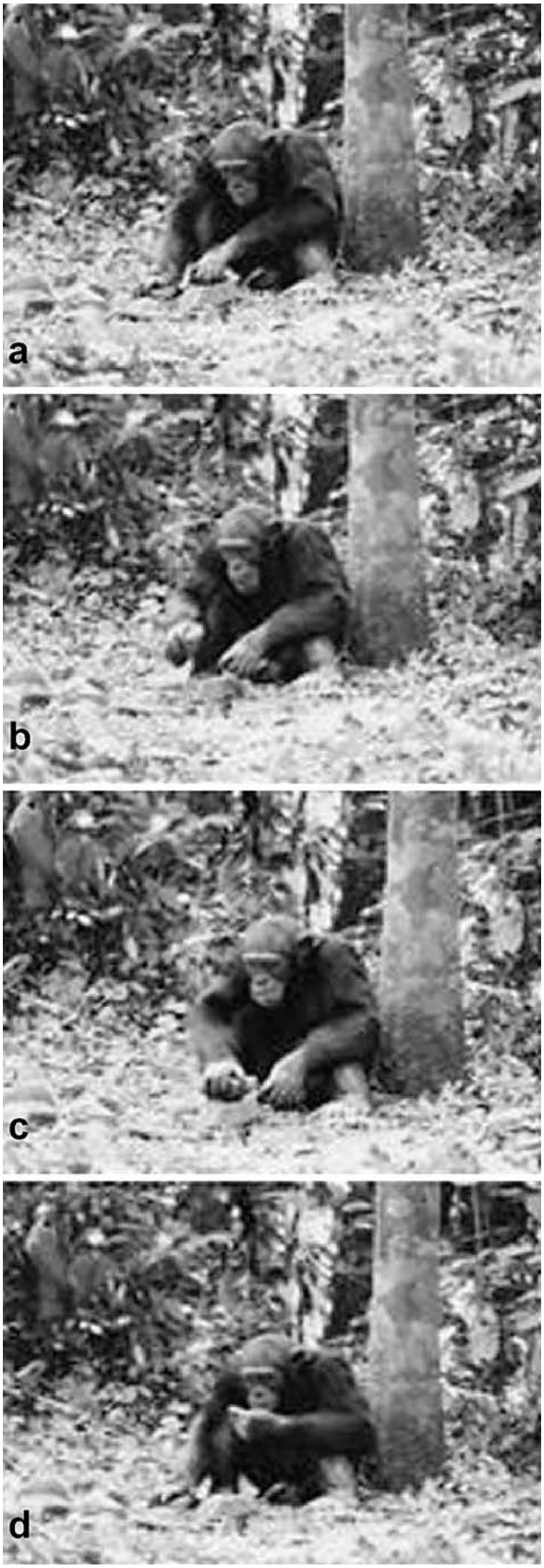

Fig. 3a–d Sequence of actions in a typical bout of nut cracking. An adult male, Na, first places a single oil-palm nut on an anvil stone using his left hand (**a**). He then uses a hammer stone, held in the right hand, to pound the nut repeatedly (**b**). Once the outer shell is broken, he retrieves the kernel with the left hand (**c**) and eats it (**d**). While members of the Bossou community include both left- and right-handed nut-crackers, for any one chimpanzee the use of the left and right hands in the four stages of nut-cracking illustrated here show perfect concordance across bouts (photos taken in Jan. 1995)

Table 3 Responses of chimpanzees in three different age classes to oil-palm nuts as well as to the presentation of novel species of nuts. *N* Number of individuals within a particular age group in given year. Values show number of individuals in each age group who attempted to crack the nuts (*Crack*), those who displayed an interest in the nuts, including handling intact nuts or eating leftovers cracked by others but did not attempt to crack themselves (*Explore*), and those who were never observed to show any interest in the nuts (*Ignore*). *Values in brackets* are proportions of the total number of individuals in the respective age group

Age group	Nut/year	Data collected by[a]	N	Crack	Explore	Ignore
Adult	Oil-palm 2000	TM, DB, CS	10	8 (0.80)	2 (0.20)	0 (0.00)
	Coula 1993	TM, NI, RT, GY	9	1 (0.11)	4 (0.44)	4 (0.44)
	Coula 1996	TM, NI	9	3 (0.33)	0 (0.00)	6 (0.67)
	Coula 2000	TM, DB, CS	10	4 (0.40)	3 (0.30)	3 (0.30)
	Coula 2002	TM, DB, CS	9	6 (0.67)	1 (0.11)	2 (0.22)
	Panda 2000	TM, DB, CS	10	2 (0.20)	0 (0.00)	8 (0.80)
Juvenile	Oil-palm 2000	TM, DB, CS	6	5 (0.83)	1 (0.17)	0 (0.00)
	Coula 1993	TM, NI, RT, GY	4	2 (0.50)	2 (0.50)	0 (0.00)
	Coula 1996	TM, NI	5	3 (0.60)	0 (0.00)	2 (0.40)
	Coula 2000	TM, DB, CS	6	4 (0.66)	2 (0.33)	0 (0.00)
	Coula 2002	TM, DB, CS	4	3 (0.75)	0 (0.00)	1 (0.25)
	Panda 2000	TM, DB, CS	6	2 (0.33)	2 (0.33)	2 (0.33)
Infant	Oil-palm 2000	TM, DB, CS	4	0 (0.00)	4 (1.00)	0 (0.00)
	Coula 1993	TM, NI, RT, GY	4	0 (0.00)	0 (0.00)	4 (1.00)
	Coula 1996	TM, NI	4	0 (0.00)	0 (0.00)	4 (1.00)
	Coula 2000	TM, DB, CS	4	0 (0.00)	4 (1.00)	0 (0.00)
	Coula 2002	TM, DB, CS	5	1 (0.20)	2 (0.40)	2 (0.40)
	Panda 2000	TM, DB, CS	4	0 (0.00)	1 (0.25)	3 (0.75)

[a] Letters indicate authors' initials: *DB* Dora Biro, *NI* Noriko Inoue-Nakamura, *RT* Rikako Tonooka, *GY* Gen Yamakoshi, *CS* Claudia Sousa, *TM* Tetsuro Matsuzawa

never approached or investigated panda nuts. This lack of interest was soon assumed by the two adult females as well, who after a single successful bout of panda-nut-cracking abandoned all further cracking efforts during subsequent sessions. Only in the two juveniles' case did cracking attempts continue, even though no further nuts were cracked.

Perhaps the most relevant analysis in the case of the panda experiment is the comparison with the initial presentation of coula nuts. For this analysis, we selected all of those individuals within the group who were present both during the coula 1993 and the panda 2000 studies, and were already within the juvenile or adult categories during both, thus creating a matched group (i.e. infants, at most 1.5 years old during coula 1993, and adults and juveniles who disappeared before panda 2000 were excluded). Although in both experiments an equal number of such individuals attempted to crack the novel nuts (2 of 10 subjects), when the proportion of individuals showing any kind of interest in the two species is examined the difference is significant, with more individuals cracking or exploring coula nuts than panda nuts, as opposed to ignoring them (Cochran's Q =4, *df* =1, *P* =0.046).

Fig. 4 An adult female, Yo, cracks newly-introduced coula nuts while two juveniles observe her actions closely. Yo was the only member of the group to crack coula nuts without initial sniffing or other exploratory behaviours. Her cracking often attracted the attention of chimpanzees from all age classes. Note the row of three panda nuts in the lower left corner (*left arrow*), which Yo completely ignored on this occasion. The pile of coula nuts is visible on the right (*up arrow*)

Observation of nut-cracking conspecifics

Individuals who made cracking attempts at unfamiliar objects often elicited great interest in conspecifics (Fig. 4). Occasionally a whole group would gather around a single nut-cracking individual. Whether some individuals were preferentially selected as models for observation was analysed by noting the identity of observers and the targets of their observation. Observation of one group member by another was said to take place when the latter approached the former to within a distance of 1 m and remained with gaze fixed upon the target individual's face or hands for at least 3 continuous seconds. Rates of observation were calculated as the number of bouts of observation per hour of nuts being handled or cracked by at least one of two or more individuals present in the outdoor laboratory.

We recorded a total of 203 observation bouts across four experiments (oil-palm, coula, and panda in 2000, and coula in 2002). Adult observers directed their observations towards related individuals (siblings, offspring, mother) in

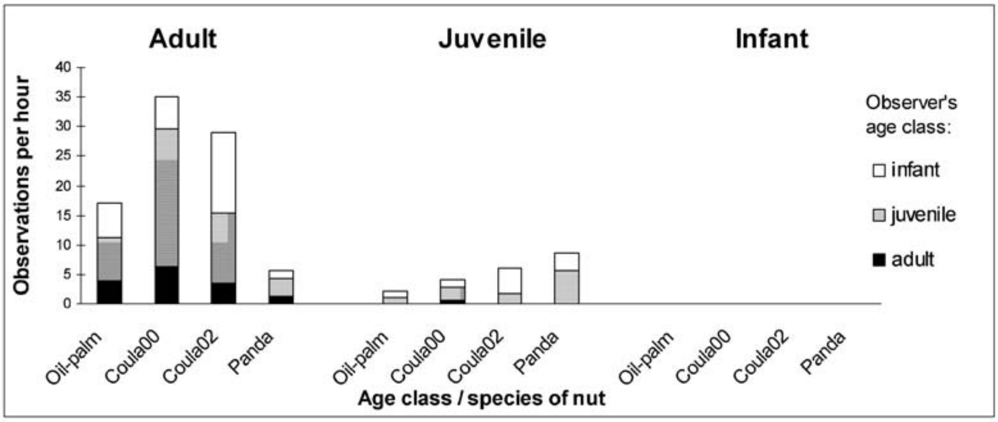

Fig. 5 Individuals in different age classes as targets of observation by conspecifics. Incidents of one chimpanzee observing another handling or cracking oil-palm, coula, and panda nuts were recorded. Observers were also assigned to one of the three age classes: adult, juvenile and infant. Values were calculated as occurrences per hour. Total time only concluded periods where either exploratory behaviours or nut-cracking attempts were being directed towards the nuts with at least two chimpanzees present in the outdoor laboratory. Data collected in 2000 (*oil-palm*, *coula00*, *panda*) and 2002 (*coula02*) by D.B. and T.M.

12.9% of cases (4 of 31 observations), juveniles in 13.3% of cases (13 of 98 observations) and infants in 55.4% cases (41 to 74 observations). Infants thus chose related individuals for observation significantly more often than adults or juveniles did (χ^2 =41.088, df =2, P <0.0001). For both juveniles and infants, the related individual chosen for observation was predominantly the mother (84.6% and 90.2% of observations of related individuals, respectively), rather than a sibling.

Adults served as the targets of observation in 170 cases, juveniles in 33, while infants were never observed. Data for rates of observation of individuals (square root transformed to meet assumptions of normality and homogeneity of variance) was analysed using a General Linear Model (rate of observation = observer's age + nut species), revealing a significant effect of age on the rate at which individuals in the three different age classes served as targets of observation ($F_{2,7}$ =21.36, P =0.001), but not of nut species ($F_{2,7}$ =1.11, P =0.383). Figure 5 shows that adults were not only the most likely to be the targets of observation but also the least likely to be observers themselves. On the other hand, juveniles were rarely targets but often observers, both of adults and of other juveniles. A one-way ANOVA showed that the rates of observations targeted towards individuals in the same age class or older were significantly higher than those targeted towards younger conspecifics ($F_{1,34}$ =20.91, P <0.001). In general, the data clearly show that the chimpanzees paid attention to the nut-cracking activities of individuals in the same age class or older, but not younger than themselves.

Discussion

The cracking of hard-shelled nuts using a pair of stones as hammer and anvil is one of the most complex tool-using skills found in the wild, which so far appears to be restricted to certain West African chimpanzee communities (Boesch et al. 1994; McGrew et al. 1997). At Bossou, Guinea, it was first discovered in 1978 (Sugiyama and Koman 1979) and has been studied extensively since 1988 (Matsuzawa 1994; Matsuzawa et al. 2001). At this site, the community's relative isolation may have facilitated the emergence of a particular constellation of behavioural traditions; in other words, the establishment of Bossou chimpanzees' own unique culture. How might the cracking of oil-palm nuts using stone anvils and hammers have entered the behavioural repertoire of the Bossou community and what ensures its continued existence? We examined three separate yet complementary lines of evidence in order to provide a model for the emergence and maintenance of such tool-using traditions in wild chimpanzee communities. Our approach combines data from an extensive geographical survey, longitudinal records of skill acquisition by individuals, and field experiments examining innovation and social transmission in the selection of targets for tool use. We will discuss the results obtained through these approaches below, focusing on (1) ecological contributions to regional variation in wild chimpanzees' tool use, (2) intra-community transmission of tool use and aspects of learning on the individual level, and (3) processes underlying inter-community transmission.

Ecological factors are not sufficient to explain regional variation in nut-cracking

Members of two of three recently discovered communities adjacent to Bossou (Yeale and Diecke) include individuals who use a pair of stones as hammer and anvil to crack open hard-shelled nuts; however, the species of nut chimpanzees use as targets of the behaviour differ among these neighbouring groups. Our survey of the vegetation in the home ranges of all four communities revealed no clear relationship between the presence of one or more of three species of nuts (oil-palm, panda, coula) at a site and the target species used in nut-cracking. Of the 12 possibilities for nut-cracking (4 sites × 3 species of nut), in four cases the behaviour is ecologically impossible (coula and panda absent at Bossou and Seringbara), while of the remaining eight possibilities, five are taken (oil-palm nut-cracking at Bossou, oil-palm- and coula-cracking at Yeale, and coula- and panda-cracking at Diecke) and three are not (oil-palm at Seringbara and Diecke, panda at Yeale). Hence, it is reasonable to conclude that ecological differences alone – such as the availability of target items – are not sufficient to explain why members of some communities use particular species of nuts as targets for nut-cracking, while others do not. What other determinants are there for these behavioural differences and how are novel nut-cracking habits incorporated into and maintained in a group's repertoire? We investigated these questions through focusing in detail on the developmental processes of acquisition.

Development of nut-cracking skill relies on individual learning aided by observation

Long-term records have allowed us to highlight various aspects of the nut-cracking skill, such as a sensitive period for the acquisition of the motor pattern involved in the activity, and the presence of perfect handedness in every individual. Furthermore, we found that all siblings, apart from a single exception, exhibited identical handedness in nut-cracking, while no such patterns were identified between mothers and their offspring. Instead, all possible combinations in mother-infant comparisons of laterality (left vs right, right vs left, right vs right, and left vs left) were exhibited. In addition, both of the non-nut-cracking mothers in the group produced several offspring who were able to crack nuts, and the single juvenile who had not fully acquired the behaviour prior to her disappearance at the age of 7 (although she frequently manipulated both nuts and stones) had a nut-cracking mother. These observed patterns invite speculation as to the factors contributing to the development of the skill.

Young chimpanzees remain in close proximity of the mother until the age of 4–5 years, continuing to suckle for as long as the first 4 years. During this period, the mother's behaviour toward her offspring is characterised by high levels of tolerance. Infants are often seen to take newly-extracted kernels from the mother's hand and interact with the stones used by her for cracking; in fact, such episodes represent 1-year-old infants' first steps toward nut-cracking. Although adults at Bossou do not engage in direct teaching (cf. two reported cases in Boesch 1991), they thus provide the setting within which individual learning occurs, aided by observation. Infants are allowed to freely explore the nuts, kernels, and stone tools used, as well as to observe closely each stage of the nut-cracking process. It is important to note that during this early stage of learning, the infants are never directly reinforced by food for their attempts, yet the latter continue for years before the first kernel is autonomously extracted (Matsuzawa et al. 2001). The motivation that drives the infants to carry on despite the lack of direct reward is a truly intriguing issue to consider. Matsuzawa et al. (2001) have described the process as "Education by master-apprenticeship", and stress that infant chimpanzees are driven not by a motivation for food but to produce a copy of the mother's actions. In this they are both motivated and aided by a strong affectionate bond with the mother, through her continuing tolerance toward them. de Waal (2001) coined the term "Bonding and identification-based observational learning" (BIOL) to refer to a similar mechanism whereby the infants' learning is "born out of the desire to be like others" (p 231). These mechanisms thus emphasise a role for models whom the infants observe and attempt to copy. In the early years of the infants' life the mother provides the most important model for observation, while as the infants grow, they begin more and more to observe other members of the community as well, including both related and unrelated individuals within the group (see Hirata and Celli 2003; Sousa et al. 2003; and Hayashi and Matsuzawa 2003, this issue, for studies exploring this topic within a captive setting).

What roles do these models play in infants' acquisition and what information is transmitted from the model to the observer? Detailed accounts at Bossou of the developmental processes involved in infant chimpanzees' acquisition of the nut-cracking skill (Inoue-Nakamura and Matsuzawa 1997; Matsuzawa 1994) do not point towards imitative learning as the underlying mechanism. Young chimpanzees go through several stages of manipulating nuts and stones, first as single objects then in various combinations, and only gradually come to approximate the correct sequence of actions. Hence, the observed models' role is likely to lie in providing the observer with information about the objects necessary and/or about the outcome of a successful bout of nut cracking – the former an example of stimulus or local enhancement, the latter a more sophisticated "emulation" learning (Tomasello 1996; see also Whiten and Ham 1992, for a taxonomy of social learning terms).

Returning to the question of inter-sibling correspondence in laterality, a number of different explanations are possible. Given the absence of clear patterns in mother-infant laterality, imitation or mirror-image imitation of the mother are unlikely to be involved. An intriguing possibility is that older siblings themselves make important models for observation, however, our data shows that these individuals are less likely to be observed by their younger siblings than are mothers or even unrelated members of the group. We favour an explanation more in line with the learning mechanisms outlined above: the possibility that some aspect of the conditions provided by each mother – under which her infants' learning takes place – may be identical in the case of each of her offspring, and encourage a particular hand being favoured in the infants' hammering. (Note that the single individual to exhibit laterality divergent from his siblings was born to a non-nut-cracking mother!) Between-mother variation may then account for the patterns in mother-infant comparisons of laterality. What features might comprise such relevant aspects of the setting within which infants' learning takes place should be elucidated in the future.

Inter-community transmission through immigration and subsequent spread of knowledge: the emergence of "cultural zones"

Our field experiments, which introduced to the Bossou group species of nuts cracked at neighbouring sites but unavailable locally, produced some interesting results relevant to the issue of cultural transmission between chimpanzee communities. In the case of coula nuts, a female named Yo stood out from the group as the only individual who proceeded to crack these nuts from the earliest presentation, with all the signs of familiarity. This suggested to us that Yo was an immigrant female, having arrived at Bossou as an adolescent prior to 1976 from a site such as neighbouring Yeale, where coula nut-cracking was part of the community's cultural repertoire. It is remarkable that she recognised the nut, presumably unseen for up to 20 years, and immediately set out to crack it without hesitation. It is also interesting that not only Yo, but also other members of the community who were observed to crack coula nuts, favoured them to the extent of temporarily abandoning oil-palm nut-cracking altogether. This was in spite of the fact that coula nuts are both tougher to break open (Boesch and Boesch 1983), and that their nutritional value is lower (energy content per 100 g of kernel of oil-palm: 663 kcal, coula: 356 kcal; Matsuzawa 1999; Boesch and Boesch 1983) than oil-palm nuts'. It is possible that novelty effects in combination with the perception of coula nuts as a limited resource among the more abundant oil-palm nuts may have been responsible.

In contrast, panda nuts are intermediate in nutritional value (407 kcal per 100 g) yet they are the hardest of the three nuts to crack: Boesch and Boesch (1983) report that in approximately 90% of cases panda nut-cracking at Tai Forest is accomplished with the aid of stone rather than wooden hammers, while the opposite is true for coula nuts which are predominantly cracked by wooden hammers. In addition, these authors found that the impulse needed to crack a single panda nut is approximately three times that required for coula (when using stone hammer on stone anvil, as at Bossou). The two Bossou females whom we observed to crack and taste panda nuts may have abandoned their efforts following this first encounter as a result of having gauged the value of these nuts as low compared to the effort invested and given the alternative nuts available. Panda nut-cracking did not continue beyond the first session in the case of adults, and in the case of juveniles became sporadic and was soon also abandoned.

The most conspicuous contrast to emerge from our behavioural observation during the coula and panda experiments was the absence in the case of panda nuts of a knowledgeable adult, possessing the equivalent of Yo's apparent familiarity with coula nuts. This may be accounted for by the low likelihood of immigration from far-away Diecke, the nearest site at which panda nut-cracking has so far been confirmed. The impact that this difference had on the overall rates, age-class distribution, and persistence of panda and coula nut-cracking within the community is perhaps best explained in terms of the reactions of individuals to others' cracking attempts. Aiming to address the question of how newly-introduced tool-using skills may spread within the community, we examined social aspects of the chimpanzees' responses to the novel nuts.

Our analysis of "observing behaviour" revealed that individuals were likely to pay close attention to the nut-cracking efforts of conspecifics in the same age group or older, but not younger than themselves. It should be noted that the juvenile as well as the adult group included successful crackers of the unfamiliar nuts and would therefore have provided similarly numerous, efficient, and salient models – yet we recorded only a single occasion where a juvenile was observed by an adult (the mother). The most general trend that emerged from this analysis was thus the tendency for chimpanzees to pay attention to the tool-using activities of conspecifics in their own age group or older, but not younger.

The contrast between the ways members of the Bossou community reacted to the two species of novel nuts is of fundamental relevance to the issue of tool-using traditions in wild chimpanzee communities. We surmise that in the presence of a "reliable" model such as an adult keenly engaged in the handling of an unfamiliar object, new behavioural traits such the cracking of novel nuts will spread rapidly and predictably within a community. On the other hand, in the absence of such models, hesitant and short-lived attempts by members of a group are not sufficient to ensure the quick spread of a behaviour among essentially neophobic individuals. Our results therefore support the hypothesis that observational learning plays a pivotal role in individuals' acquisition of population-specific behaviours such as nut-cracking. This is consistent with the "culture" interpretation, whose key prerequisite it is that a behaviour that is shared by members of a community be passed from generation to generation through non-genetic channels (Matsuzawa 1999; see also McGrew 1998 for a historical review). If a model's behaviour indeed facilitates subsequent attempts in observers, then cultural innovations are likely to spread horizontally (e.g. between unrelated juvenile playmates) or vertically/orthogonally downwards (e.g. from mother to offspring or from juvenile to unrelated infant, respectively), but not, in this case, upwards. Without the influence of immigrant adults, new cultural traditions such as the incorporation of novel targets for tool use are likely to be introduced into chimpanzee communities by juvenile members of the group, who appear to be less conservative in their food choice and more motivated to innovate. These dual aspects of innovation and transmission are thus jointly responsible for the existence of unique behavioural traits within communities, and the rates at which they take place will in turn influence the speed with which cultural traditions are assimilated over time.

Finally, it is important to note that our experiments dealt not with the introduction of an entirely novel behaviour into the community, but the adaptation of an existing tool-using skill to novel target items. We observed transmission among adult members of the group, who were well past the end of the sensitive period during which the motor patterns involved in nut-cracking emerge (despite the fact that some adults were relatively young due to our classification based on reproductive age). It is possible that such generalisation of an existing skill is supported by different learning mechanisms than the acquisition of novel actions. Precisely which aspects of a behaviour are transmitted before and after the end of the sensitive period remain to be elucidated.

Our data thus illuminates both inter-community and transgenerational aspects of cultural propagation. The three-way approach we have employed – extensive regional survey, intensive developmental tracking, and a field experiment introducing novel target items for tool use – clearly emphasises the role of observational learning both in introducing and maintaining behavioural traditions in wild chimpanzee communities. Through immigration, social transmission, and subsequent "education" through generations, sets of neighbouring chimpanzee communities can come to comprise "cultural zones" characterised by the possession of certain shared behavioural traditions. The observation that communities that share migrants do not necessarily possess identical sets of behavioural traditions further highlights the importance of within-community propagation following introduction.

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