

Ontogeny and Cultural Propagation of Tool Use by Wild Chimpanzees at Bossou, Guinea: Case Studies in Nut Cracking and Leaf Folding

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1 Introduction

The discovery more than four decades ago that wild chimpanzees habitually made and used tools (Goodall 1964) helped to put a fairly abrupt end to the notion that tool use was a defining characteristic unique to humans. Since then, reports of the skilful use of tools from a wide variety of primate and non-primate species have been accumulating steadily. As somewhat of a parallel, initial observations on the establishment and spread of sweet-potato washing behaviour by Japanese monkeys on Koshima island (Kawai 1965) as well as McGrew and Tutin's (1977) original report on regional differences in wild chimpanzee behaviour have been elaborated to such an extent since then (McGrew 1992; Whiten et al. 1999, 2001) that the issue of "culture" in nonhuman primates has become one of the hottest topics in current primatology. The debate centres on behaviours spanning the tool-using, self-maintenance, and social domains, and which are shared by individuals within specific communities but are known to be absent from or assumed different forms in other communities. Such regional variation, when it cannot be explained by ecological or genetic factors, gives rise to questions about processes underlying the emergence, maintenance, and propagation of community-specific behaviours as well as the terminology used to describe them.

Do nonhuman animals possess culture? As is often the case with questions of this sort, the answer depends on what we understand to constitute "culture"; different definitions will yield more or less inclusive pictures of how widespread the phenomenon is across the animal kingdom (see McGrew 2004 for a comprehensive review of the controversy regarding membership in the "Culture Club"). For the purposes of this chapter, we rely on a useful working definition provided by Matsuzawa (1999): culture can be thought of as "a set of knowledge, techniques, and values that are shared by members of a community and transmitted from one generation to the next through non-genetic channels."

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focus on two tool-using behaviours which, although in general aspects not unique to our study site at Bossou, Guinea, are not found universally across all chimpanzee populations in Africa. One, the cracking of hard-shelled oil palm nuts (*Elaeis guineensis*) with the aid of a pair of stones as hammer and anvil, is restricted to West African chimpanzees, which is surprising as both nuts and stones are readily available in the habitats of Central and East African populations. The other, the use of leaves for drinking water, has been observed at many sites; however, the precise techniques used vary considerably across populations. At Bossou, leaf folding (the use of leaves that are folded, accordion-like, inside the mouth before being dipped into water and retrieved) dominates over other forms of leaf use in drinking (such as leaf sponging or leaf spooning). For both these behaviours we examine general features common to skilful users of the tools, such as tool selectivity and technique, as well as developmental aspects involved in the acquisition of the skill by young members of the group. Our setup provides us with a unique window of observation, allowing us to study the two behaviours side by side: at the same place, at the same time, and in the same individuals across several years. In accordance with the definition of culture outlined here, we examine what forms of social transmission may be responsible for the maintenance of these behaviours within the Bossou group, leading ultimately to the kind of community specificity that may be regarded as a hallmark of primate cultures.

2 The Study Site

2.1 Bossou

Bossou, located in the southeastern corner of the Republic of Guinea and home to a small group of chimpanzees of the Western subspecies (*Pan troglodytes verus*), is one of eight major long-term chimpanzee research sites around Africa. Study at the site began in 1976 and is about to enter its fourth decade. Research has focused on a variety of disciplines, including chimpanzee ecology, behaviour, genetics, physiology, and conservation. Until 2003, the size of the Bossou community had remained relatively stable around 20 individuals (minimum 16, maximum 22). However, a flu-like epidemic at the end of 2003 took the lives of 5 community members (Matsuzawa et al. 2005), and the disappearance (probable emigration) of 3 more individuals in 2004, followed by the birth of a single infant, means that the group currently numbers only 12 individuals, the lowest in the past 29 years.

The core area of the Bossou community measures about 5 to 6 km², consisting mainly of primary and secondary forest. This core area is surrounded by savanna and cultivated fields, which the chimpanzees do not commonly traverse. Beyond a stretch of about 3 to 4 km of this savanna lie the Nimba Mountains, West Africa's largest mountain range and home to a large number of chimpanzees.

Because of the isolated nature of Bossou, both immigration and emigration—common features of wild chimpanzee societies—have been rare. Only three cases of transient immigration have been recorded; none of these individuals remained permanently at Bossou (the three visits lasted 1 day, 20 days, and somewhere between 3 months and a year, respectively; Sugiyama 1999). Emigration has likely occurred more often, as several community members (mainly adolescents or young adults of both sexes) have disappeared, although in none of these cases is it known whether these individuals successfully joined adjacent communities because their presence at neighbouring sites has never been directly confirmed.

Bossou chimpanzees are known to utilize a variety of tools in feeding contexts; these include nut cracking, the use of leaves for drinking water, ant dipping, termite fishing, algae scooping, and pestle pounding (see Sugiyama 1998; Matsuzawa 1999, for extensive reviews). In addition, examples of tool use in non-feeding contexts have also been reported (Hirata et al. 1998, 2001b; Matsuzawa 1997).

2.2 Outdoor Laboratory at Bossou

Witnessing tool-using behaviours in the chimpanzee's natural habitat, particularly obtaining longitudinal records on specific individuals, is often complicated by the unpredictability of encounters with community members as well as the often dense vegetation through which the behaviours must be observed. In 1988, T. Matsuzawa set up a facility for the intensive observation of tool-using behaviours at Bossou (Matsuzawa 1994). In a clearing at the top of one of the hills within the Bossou groups' core area, an "outdoor laboratory" was established, with the aim of increasing rates of encounters with all members of the community as well as the opportunity to observe tool-using behaviours in a visually uncluttered environment (Fig. 1). The laboratory is opened once each year for a period of approximately 1 to 2 months during the dry season (in December, January, or February), during which time researchers control the availability of various items inside the clearing. The location of the clearing is such that it is at the crossroads of several paths used frequently by all members of the Bossou group, and as a result chimpanzee parties of various sizes visit the outdoor laboratory on average once a day. Observers, hidden behind a grass screen at one end of the clearing, monitor the site from 0700 until 1800 each day and video record all visits by chimpanzees from at least two different angles simultaneously.

Besides easy and regular visual access to individuals, there is another important advantage associated with the outdoor laboratory. The setup facilitates extremely detailed observation of the same community members across many years, focusing not only on a single behaviour but on various different skills. These skills can be observed at the same place, often within no more than a few minutes of each other, as is the case with nut cracking and leaf folding. For

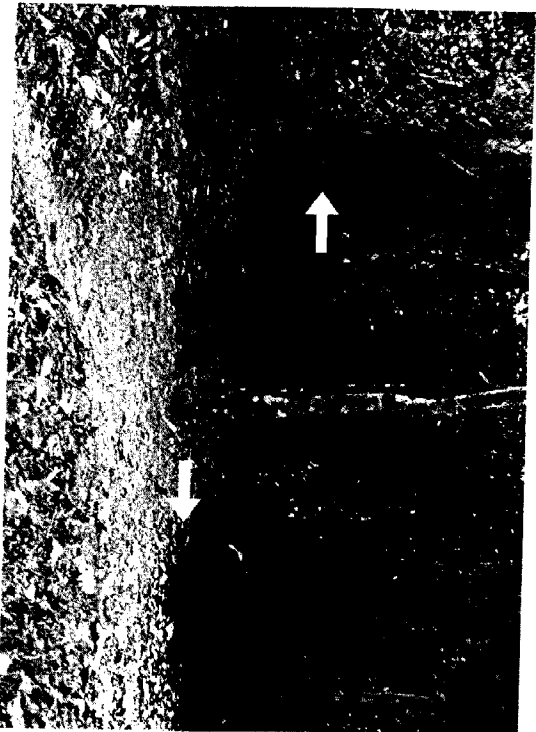


Fig. 1. "Outdoor laboratory" where intensive observations of tool-using behaviours were conducted. The arrow on the left points to a tree with an enlarged natural hollow containing water (only the forward-facing hole is visible; a second hole is located in the side of the tree, facing right; see Fig. 2B), from which chimpanzees drank with the aid of folded leaves. An adult female can be seen putting a leaf tool into her mouth, having just retrieved it after dipping it into the water inside the tree hollow. The arrow on the right shows the location of about 50 stones laid out within a small rectangular area (see Fig. 2A); from among these, chimpanzees selected their tools for use in nut cracking. Piles of oil-palm nuts were scattered on the ground within the clearing before the group's arrival, and several individuals can be seen performing the behaviour (most prominently an adult male in the centre). Photograph was taken from behind a grass screen that separated the observers from the chimpanzees inside the outdoor laboratory.

example, we might observe a 3-year-old infant chimpanzee rolling stones and nuts on the ground and scrounging freshly extracted kernels from his mother, then shortly thereafter picking up a leaf tool discarded by an older individual and dipping it into a tree hollow to retrieve water. In a couple of years' time, we may see the same individual successfully cracking nuts by himself, then not only using but also making his own drinking tool. Such longitudinal records provide us with data on individual acquisition of skills, as well as the relative course of development of different behaviours within individuals.

2.2.1 Nuts and Stones for Cracking

The initial focus of the outdoor laboratory studies was nut cracking: researchers provided a set of numbered stones of known weights and dimensions (while clearing the area of all other naturally occurring stones) as well as 2 to 5 kg of oil-palm nuts laid out in several piles (Fig. 2A). Chimpanzees that visited the



Fig. 2. Materials at the outdoor laboratory used in the nut-cracking and leaf-folding study reported here. A Stones available within the clearing as arranged before the arrival of a party of chimpanzees. A pile of oil-palm nuts is visible to the right of the top-right corner of the stone matrix; another can be seen above the top-left corner. B The tree at the back of the outdoor laboratory from which chimpanzees drank using leaf tools. The two holes are approximately right angles to each other

clearing utilized the nuts and stones present. After each visit, the supply of palm nuts was replenished and the stones were returned to their original positions. Analyses of these episodes provided data on various aspects of behaviour. For example, in the following sections we explore topics such as characteristics of objects that were preferentially selected as hammers or anvils, individual differences in technique, and stages of development that young chimpanzees pass through before they acquire the skill.

2.2.2 Artificial Tree Hollow for Drinking

In addition to nut cracking, the outdoor laboratory also provided an excellent opportunity to observe leaf-folding behaviour. Particularly in the dry season when the nut-cracking experiments were conducted, water is a relatively scarce resource and the provision of water at this site meant that chimpanzees drank here with the aid of leaves gathered inside or at the edge of the clearing. A natural hollow in a large tree (*Richinodendron heudelotii*) at the back of the clearing was cleaned and filled with clear water, the natural entry hole enlarged and an extra hole drilled (Fig. 2B). The hollow had a capacity to hold about 17 l water. The amount of water drunk during each visit by a party of chimpanzees was measured by refilling the water to the brim once all chimpanzees had exited the clearing. At the same time, the locations of all discarded leaves (clumps of folded leaves) on the ground were noted for subsequent matching to the user based on video records, then at the end of the day (or, in the case of years of the study, just after the party's departure) removed from the clearing for laboratory for further analysis.

3 Nut Cracking and Leaf Folding: Techniques and Individual and Age-Related Differences

In this section, we summarize what long-term records have revealed about the characteristics of nut cracking and leaf folding, focusing on both the details of techniques that skilled adult performers apply in the tasks and the developmental stages in young chimpanzees' acquisition of the skill. Figures 3 and 4 illustrate the two tasks and provide outlines of the different behavioural components involved in their performance.

3.1 Skilled Performers

Nut cracking by chimpanzees using a pair of stones as hammer and anvil was first reported by Sugiyama and Koman (1979) and is regarded as one of the most complex forms of tool use found in the wild. According to Matsuzawa's (1996) scheme, nut cracking constitutes 'level 2' tool use: three objects must be related to each other in a specific temporal and spatial pattern. Thus, a typical bout of nut cracking would proceed as follows. First, a nut (object 1) must be stably

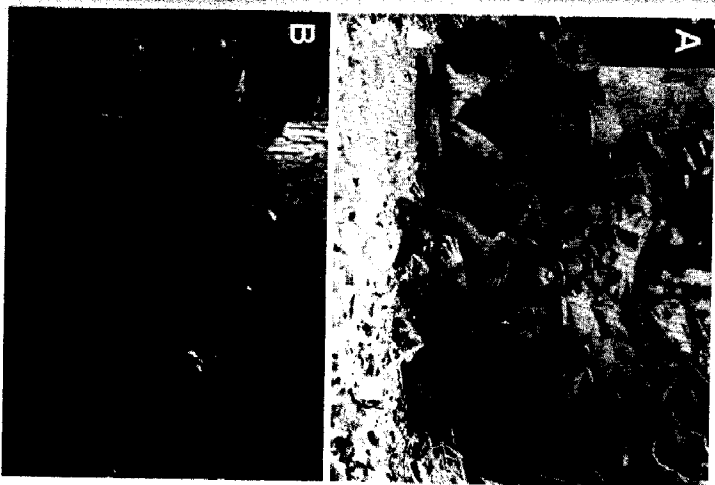


Fig. 3. Chimpanzees at Bossou performing the tool-using tasks examined in the present chapter. A Two adult females, Velu and Jire, crack oil-palm nuts with the aid of a pair of stones. Velu (left) has just placed a nut on an anvil stone with her left hand and is about to strike it with a hammer stone held in her right hand. Jire (right) has just struck the nut with a hammer held in her left hand, while her infant observes her actions from close range. B An adult female, Jire, drinks water from the artificial tree hollow with the aid of leaves. The leaves are visible in Jire's right hand, held between the index and middle fingers, being withdrawn from the hole. A younger female, Vuavua, is visible on the right, observing Jire's actions

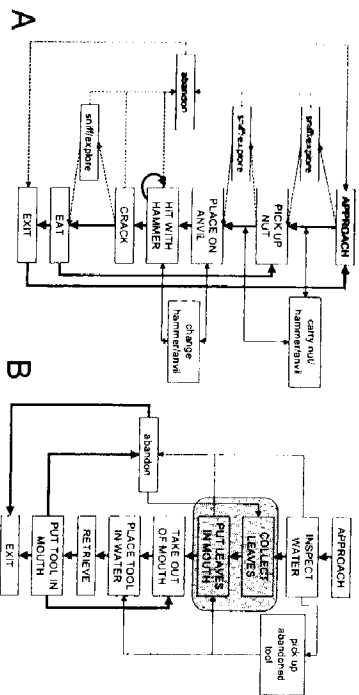


Fig. 4. Flowcharts illustrating main behavioural stages in (A) nut cracking and (B) leaf folding for drinking water. *Capital letters* and *thick arrows* correspond to a typical bout as performed by adult users of the tools; *lowercase letters* and *thin arrows* correspond to variations less frequently observed in adults and more common in infants and juveniles. *Dashed arrows* in A show behaviours observed during the presentation of unfamiliar species of nuts (see Section 4.2), not normally seen in the case of oil-palm nuts. *Grey box* in B indicates the tool-making phase observed from the age of about 3.5 years (younger individuals use tools abandoned by others only; see Section 3.3.1).

placed on an anvil stone (object 2). Next, a hammer stone (object 3) must be used to strike the nut with a force appropriate for cracking the shell, but leaving the contents (the kernel) relatively unharmed. The kernel can then be retrieved and eaten, and the process repeated with the next nut.

Leaf folding, in contrast, is an example of a “level 1” tool use. One object (crumpled leaf or, more often, two or more leaves folded in parallel) is related to another (water). However, unlike nut cracking, leaf folding incorporates a tool-manufacturing as well as a tool-using phase, both of which the individual must perform to succeed. A typical bout of drinking water with the aid of folded leaves may begin by a chimpanzee approaching a drinking source (tree hollow filled with water, in our experiments) and inspecting it. He will then retreat to collect from one to about four leaves of a plant (generally one fairly close by, up to about 2 m away, although individuals sometimes move further away or even arrive with a tool already in the mouth) (Sugiyama 1995; Tonooka 2001). The leaves will then be put into the mouth, and parts of the leaves may be trimmed away with the hand and teeth. The leaves inside the mouth are occasionally chewed, but mainly just laid parallel and folded accordion-like (Fig. 5) with 2 to 3 cm between ridges. The tool thus made is then taken out of the mouth and, held between the index and middle fingers, inserted into the tree hollow, dipped into the water, then retrieved and returned to the mouth, and the water carried between the folds of the leaves is drunk. The tool can be reused several times by reinserting it into the water, and is eventually dropped when the drinking bout is over or if the individual begins to make another tool from fresh leaves.



Fig. 5. Leaf tool (*Hybophyllum brauniium*, the most commonly used species in the outdoor laboratory) for retrieving water from a tree hollow. **A** The tool as it was found immediately after the user had dropped it following a bout of drinking. **B** The same tool unfolded to reveal the characteristic accordion-like shape, achieved by folding several leaves inside the mouth.

3.1.1 Tool Selectivity

Are chimpanzees specific in their choice of tools they use for cracking nuts and drinking water? In both cases, it is clear that certain objects will make more efficient tools than others: for example, a stone that is too large will not make a good hammer if the individual has difficulty lifting it; leaves that are too small or too fragile will reduce the volume of water retrieved.

We examined tool choice in nut cracking in the outdoor laboratory, where the weight and dimensions of each available stone were known (52 stones, ranging in weight from 0.2 to 5 kg). During observation at the outdoor laboratory, as well as from video data, we recorded where possible the identity of the stones being used as hammer and anvil, as well as the chimpanzee who used them. From a total of 550 such stone identifications (between 1999 and 2002), we calculated average hammer weights to be 1.0 kg and anvil weights to be 2.5 kg. This tendency was clear at the individual level as well: all individuals observed nut cracking showed a preference for heavier anvils than hammers on average. Of all hammer-anvil sets where both stones could be identified, only in 12% of cases was the hammer heavier than the anvil.

Figure 6 shows patterns in the use of stones of different sizes as hammer and anvil. The data confirm that while small stones tended to be used primarily as hammers and large stones as anvils (indeed, anything over 2.5 kg almost exclusively so), stones of intermediate sizes were used as both anvil and hammer with comparable frequencies. Seven stones were never used; all of these weighed 0.5 kg or less. Weight was not the only factor determining use, however, as several stones around 0.5 kg were in fact quite popular: these tended to be stones with a more compact shape rather than elongated, with one or more wide, flat surfaces.

In a similar vein, chimpanzees showed selectivity in the species of plants whose leaves they use in manufacturing drinking tools. Leaf tools generally consist of several leaves (usually between one and four) of the same species, torn

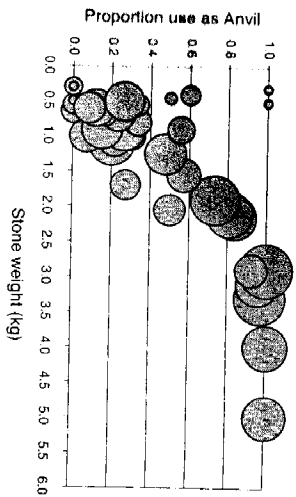


Fig. 6. Use of stones provided at the outdoor laboratory as hammer and anvil as a function of weight. Each circle represents a single stone, with the diameter of the circles corresponding to the relative frequencies with which the stones were used (the smallest circles indicate a single use; the largest represents 35 uses). Height on the y-axis corresponds to the ratio of use of the stone as anvil; i.e., 1 = exclusive use as anvil, 0 = exclusive use as hammer.

off at the same time by grasping them in one hand and pulling them off a live branch. We found that in the outdoor laboratory the majority (about 75% in 2002 and 50% in 2003) of the tools were made from *Hybophyrium braunianum* leaves, with *Napoleona vogelii* and *Carapa procera* becoming more common over the course of the 2003 field season (M. Hayashi, personal communication). In Tonooka's (2001) study, carried out at a different tree outside the outdoor laboratory, the majority (76%) of leaf tools belonged to *H. braunianum*, with three more species (*Aningueria robusta*, *Blighia sapida*, and *Thaumatococcus daniellii*) making up most of the rest. Sugiyama (1995) also reports that most drinking tools were made from *H. braunianum* and *C. procera*. Thus, in all these studies, *H. braunianum* seemed to be a strongly preferred candidate for tool-making over other species that were equally accessible around the vicinity of the drinking sites. The leaves of this species are fairly soft and are characterised by a large, smooth, hairless surface. Leaves of the other species listed are smaller, but are also hairless, smooth, and soft. It is likely that such characteristics contribute to tool effectiveness, and empirical evidence regarding, for example, the amount of water that comparably sized tools made from different species can hold is currently being evaluated.

3.1.2 Tool Fidelity

Within a nut-cracking bout, adult chimpanzees rarely exchanged their hammers or anvils for other stones. When individuals entered the outdoor laboratory, they often approached the stone matrix first, selected two stones, and transported them to one of the piles of nuts scattered around the clearing. Once that pile was exhausted, chimpanzees often transported both hammer and anvil across the clearing to the next pile. Such transports have been studied extensively at the Tai Forest, Ivory Coast (Boesch and Boesch 1984), where chimpanzees have been observed to carry stones over distances of several tens or even hundreds of

metres when nut trees of a rarer species did not have any suitable stones around them. In general, in Bossou such transports tend to be much shorter, as stones are readily available throughout the forest (Sakura and Matsuzawa 1991).

Similarly, adult chimpanzees began a drinking bout by manufacturing a tool, which they then continued to reuse until the end of the bout (on average, about 25–30 times in roughly 10-min bouts). Additional leaves were sometimes added to the existing tool (26% of bouts), but rarely did they drop the current tool to make a new one to continue drinking (Tonooka 2001). In both cases, the fate of the tools left behind by adults (whether a pair of stones balanced on top of or next to each other, or a clump of folded leaves) is extremely interesting in itself. We return to this point in more detail in Section 3.3.1.

3.1.3 Metatools

In addition to serving as hammers and anvils, stones in the outdoor laboratory very occasionally took on another role as well: that of a meta-tool. Matsuzawa (1994) reports three instances (an adult female in 1991, and an adult and a juvenile male in 1992) when chimpanzees at Bossou placed a third stone beneath their anvil as a wedge, stabilizing the anvil and maintaining a flat, horizontal upper surface. We have observed such cases in subsequent years as well (Fig. 7); however, it is sometimes difficult to ascertain to what extent individuals understand the function of the metatool. We suspect that the construction in Fig. 7, for example, was accidental rather than deliberate, as it came about after the individual turned the anvil stone over several times, probably in an attempt to stabilize the upper surface, until it rolled onto the stone that then served as the wedge. Nevertheless, genuine metatools in the nut-cracking context raise the stakes considerably in the search for the most complex tool use found in the wild: at present the wedge is the only example of a 'level 3' tool (Matsuzawa 1996).

An analogous example in the case of the use of leaves for drinking water has been reported (Matsuzawa 1991; Sugiyama 1995), this time performed by a 4-



Fig. 7. Use of a 'metatool' in nut cracking. A wedge stone (number 8) is inserted under the anvil stone (number 67), which in turn now has a flat upper surface. Note the nut-shell leftovers on top of the anvil; photograph was taken immediately after the chimpanzee user exited the scene.

year old female. This individual was seen to use a dead twig to push a leaf tool deep into a tree hole, then use the twig to retrieve it, before putting it into her mouth and drinking.

3.1.4 Laterality

One of the benefits of the outdoor laboratory setup is that individuals' performance in the tool-using tasks can be followed within a bout of tool use, across a field season, and over several years. This advantage has allowed us to collect data on longitudinal aspects of the behaviours. Table 1 shows, for each of the individuals at Bossou since the start of the outdoor laboratory experiments in 1988, records of nut-cracking ability and the hand used in hammering. Of these 34 chimpanzees, 11 were never seen to succeed at cracking nuts: 2 were adult females, 2 were infants who disappeared together with their mothers, 4 were infants who died, 1 is a current infant, and 2 were juveniles who both disappeared before they reached adulthood although they had already shown some form of hammering action, albeit without success. The remaining 23 chimpanzees show a striking pattern: they exhibit perfect laterality on the individual level. The hand used to hold the hammer stone is consistent from nut-to-nut, day-to-day, and year-to-year. The only two exceptions are Fana, who in 1996 switched from the left to the right hand for hammering following paralysis of the left arm, and Jeje, who has just begun to crack nuts successfully and currently uses both hands alternately (a phase observed in other new crackers as well; see Section 3.2.3).

Taking all crackers (excluding Fana and Jeje) into consideration, right-handers outnumber left-handers at 62% versus 38%, respectively, but this does not correspond to a significant community-level bias (binomial test; $n = 22$, $P = 0.097$). It has recently been argued (Lonsdorf and Hopkins 2005) that given larger sample sizes, such differences should emerge as significant, demonstrating population-level handedness in nut cracking as well as other tool-using tasks, such as termite fishing and leaf sponging (a variation on leaf folding where leaves are chewed to produce a sponge-like waedge which is then dipped into water). This intriguing possibility remains to be seen at Bossou.

Other interesting patterns in Table 1 concern the distribution of right- and left-handed crackers within matriline. Arguing against a genetic explanation for handedness, congruence in laterality is found in only 4 of the 16 mother-infant pairs where the infant's handedness was known. In 6 cases, laterality was incongruent, while in the remaining 6 pairs nut-cracking offspring belonged to non-nut-cracking mothers. On the other hand, between siblings we found near-perfect congruence in handedness: only a single infant (Peley) developed a cracking hand different from his siblings. Note that Peley and his siblings were descended from a non-nut-cracking mother, Pama. The implications of this interesting pattern are discussed in Section 3.3.3.

In terms of general patterns in laterality, leaf-folding behaviour presents a contrast. Figure 8 shows data collected in 2000 on individuals' use of the left and

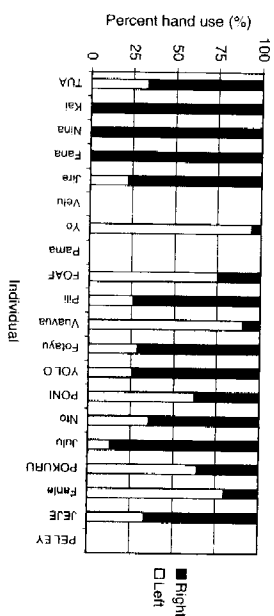


Fig. 8. Laterality during use of folded leaf tools. The hand used to dip the tool into the water, retrieve it, and place it into the mouth was recorded for each dipping action. Males are in *capitals*, females in *lowercase*. Data were collected in 2000; individuals for whom no data were obtained during the period of observation that year (Velu, Pama, and Peley) were seen performing the behaviour in other years.

right hand in dipping leaf tools into the tree hollow. Although a few individuals do show consistency in the use of hand, the majority have been observed to use both the left and the right hand to perform the action. Even within the same drinking bout, chimpanzees will change the hand used to dip the tool into the water (adults at a rate of about 0.27 times per bout). It is more difficult to assign clear left- or right-handedness to individuals than in the case of nut cracking, although some degree of preference for a particular hand is shown by most individuals.

There are several factors that may contribute to the lack of perfect laterality in individuals performing the drinking task. Tree holes are often located in hard-to-reach places where the orientation of the hole and nearby branches which chimpanzees grasp for stability may determine which hand is free for performing the task. At the tree in the outdoor laboratory, two individuals could drink from the hollow simultaneously, which meant that the hand used in the dipping action was strongly influenced by the hole next to which the individual happened to be or was forced to assume position.

Table 2 examines concordance in hand preference between nut cracking and leaf use within individuals and within mother-infant pairs. Neither shows a clear pattern, with about half the individuals preferring the same hand in both tasks, while the other half use different hands, and about half of the mother-infant pairs showing concordance in the preferred hand while the other half do not. This observation argues both in favour of "handedness" being task specific rather than task independent and against a genetic explanation for individual patterns.

3.2 Ontogeny

The longitudinal data on nut cracking presented in Table 1 are clearly also informative regarding the processes of acquisition. None of the infants born at

Table 1. Longitudinal record of stone-tool use by chimpanzees at Bossou, Guinea

Name	Sex	Age	Mother	Year observed															
				88	90	91	92	93	94	95	96	97	98	99	00	02	03	04	05
Tua	m	Adult	N.A.	?	L	L	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*	f	29	Kai	?	R	R	—	—	—	—	—	—	—	—	—	—	—	—	—
Kakuru*	f	18	Kie	?	A	R	—	—	—	—	—	—	—	—	—	—	—	—	—
Nina*	f	(Adult)	N.A.	?	X	X	X	X	X	X	X	X	X	X	X	X	X	—	—
Na*	m	19	Nina	?	R	R	R	R	R	R	—	—	—	—	—	—	—	—	—
Nto*	f	11	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	R	R
Foaf	m	24	Fana	?	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
Fotayu*	f	13	Fana	—	—	—	X	X	X	AR	R	R	R	R	R	R	R	R	—
Fokaiye*	m	3.5	Fotayu	—	—	—	—	—	—	—	—	—	—	—	—	X	X	X	—
Fanle	f	7	Fana	—	—	—	—	—	—	—	—	—	X	X	X	R	R	R	R
Jire	f	Adult	N.A.	?	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Ja*	f	21	Jire	?	R	R	R	R	—	—	—	—	—	—	—	—	—	—	—
Jokro†	f	(3)	Jire	—	X	X	X	—	—	—	—	—	—	—	—	—	—	—	—
Juru*	f	11	Jire	—	—	—	—	—	X	X	X	X	r	r	r	—	—	—	—
Jeje	m	7	Jire	—	—	—	—	—	—	—	—	—	X	X	X	X	X	X	A
Jimato†	m	(1.5)	Jire	—	—	—	—	—	—	—	—	—	—	—	—	X	X	—	—
Joya	f	0.5	Jire	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X
Velu	f	Adult	N.A.	?	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
Vube*	f	22	Velu	?	L	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vui*	m	18	Velu	?	X	X	L	L	L	L	L	L	L	L	L	L	L	L	—
Vuavua*	f	13	Velu	—	—	—	X	X	X	AL	L	L	L	L	L	L	L	L	—
Veve†	f	(2.5)	Vuavua	—	—	—	—	—	—	—	—	—	—	—	—	X	X	—	—
Yo	f	Adult	N.A.	?	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Yunro*	f	20	Yo	?	X	X	X	l	—	—	—	—	—	—	—	—	—	—	—
Yela†	m	(0.5)	Yo	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Yolo	m	13	Yo	—	—	—	X	X	X	X	L	L	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	X	X
Puru*	m	24	Pama	R	R	R	—	—	—	—	—	—	—	—	—	—	—	—	—
Pili*	f	17	Pama	?	X	R	R	R	R	R	R	R	R	R	R	—	—	—	—
Pokru*	m	8	Pili	—	—	—	—	—	—	—	—	X	X	X	X	—	—	—	—
Poni†	m	(9)	Pama	—	—	—	—	X	X	X	R	R	R	R	R	R	R	—	—
Peley	m	6	Pama	—	—	—	—	—	—	—	—	—	—	X	X	AL	L	L	L

Individuals are sorted according to matrilineal kinship

Oil-palm-nut-cracking ability and hand used to hold hammer stone recorded for all individuals since 1988

Age represents estimate in years as of January 2005; numbers in parentheses represent age in years at which individual died

*Individual disappeared before January 2005

†Individual confirmed dead

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 because of lack of observation; —, data unavailable as subject had not yet been born, had disappeared, or died; N.A., not available

Table 2. Comparison of hand preference in nut cracking and the use of leaves for drinking water

Name	Sex	Mother	Hand preference		Mother-infant concordance	
			(a) Nut cracking	(b) Leaf folding	(a)-(b) concordance	(a) (b)
Tua	m		L	R	X	
Kai	f		R	R	✓	
Nina	f		—	R		
Fana	f		R	R	✓	
Jire	f		L	R	X	
Velu	f		R	—		
Yo	f		L	L	✓	
Pama	f		—	—		
Foaf	m	Fana	R	L	X	✓
Pili	f	Pama	R	R	✓	(X)
Vuavua	f	Velu	L	L	✓	X
Futayru	f	Fana	R	R	✓	✓
Yolo	m	Yo	L	R	X	✓
Poni	m	Pama	R	L	X	X
Nto	f	Nina	R	R	✓	(X)
Juru	f	Jire	—	R	✓	✓
Pokuru	m	Pili	—	L		X
Fante	f	Fana	R	L	X	✓
Jeje	m	Jire	A	R	?	X
Peley	m	Pama	L	—		✓

Column for hand preference in leaf folding is based on hand used more often during the task. Data are for individuals present at Bossou in 2000 (arranged in order of decreasing age). Hammering hand for the youngest individuals not yet able to nut crack in 2000 was determined in subsequent years. (X), concordance was not possible to evaluate as the mother never engaged in nut cracking. ?; Jeje is at present ambidextrous in nut cracking, hence concordance cannot yet be determined.

Bossou during the period covered by the outdoor laboratory studies was able to successfully crack nuts before the age of 3 to 3.5 years. In addition, individuals who did not begin to crack by the age of about 7 years were never seen to acquire the skill later in life, which has led to the proposition that there exists a critical period for learning the skill (Matsuzawa 1994). Similarly, no infant younger than about 2 years has been seen drinking water with the aid of folded leaves, and none younger than 3.5 years has been observed manufacturing and using their own drinking tool. Nevertheless, all infants who remained at Bossou beyond that age were eventually seen to perform the behaviour. What stages do infants go through on their way to acquiring these skills?

3.2.1 Overview of the Stages of Learning

Inoue-Nakamura and Matsuzawa (1997) examined in detail the learning processes in young chimpanzees' acquisition of nut cracking. Three infants' progress was followed from 0.5 to 3.5 years of age over four consecutive field seasons. Fine-scale analysis of the infants' interactions with nuts and stones revealed that in the early stages of development such interactions were restricted to the manipulation of single objects on their own, such as holding a stone or rolling a nut. This stage was followed by multiple actions on multiple objects in combinations of increasing complexity and appropriateness in terms of the demands of the task. By the age of 1.5 years, infants had performed all the actions that constitute components of the nut-cracking sequence, albeit they had never combined them in the appropriate order. For example, they would pick up a nut and place it on an anvill, but then hit it with the hand, or pick up a hammer but use it to hit another stone or a nut not yet positioned on an anvill. It took 2 more years before the separate actions condensed into the correct temporal and spatial order and the infants were able to crack their first nut by themselves.

Drinking water with the aid of folded leaves differs from nut cracking in that it involves two distinct phases: a tool-making and a tool-using phase. Infant chimpanzees begin with the tool-using phase. At around the age of 2 years, they are first observed using leaf tools for drinking, but these tools are not yet the infants' own: they rely instead only on the discarded drinking tools of older individuals.¹ These they pick up off the ground, or occasionally take from their mother's hand, suck on, then place in the water and retrieve for drinking. Infants use such discarded leaf tools exclusively until the age of about 3.5 years, after which they begin to manufacture and use their own tools. In fact, tool manufacture begins slightly earlier than 3.5 years, but in those cases infants drop their own tools immediately after making them, picking up and using those discarded by adults instead. Infants' tools are generally smaller than those of adults (see next section), consisting of fewer leaves, or are made of species with leaves smaller than the *H. brachiumum* favoured by adults. Tonooka (2001) also reports that younger chimpanzees are more likely to chew the leaves they place in their mouth, thus producing "sponges" rather than the much more common accordion-like folds.

3.2.2 Tool Efficiency

The skills of adult tool users appear almost stereotyped: in the case of nut cracking, for example, an individual chimpanzee's sitting posture, nut manipulation, hammer use, etc., all appear very similar from one cracking bout to the next.

¹An earlier report (Tonooka 2001) estimated the age at which this tool use first appears in infant chimpanzees as 2.5 years. Our slightly earlier estimate may be due to methodological differences, such as the observation of a larger number of infants over several years, and our procedure to leave abandoned leaf tools in place, rather than remove them immediately after the chimpanzee party's departure, thus facilitating the behaviour in individuals not yet able to make their own tools.

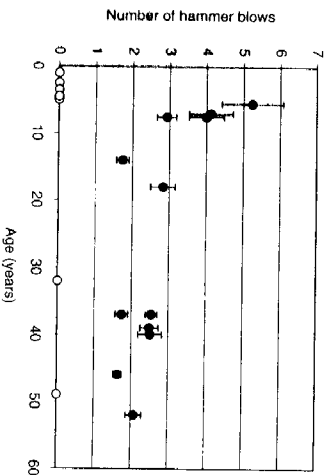


Fig. 9. Average number of hammer blows required to crack a single oil-palm nut as a function of age. Data were collected in 1999. Each filled circle represents the performance of a single individual who was able to crack nuts; open circles show age distribution of individuals who were never seen to succeed at cracking in 1999. Ages of oldest individuals are estimates. Error bars are standard errors of the mean

However, there are various ways in which the performance of younger chimpanzees changes as they hone their skills, such as setting on a particular hand to use for hammering after an initial ambidextrous phase. To assess whether more experience with a task leads to more efficient use of tools, we examined age-related differences in chimpanzees' performance of these tasks.

Figure 9 shows the number of hammer blows that individual chimpanzees used to open single oil palm nuts. The data show that, with increasing age, chimpanzees need progressively fewer blows to crack open nuts, reaching an asymptote around an average of only two blows per nut in the most experienced individuals. The increased effort that younger individuals seem to put into obtaining the same reward may be the result of lack of muscular development (weak blows), the choice of suboptimal tools for the task (such as hammers or anvils that are too small), or inferior technique (incorrectly aimed blows).

We also examined the efficiency of leaf tools as a function of age. In 2002, we collected tools discarded in the outdoor laboratory just after chimpanzees moved away following drinking bouts. These tools were immediately weighed and tested for their capacity to carry water by being dipped into a bucket of water and then squeezed over a measuring jug ten times consecutively. The amount of water thus carried by each tool was noted, and wherever possible assigned to the individual who manufactured and used the tool (as determined from onsite observation and video records). These data are plotted in Fig. 10. There was a significant correlation between tool weight and water-carrying capacity (Pearson's correlation: $n = 31$, $r = 0.83$, $P < 0.001$), which is unsurprising as larger tools would be expected to hold more water; however, the graph also shows that tools made by juveniles had much lower capacity than those of adults [one-way analysis of variance (ANOVA) on log-transformed data, $F_{1,30} = 23.58$, $P < 0.001$] because they were generally smaller ($F_{1,30} = 38.56$, $P < 0.001$).

3.2.3 Adjustments During Execution

Related to younger chimpanzees' generally lower efficiency in tool use is a lower fidelity to tools and techniques during the execution of the tasks. Juveniles in

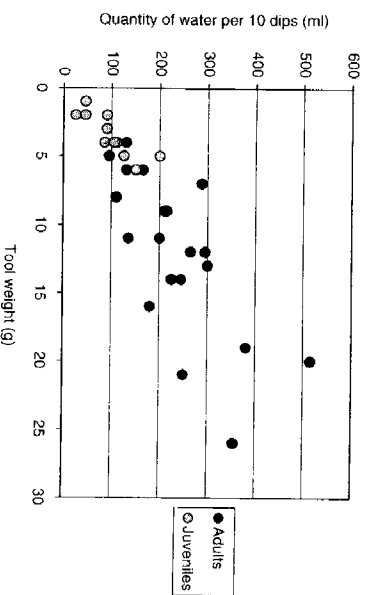


Fig. 10. Weight and efficiency of leaf tools made by individuals in different age classes. Each circle represents a single leaf tool; solid circles are tools made by adults and shaded circles are those made by juveniles. Data were collected in 2002

particular often change their hammers and anvils during bouts, sometimes selecting fresh stones, at other times taking those just abandoned by another individual. In addition, in their first year of successful cracking, young chimpanzees are often ambidextrous in hammer use and will switch hands in the course of a bout, something that is never observed in adults. During the use of leaf tools for drinking water, such hand changes occur even in adults, albeit at a much lower rate than in juveniles and infants (adults, 0.27 times per bout; juveniles, 1.3 times; infants, 0.83 times).

The switching of tools as well as hands during the execution of a tool-using task may represent a trial-and-error process in young individuals' learning. It may be that such incidents constitute a form of practice whereby chimpanzees develop their own favoured techniques.

3.3 Social Influences

Although both nut cracking and the use of leaves for drinking water are essentially solitary activities, members of chimpanzee parties travelling together often engage in these behaviours simultaneously. Furthermore, infants always travel with the mother and thus are exposed to her and other community members' tool-using activities long before they themselves begin to make any attempts. Similarly, juveniles who travel with the mother or other members of the community have access to the performance of skilled tool users. Thus, unless these tool-using skills rely entirely on genetically "preprogrammed" behaviour or individual trial-and-error learning (both of which are unlikely considering patterns of regional distribution; see Section 4), young chimpanzees are provided with a rich social environment that may well trigger and guide the acquisition process.

