28 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 (1978) 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 assume 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 are transmitted from one generation to the next through non-genetic channels." We

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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 km^2, 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 group's 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

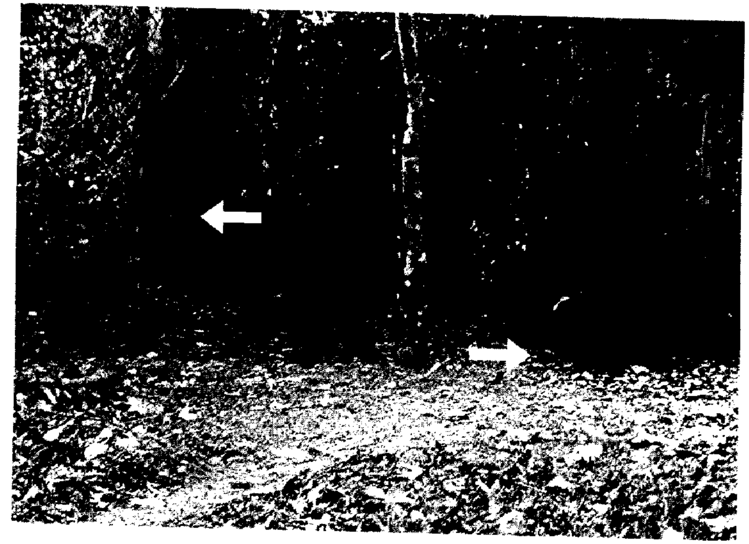

Fig. 1. "Outdoor laboratory" where intensive observations of tool-using behaviours were conducted. The *arrow on the left* points to a tree with an enlarged natural hollow containing water (only the forward-facing hole is visible; a second hole is located in the side of the tree, facing right; see Fig. 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

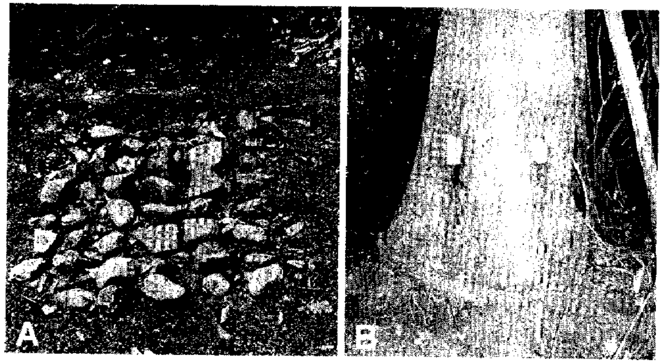

Fig. 2. Materials at the outdoor laboratory used in the nut-cracking and leaf-folding st[...] reported here. A Stones available within the clearing as arranged before the arrival of [...] party of chimpanzees. A pile of oil-palm nuts is visible to the right of the top-right corn[...] the stone matrix; another can be seen above the top-left corner. B The tree at the back of [...] outdoor laboratory from which chimpanzees drank using leaf tools. The two holes a[...] 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 p[...] tions. 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 a[...] individual differences in technique, and stages of development that young c[...] panzees 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 exce[...] opportunity to observe leaf-folding behaviour. Particularly in the dry se[...] when the nut-cracking experiments were conducted, water is a relatively sc[...] 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 clea[...] A natural hollow in a large tree (*Richinodendron heudelotii*) at the back of [...] clearing was cleaned and filled with clear water, the natural entry hole enla[...] and an extra hole drilled (Fig. 2B). The hollow had a capacity to hold abo[...] to 17 l water. The amount of water drunk during each visit by a party of c[...] panzees was measured by refilling the water to the brim once all chimpa[...] had exited the clearing. At the same time, the locations of all discarded [...] (clumps of folded leaves) on the ground were noted for subsequent matchi[...] the user based on video records, then at the end of the day (or, in the e[...] years of the study, just after the party's departure) removed from the ou[...] 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

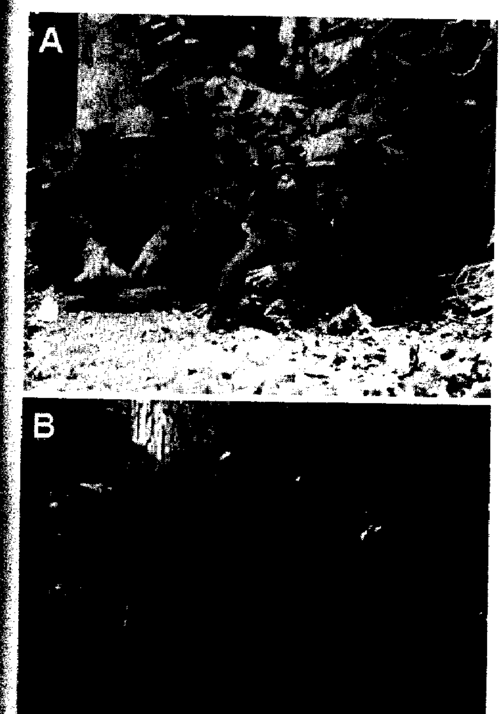

Fig. 3. Chimpanzees at Bossou performing the tool-using tasks examined in the present chapter. A Two adult females, Velu and Jire, crack oil-palm nuts with the aid of a pair of stones. Velu (*left*) has just placed a nut on an anvil stone with her left hand and is about to strike it with a hammer stone 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

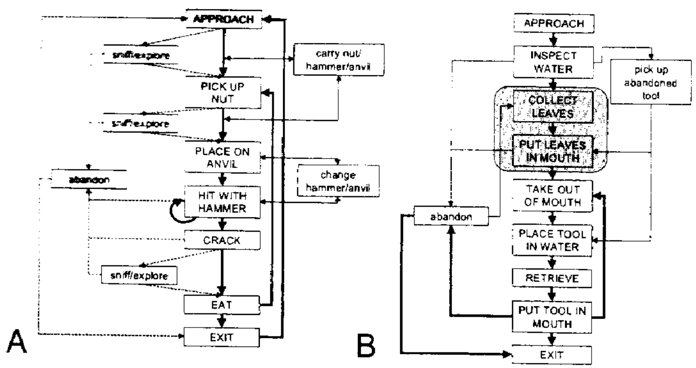

Fig. 4. Flowcharts illustrating main behavioural stages in (A) nut cracking and (B) leaf folding for drinking water. *Capital letters* and *thick arrows* correspond to a typical bout as performed by adult users of the tools; *lowercase letters* and *thin arrows* correspond to variations less frequently 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 (*Hybophrynium braunianum*, 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

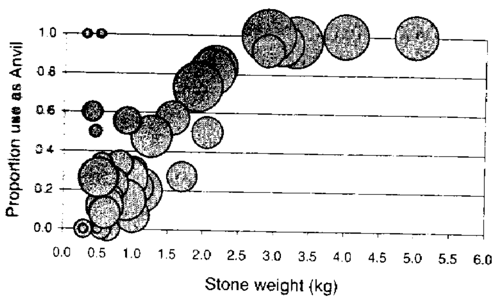

Fig. 6. Use of stones provided at the outdoor laboratory as hammer and anvil as a function of weight. Each *circle* represents a single stone, with the diameter of the circles corresponding to the relative frequencies with which the stones were used (the smallest circles indicate a single use; the largest 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 *Hybophrynium 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 Taï 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 nutshell 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 wadge 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 matrilines. 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 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.

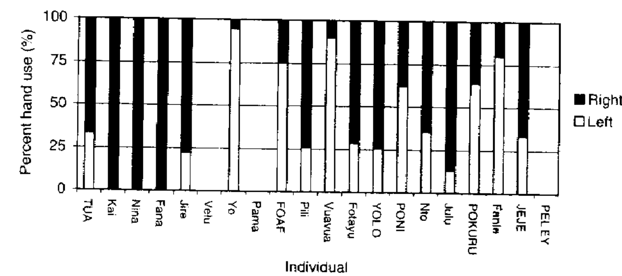

Fig. 8. Laterality during use of folded leaf tools. The hand used to dip the tool into the water, retrieve it, and place it into the mouth was recorded for each dipping action. Males are in *capitals*, females in *lowercase*. Data were collected in 2000; individuals for whom no data were obtained during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

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

				Year observed															
Name	Sex	Age	Mother	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	—	—	—	—	—
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 matrilinial 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

			Hand preference				
						Mother–infant concordance	
Name	Sex	Mother	(a) Nut cracking	(b) Leaf folding	(a)–(b) concordance	(a)	(b)
Tua	m		L	R	✗		
Kai	f		R	R	✓		
Nina	f		—	R			
Fana	f		R	R	✓		
Jire	f		L	R	✗		
Velu	f		R	—			
Yo	f		L	L	✓		
Pama	f		—	—			
Foaf	m	Fana	R	L	✗	✓	✗
Pili	f	Pama	R	R	✓	(✗)	
Vuavua	f	Velu	L	L	✓	✗	
Futayu	f	Fana	R	R	✓	✓	✓
Yolo	m	Yo	L	R	✗	✓	✗
Poni	m	Pama	R	L	✗		
Nto	f	Nina	R	R	✓	(✗)	✓
Juru	f	Jire	—	R			✓
Pokuru	m	Pili	—	L			✗
Fanle	f	Fana	R	L	✗	✓	✗
Jeje	m	Jire	A	R	?	?	✓
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
(✗), 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 anvil, 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 anvil. 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. braunianum* 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.

[1] *An 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.*

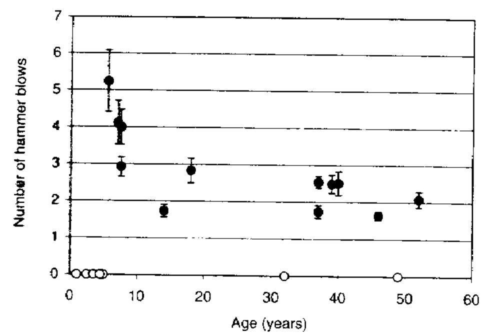

Fig. 9. Average number of hammer blows required to crack a single oil-palm nut as a function of age. Data were collected in 1999. Each *filled circle* represents the performance of a single individual who was able to crack nuts; *open circles* show age distribution of individuals who were never seen 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 settling 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 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).

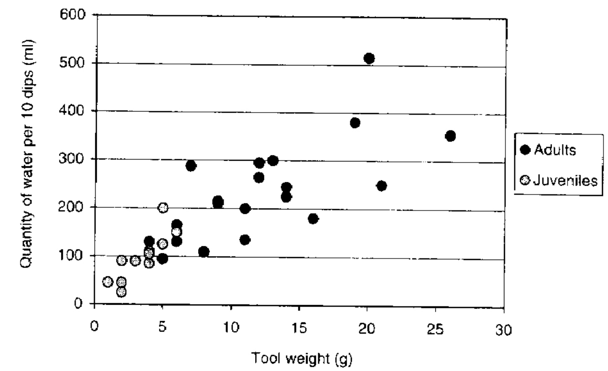

Fig. 10. Weight and efficiency of leaf tools made by individuals in different age classes. Each *circle* represents a single leaf tool; *solid circles* are tools made by adults and *shaded circles* are those made by juveniles. Data were collected in 2002

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.

3.3.1 Scrounging and the Use of Abandoned Tools

Infants are allowed to scrounge freshly cracked nuts from their mothers (and also, to a lesser degree, from other individuals) and are allowed to interact with their stones during a nut-cracking bout. For example, infants reach out to touch their mother's anvil, even hold her hammering hand or arm as she is delivering blows, and take nuts and shells off her anvil. Such scrounged nuts constitute the infants' only tangible reinforcement in the nut-cracking context until the age of about 3.5 years when they begin to crack nuts by themselves. We have also observed that young infants, when held by their mothers engaged in leaf-tool use, sometimes reach into a tree hollow and dip their hand into the water within, which they can then lick off their fingers. Although not strictly speaking scrounging, this does parallel infants' access to oil palm kernels in an important way: through the mother's nut cracking or through the mother holding the infant up high enough to reach the water, infants may be "getting a taste" for what is to be gained from successful tool use well before they begin to attempt it themselves.

As mentioned earlier (Section 3.2.1), infants' tool use for drinking water begins at the age of around 2 years with the picking up of leaf tools abandoned by previous users. Moreover, infants have also been observed to take leaf tools from their mother's hand during a drinking bout and to continue to use the tool by themselves. A parallel in nut cracking is seen in infant and juvenile chimpanzees' propensity to use anvil–hammer sets freshly abandoned by adult users. Even if they are already engaged in cracking themselves, if an adult nearby walks off leaving behind his or her set, juveniles in particular will walk over and either crack in the adult's place or take one or both of the abandoned stones away with them.

Laboratory work confirms the importance of leftover tools in individuals' acquisition of tool-using skills. In a captive simulation of ant/termite fishing by wild chimpanzees, Hirata and Morimura (2000; see also Chapter 12 by Hirata in this volume) showed that adult chimpanzees naïve to the task (honey-fishing) were more successful in their attempts if they used those objects as tools that had just been abandoned by a previous user than if they made their own tool selection from the many different objects provided. When the experiment was repeated using mother–infant pairs of chimpanzees (Hirata and Celli 2003), the infants' tendency to scrounge from their mother performing the honey-fishing tasks was prominent: they would lick the honey off the mother's tool, or even attempt to steal the latter. Similarly for wild chimpanzees, such opportunities to scrounge, as well as the presence of leftover tools, may have much to contribute to individuals' acquisition of the task.

It is interesting to note that juveniles at Bossou, who also occasionally reuse discarded leaf-tools, are not granted the same liberties to scrounge as infants. Although the mother may show some degree of tolerance towards her juvenile offspring's attempts to interact with her objects during nut cracking, scrounging from others becomes impossible. Juveniles are often chased away when they approach an older individual engaged in nut cracking and are certainly not permitted to take nuts from them. This propensity may contribute to the end of the "critical period" for learning; once a juvenile, opportunities for direct interaction with older, skilled group members during the tool-using task disappear.

3.3.2 Conspecific Observation

While scrounging involves direct interaction with older tool users in the community, the social setting in which tool-using behaviour often takes place provides younger individuals not only with leftover tools but also with an opportunity to observe closely the actions of other group members. Such observation may be an important building block of socially transmitted behaviours.

We examined patterns in the observation of conspecifics carried out by individuals in the Bossou community (Biro et al. 2003; Sousa et al., in preparation). An episode of observation of one community member by another was said to take place when the latter approached the former to within about 1 metre and remained with gaze fixed upon the target individual's face or hands for at least 3s. Figure 11 shows the rates of occurrence of such observational episodes during periods in the outdoor laboratory when at least two individuals were present and at least one of them was engaged in nut cracking (including the handling of nuts and stones) or the use of leaves for drinking water. The data are strikingly similar for the two tool-using tasks, and three main conclusions can be drawn. (1) Adults are the most popular targets for observation by individuals in all three age classes. Juveniles are observed less often, while infants are almost never observed (the bar for infants in Fig. 11B corresponds to a single episode of observation of an infant by a juvenile). (2) Juveniles and infants are the most likely to observe, while adults are the least likely to act as observers.

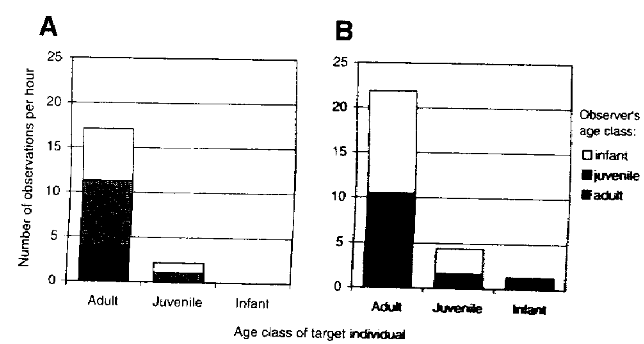

Fig. 11. Individuals in different age classes as targets of observation by conspecifics during (A) nut cracking and (B) using leaves for drinking water. *Bars of different colours* correspond to the observer's age class. Rates were calculated as number of episodes of observation divided by the amount of time individuals in the three different age classes spent in the outdoor laboratory engaged in the handling or cracking of nuts or in drinking water with the aid of leaf tools. Data were collected in 2000

(3) Individuals almost exclusively observe conspecifics in the same age group or older, but not younger, than themselves.

This pattern of conspecific observation has implications for any model of the social transmission of behaviour in chimpanzee communities. We return to this point in Section 4.2.

3.3.3 "Education by Master-Apprenticeship"

Previous work at Bossou has illuminated many aspects of the developmental changes that young chimpanzees go through as they learn to use tools (Inoue-Nakamura and Matsuzawa 1997; Tonooka 2001). Furthermore, elucidating the underlying mechanisms of learning and the role that skilled community members play in the acquisition process is crucial for understanding how community-specific behaviours are maintained among wild chimpanzees. Drawing together evidence from the individual as well as the social aspects of behavioural development, Matsuzawa et al. (2001) proposed a model to describe how tool-using skills may be propagated in wild chimpanzee communities, referred to as "education by master-apprenticeship." The central theme of this model is that infant chimpanzees, who remain in extremely close proximity to the mother for the first 4 to 5 years of life, are provided with an excellent setting in which learning aided by observation can take place, while the bulk of the work is then done at the individual level. The models whom the infants observe (primarily the mother) are highly tolerant: they will allow infants to scrounge, to observe from close range, and to interact with the objects involved in their actions, but they play no active role in the infant's learning. Infants in turn are driven by an intrinsic motivation to do as the others in the community [de Waal (2001) refers to this as "the desire to be like others"].

The underlying mechanism responsible for the social transmission of the skill from model to observer is a particularly intriguing, much-debated issue. Although imitative learning, where a model's behaviour is copied motor-pattern-by-motor-pattern by an observer, would in theory facilitate high-fidelity copies of behaviour, it does not seem to satisfactorily account for the years spent by infants gradually approximating the correct motor sequence necessary for the task. (Bear in mind that young chimpanzees receive no direct food reward from their interactions with nuts and stones for several years, yet they continue to handle these objects.) Facilitated by their tolerance, models draw attention to the tools and targets, as well as to the possible outcomes of a successful bout of tool-use. In that sense, infants' progress may be aided by a form of stimulus or local enhancement, or emulation learning (Tomasello 1996), where the details of the motor pattern have to be established through individual trial-and-error learning. This idea is supported also by our long-term record of laterality in tool use, which shows no consistent patterns in mother–infant congruence in handedness in either nut cracking or the use of leaves for drinking water. Near-perfect inter-sibling congruence in laterality, however, is a very striking feature of the data. We have tentatively suggested a way in which this pattern is consistent with

the education by master-apprenticeship model (Biro et al. 2003): it may be that individual mothers provide specific learning environments for their offspring which will favour a particular hand for hammering across all siblings. For example, a mother who always places her offspring on her right during nut cracking may encourage the infant's right hand to be used for exploring objects within reach from an early age. The only individual who shows divergence from the pattern of inter-sibling consistency (Peley) was born to a non-nut-cracking mother (Pama), such that he—as well as his siblings—must have relied on other individuals as models for observation.

Various alternatives accounting for infants' learning can be discounted. In contrast with Boesch's (1991) observations of rare examples of active teaching by chimpanzee mothers at Taï, we have never encountered such cases at Bossou. Mothers do not mould the hands of their young, nor do they perform what appear to be deliberate slow-motion demonstrations of the appropriate techniques in front of them. At the other end of the scale, if models contributed nothing to learning and the behaviour arose independently in each individual in the community, then it would be difficult to account for regional variation in the presence or absence of specific tool-using skills in different communities. We turn our attention now to such inter-community differences and the processes that may contribute to their emergence, propagation, and maintenance in wild chimpanzee populations.

4 Regional Variation and Culture

In common with many other behavioural patterns (Whiten et al. 1999, 2001), nut cracking and the use of folded leaves for drinking water are not found in all wild chimpanzee communities across Africa. The reasons behind the patchy distribution of such behaviours and related issues of "cultural" variation are currently much debated. So far in the present chapter we have discussed possible mechanisms contributing to the maintenance of these behaviours within a community, but how can the absence of the same behaviours from other communities be explained? One simple hypothesis is that ecological factors, such as the absence of the target species from the chimpanzees' habitat, account for the absence of a particular behaviour; this is certainly true in some cases (Baldwin et al. 1991) but certainly not true in others. As mentioned at the start, for example, the cracking of hard-shelled nuts is restricted to West African communities (Boesch et al. 1994), yet the raw materials needed to perform the task are present in Central and East African communities' habitats. The use of leaves for drinking water is geographically more widespread (McGrew 1977; Nishida 1990; Quiatt and Kiwede 1994; Wrangham 1992; Boesch and Boesch 1990; Ghiglieri 1984), so much so that Whiten et al. (2001) putatively refer to it as a "chimpanzee universal." However, this universal is in fact the "leaf-sponge," a relatively rare variant at Bossou, whereas the folded leaves typical among Bossou chimpanzees have not been reported from any other site. Such community specificity in the characteristics of a tool is mirrored also in nut cracking, where although the goal of the behaviour is shared between Bossou and Taï, certain fine details are not: for example, only Taï chimpanzees are known to use wooden hammers and wooden anvils as well as stone, while those at Bossou use only stone.

In an attempt to examine questions related to such regional variation, we looked at the distribution of tool use (nut cracking, in particular) in detail at sites adjacent to Bossou and carried out a series of field experiments to explore possible mechanisms underlying cultural innovation and transmission.

4.1 Tool Use at Sites Adjacent to Bossou

Preliminary work has begun at three sites located at various distances from Bossou known to be inhabited by chimpanzees. The closest, Seringbara at the foot of the Nimba Mountains, is located about 6 km to the east of Bossou, and efforts are currently underway to habituate this community. From trace evidence (discarded tools and abandoned tool-using sites), it has already been possible to document the use of wands for ant dipping in this community, but not stone tools for nut cracking even though oil palms are available within the habitat (Humle and Matsuzawa 2001).

The second site, Yealé in the Ivory Coast, is 12 km southeast of Bossou (Matsuzawa and Yamakoshi 1996). At this site also, chimpanzees are known to ant dip, and furthermore traces of nut cracking have also been found. Yealé is home to two more species of nut besides the oil palm, neither of which occurs naturally at Bossou: the coula nut (*Coula edulis*) and the panda nut (*Panda oleosa*). Only coula and oil palm are cracked at Yealé; panda is not.

The third site, Diecke, 50 km to the west of Bossou, has been surveyed by Matsuzawa et al. (1999). Here, neither ant dipping nor oil-palm nut cracking has so far been found; however, chimpanzees do crack both coula and panda nuts.

Table 3 summarizes nut-cracking activity at these sites. Examining patterns in chimpanzees' utilization of different species of nut for cracking, it is clear that while in some cases the behaviour is ecologically impossible (coula and panda are not available at Bossou and at Seringbara, and no oil palm at Diecke), in three cases such explanations are not sufficient. Oil-palm nuts at Seringbara and Diecke, and panda nuts at Yealé, are available but not cracked. Although Seringbara chimpanzees have not been found to nut crack at all, those at Diecke and Yealé are known to utilize some but not all of the nuts available in their habitat.

Table 3. Species of nuts cracked by wild chimpanzees at Bossou, Seringbara, Yealé, and Diecke

Site	Distance from Bossou	Species of nut: Oil palm (*Elaeis guineensis*)	Coula (*Coula edulis*)	Panda (*Panda oleosa*)
Bossou		Yes	—	—
Seringbara	6 km	No	—	—
Yealé	12 km	Yes	Yes	No
Diecke	50 km	No	Yes	Yes

—, target nut species is not available at the site; No, no evidence of cracking by the chimpanzees has so far been found even though the nuts are available

4.2 Nut-Cracking Field Experiment

At the heart of all models of culture lies an invention. Behaviours that show regional variation and are propagated through social learning must have originated with an inventor. Just as Imo, the Japanese macaque, has become famous as the first individual on Koshima island to perform sweet-potato washing (Kawai 1965; see also recent review by Hirata et al. 2001a), there must have lived many uncelebrated primates whose innovations have spread within their communities and often beyond. Such instances of invention are, however, extremely difficult to document in nature.

To investigate how novel tool-using behaviours (such as the cracking of previously neglected nut species) may emerge in wild chimpanzee communities, we carried out a field experiment involving the introduction of novel species of nuts in the Bossou community. We used the nuts available at neighbouring sites, but not at Bossou: coula and panda nuts (Fig. 12). Coula nuts were presented in five separate field seasons (January 1993, 1996, 2000, 2002, and 2005), whereas panda nuts were presented once (in January 2000). Initial presentation involved placing three of the unfamiliar nuts in the outdoor laboratory, along with the usual piles of oil-palm nuts, and replenishing them when they had been used up. In later years, coula were provided in two piles of about 30 nuts (see Matsuzawa 1994, Matsuzawa and Yamakoshi 1996, and Biro et al. 2003 for further detail). In each year, we continued presentation until all individuals present in the group had visited the outdoor laboratory at least four times with the novel nuts present (except in 2005, when one individual did not visit throughout the entire period of coula nut presentation).

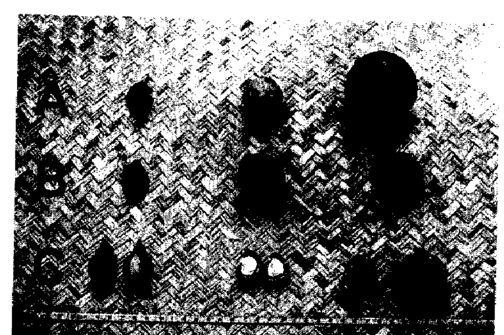

Fig. 12. Three species of hard-shelled nut presented in the outdoor laboratory: oil-palm nuts (*left*), coula nuts (*centre*), and panda nuts (*right*). For each species, three stages are shown: fruit (A), hard-shelled contents of fruit before cracking (B), and after cracking, with edible kernels visible (C)

We examined Bossou chimpanzees' responses to these novel items. We classified behaviours displayed by individuals into three general categories: "ignore," "explore," and "crack." First, "ignore" described individuals who displayed no visible signs of interest toward the nuts: they neither approached them nor looked at or handled them in any way. Second, individuals were said to "explore" if they looked at closely, handled, sniffed, mouthed, or bit into nuts but did not attempt to crack them. 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. In addition, individuals present at Bossou at the time of the experiments were also classified into three different age groups based on known aspects of life history (weaning and age of first parturition): infants from 0 to 4 years, juveniles from 5 to 8 years, and adults 9 years and above.

4.2.1 Initial Responses: Coula in 1993, Panda in 2000

Table 4 shows the proportion of individuals in the three different age groups who displayed each of the three responses during the very first presentation of coula nuts (in 1993) and panda nuts (in 2000). In both cases, a small proportion of the group attempted to crack the nuts: 3 of 17 individuals in the case of coula (one adult and two juveniles), and 4 of 20 for panda (two adults and two juveniles). This result was in sharp contrast with oil-palm nut cracking, which 10 of 17 individuals performed in 1993 and 13 of 20 in 2000.

Thus, the cracking of oil-palm nuts did not immediately generalize to novel species of nuts. Of the individuals who did attempt to crack, only in one case was cracking not preceded by some form of exploration: a single adult, Yo, proceeded to crack coula nuts without any exploratory behaviours. All other individuals who cracked either type of nut (including Yo subsequently attempting panda nuts) did so after extensive sniffing and handling of the novel items. Yo also correctly selected ripe (dark) coula nuts over unripe (green) ones for cracking, even though neither showed obvious signs of either containing something edible inside or requiring the use of hammer and anvil. These observations have prompted the intriguing suggestion (Matsuzawa 1994; Matsuzawa and Yamakoshi 1996) that Yo may have been an immigrant, having transferred to Bossou some time before 1976 from a community where coula nut cracking was habitual. Her apparent lack of knowledge regarding panda nuts would suggest that of the nearby communities surveyed, she most likely hails from the region of Yealé, where both oil-palm and coula nuts are cracked but panda is not.

Table 4. Responses of chimpanzees in three different age classes to the initial presentation of novel species of nuts

Age group	Nut (year)	*n*	Crack	Explore	Ignore
Adult	Oil palm (2000)	10	8 (80%)	2 (20%)	0 (0%)
	Coula (1993)	9	1 (11%)	4 (44%)	4 (44%)
	Panda (2000)	10	2 (20%)	0 (0%)	8 (80%)
Juvenile	Oil palm (2000)	6	5 (83%)	1 (17%)	0 (0%)
	Coula (1993)	4	2 (50%)	2 (50%)	0 (0%)
	Panda (2000)	6	2 (33%)	2 (33%)	2 (33%)
Infant	Oil palm (2000)	4	0 (0%)	4 (100%)	0 (0%)
	Coula (1993)	4	0 (0%)	0 (0%)	4 (100%)
	Panda (2000)	4	0 (0%)	1 (25%)	3 (75%)

Data for oil-palm nuts are also shown for reference (data from 2000)
n, number of individuals within a particular age group in given year
Values show number of individuals in each age group who displayed the three different behaviours towards the nuts (see text for details)
Values in brackets are percentages of the total number of individuals in the respective age group

With both species of unfamiliar nuts, it appears that juveniles were more likely than adults to show interest in (explore or crack) the novel objects. Adults were relatively more conservative, being more likely to ignore (particularly in the case of panda) the unfamiliar nuts. The two adults who did crack panda nuts abandoned their attempts after a single successful bout, while juveniles continued to explore and try to crack over subsequent days of presentation.

4.2.2 Coula Cracking Through the Years 1993–2005

The repeated presentation of coula nuts revealed various trends across the years (Table 5). The proportion of individuals who cracked these nuts increased

Table 5. Responses of individuals in the three age groups to coula nuts as across the 5 separate years when these nuts were presented

Age group	Nut (year)	*n*	Crack	Explore	Ignore
Adult	Coula (1993)	9	1 (11%)	4 (44%)	4 (44%)
	Coula (1996)	9	3 (33%)	0 (0%)	6 (67%)
	Coula (2000)	10	4 (40%)	3 (30%)	3 (30%)
	Coula (2002)	9	6 (67%)	1 (11%)	2 (22%)
	Coula (2005)	7[a]	5 (72%)	1 (14%)	1 (14%)
Juvenile	Coula (1993)	4	2 (50%)	2 (50%)	0 (0%)
	Coula (1996)	5	3 (60%)	0 (0%)	2 (40%)
	Coula (2000)	6	4 (66%)	2 (33%)	0 (0%)
	Coula (2002)	4	3 (75%)	0 (0%)	1 (25%)
	Coula (2005)	3	2 (67%)	1 (33%)	0 (0%)
Infant	Coula (1993)	4	0 (0%)	0 (0%)	4 (100%)
	Coula (1996)	4	0 (0%)	0 (0%)	4 (100%)
	Coula (2000)	4	0 (0%)	4 (100%)	0 (0%)
	Coula (2002)	5	1 (20%)	2 (40%)	2 (40%)
	Coula (2005)	1	0 (0%)	1 (100%)	0 (0%)

[a]The 8th adult (Velu) present at Bossou in 2005 could not be tested as she did not visit the outdoor laboratory during the period of coula nut presentation; this individual had cracked coula nuts in previous years of presentation

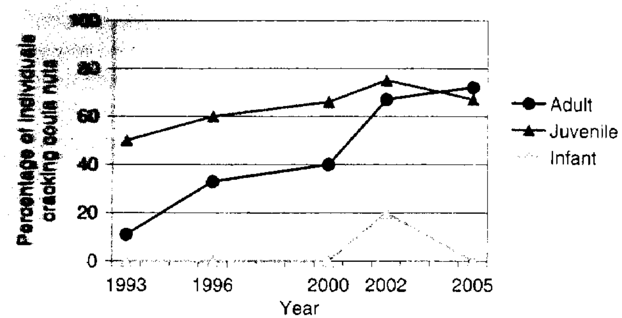

Fig. 13. Percentage of individuals in the three age classes who attempted to crack coula nuts on the five occasions when these nuts were presented at the outdoor laboratory

gradually among both adults and juveniles (Fig. 13), such that they are now roughly comparable to the proportion cracking oil-palm nuts. The rise among adults was partly the result of juvenile crackers from previous years reaching adulthood and partly adults who in previous years showed only exploratory behaviours eventually moving on to cracking.

Exploratory behaviours towards coula nuts also waned over the years. By 2002, seven of the ten individuals who cracked did so without any exploration on their first encounter of the year, as did five of the seven crackers in 2005. In addition, by 2005 only one individual (the adult female Fana) ignored coula nuts completely; this result again is comparable to oil-palm nuts (see Table 4), which all individuals of the group (except the youngest of infants) handle, scrounge on, or crack.

4.2.3 Conspecific Observation with Coula and Panda Nuts

As with oil-palm nuts, we recorded episodes of conspecific observation when coula and panda nuts were present. The overall patterns were similar to the data obtained from oil-palm nuts: adults were the most likely and infants the least likely to be observed, juveniles and infants performed most of the observing, and the targets of observation tended to be in the same age group or older than the observers themselves (Fig. 14). In addition, rates of observation were about twice as high when coula nuts were present as during oil-palm-only periods. Adults engaged in the cracking of coula nuts generated a great deal of interest in the rest of the group. Yo's cracking of coula nuts, in particular, often attracted several individuals (Fig. 15). In contrast, adults cracking panda nuts were observed at lower rates, partly because only relatively few interactions with the nuts occurred, and some of these took place with few other individuals present (for example, Yo was on her own in the outdoor laboratory when she first cracked panda nuts).

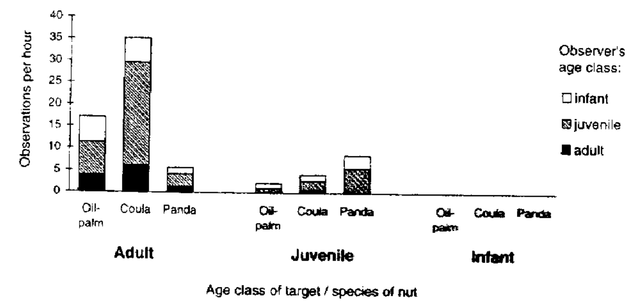

Fig. 14. Individuals in different age classes as targets of observation by conspecifics during the cracking of three different species of nuts. See legend to Fig. 11 for further detail. Data for all three nuts were collected in 2000

Fig. 15. An adult female (Yo) cracking coula nuts, while two juveniles observe her actions closely. A pile of coula nuts is visible on the right (*upward-pointing arrow*). A row of panda nuts that can be seen near the bottom-left corner (*left-pointing arrow*) was ignored by all three individuals present

4.2.4 Toward a Model for Cultural Innovation and Propagation

Together with our intensive observations of the development of nut-cracking skills at the individual level and patterns in the regional distribution of the behaviour, this experiment completes a three-way approach to tracing the emergence and propagation of cultural traditions in wild chimpanzee communities. As the regional survey has shown, ecological factors cannot fully account for the observed patterns in the utilization of different target species for cracking in communities adjacent to Bossou. In addition, intensive longitudinal study of developmental processes suggests that the social environment contributes significantly to the individual acquisition of the skill. There are two main ways in which such non-genetically based, socially transmitted behaviours can first appear in a community: through invention by one or more individuals independently, or through the arrival in the group of an immigrant possessing knowledge gained in her natal group.

We believe that our novel-nut experiments can contribute to our understanding of both these processes, as well as to the subsequent diffusion within the community that then serves to incorporate the behaviour into the group's repertoire. First, the contrast between the initial presentation of coula and panda nuts suggests that the actions of a knowledgeable immigrant (which Yo quite likely was) can have an effect on other group members' reactions to unfamiliar or neglected items in the environment. Yo's behaviour toward coula elicited high levels of interest among individuals in all age groups, such that most proceeded to at least investigate the novel nuts. Because our analysis shows that adult observers pay attention almost exclusively to the actions of other adults in the group, novel behaviours are likely to spread to them from adult performers only. That no individual at Bossou seemed to be familiar with panda nuts meant that adult chimpanzees—more conservative than juveniles or infants—showed only a transient interest in these nuts and abandoned them after a single successful attempt. Possibly, these adults gauged that the amount of effort that went into cracking panda nuts, the toughest of the three nuts by far (Boesch and Boesch 1983), was too high compared to the rewards gained (one of the adults was observed to strike the same panda nut 78 times consecutively before she was able to crack it, changing her hammer eight times and her anvil four times in the process!). Meanwhile, the more persistent interest shown by juveniles towards panda nuts, as well as the generally higher levels of interest in coula nuts from the start, might suggest that newly invented behaviours may be most likely to originate in this group. Bearing in mind patterns of conspecific observation, such new inventions would then be likely to spread horizontally to other juveniles or downwards to infants, but not upwards to adults.

Over the five different years of presentation, coula-nut cracking seems to have been assimilated by members of the Bossou community, even though encounters with these nuts were brief and occurred as much as 3 to 4 years apart. Most individuals now crack coula nuts without any form of prior exploratory behaviour. It is difficult to predict what the fate of panda-nut cracking would be if these nuts were reintroduced at Bossou. Without a knowledgeable adult as a model for observation but given sustained interest among juveniles, it may be that this nut would also come to be accepted over time, albeit less quickly, through the maturation of younger innovators and their contemporaries.

It may be reasonable to suggest that the rates at which migration, innovation, and within-community transmission take place will ultimately influence how quickly novel cultural traditions are assimilated by wild chimpanzee communities. The finding that communities that share migrants do not necessarily possess identical behavioural repertoires confirms that transmission within communities plays an indispensable role in the maintenance of such traditions. Exploring the channels through which information travels from knowledgeable individuals within and across generations will illuminate how community-specific behaviours come to be established. The emergence of "cultural zones" (Matsuzawa et al. 2001; Biro et al. 2003) where sets of neighbouring communities come to develop similar but not necessarily identical behavioural traditions may be the result of such interplay between inter-community migration and within-community propagation.

5 Future Perspectives

This chapter has provided an overview of results obtained through the long-term study of two chimpanzee tool-using behaviours at Bossou. Observations and field experiments continue at this site year after year, and neighbouring communities continue to be explored in efforts to build a comprehensive picture of the cultural life of chimpanzees in this corner of Africa (Humle and Matsuzawa 2001, 2002, 2004). Genetic analyses of these populations are also helping to illuminate local migration patterns (Shimada et al. 2004) and thus possible channels for the flow of knowledge between communities.

Current research at the outdoor laboratory is examining further the developmental and social aspects of skill acquisition in both nut cracking and the use of leaves for drinking water. One of the focuses of the work concerns object manipulation during the performance of these tasks (M. Hayashi et al., in preparation). For example, chimpanzees occasionally adjust the position of their anvil, rotating or rolling the stone before placing the next nut on the upper surface. Whether these adjustments are based on an understanding of the properties of the objects involved (such as a slanted upper surface not being able to support a round object on top) are being examined by presenting chimpanzees with ready-made anvil–hammer sets in which the anvil is positioned incorrectly. Fine-scale analysis of the actions performed by individuals when encountering such situations will shed light on chimpanzees' perception of the physical world.

Meanwhile, at the Primate Research Institute of Kyoto University, researchers are investigating tool use by chimpanzees in a captive setting, including experiments on nut cracking (Hayashi et al. 2005), the use of leaves for drinking (Tonooka et al. 1997; Celli et al. 2004), and the transmission of such behaviours from mother to infant (Hirata and Celli 2003). In addition, a new series of experiments that began with the birth of three chimpanzee infants in 2000 are examining various issues related to cognitive development (Matsuzawa 2003; see also other chapters in this book). Many of these are intricately related to the developmental aspects discussed in the present chapter. For example, Hayashi and Matsuzawa (2003) have shown that in infant chimpanzees' free manipulation of objects, the appearance of "inserting" actions precedes that of "stacking". Infants from the age of about 1 year begin to insert one object into another, but it takes another year before they begin to spontaneously stack objects on top of one another. The significance of this finding becomes clear when data from the wild are considered in parallel. The use of leaves for drinking water is essentially an inserting action whereas nut cracking requires precise stacking of objects: much as the captive data would predict, in infants at Bossou the former emerges earlier than the latter.

Field and laboratory work can thus go hand-in-hand to shed light on various aspects of wild chimpanzee cognition and behaviour. The combination of such parallel efforts is likely to emerge as a whole greater than the sum of its parts.

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