



Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon

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ABSTRACT

Homo faber was once proposed as a label for humans specifically to highlight their unique propensity for tool use. However, new observations on complex tool use by the chimpanzees of Loango National Park, Gabon, expand our knowledge about tool-using abilities in *Pan troglodytes*. Chimpanzees in Loango, when using tools to extract honey from three types of bee nests, were observed to regularly use three- to five-element tool sets. In other words, different types of tools were used sequentially to access a single food source. Such tool sets included multi-function tools that present typical wear for two distinct uses. In addition, chimpanzees exploited underground bee nests and used ground-perforating tools to locate nest chambers that were not visible from the ground surface. These new observations concur with others from Central African chimpanzees to highlight the importance of honey extraction in arguments favoring the emergence of complex tool use in hominoids, including different tool types, expanded tool sets, multifunction tools, and the exploitation of underground resources. This last technique requires sophisticated cognitive abilities concerning unseen objects. A sequential analysis reveals a higher level of complexity in honey extraction than previously proposed for nut cracking or hunting tools, and compares with some technologies attributed to early hominins from the Early and Middle Stone Age. A better understanding of similarities in human and chimpanzee tool use will allow for a greater understanding of tool-using skills that are uniquely human.

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Introduction

Homo faber was once proposed as a label for humans in order to capture their unique aptitude for tool use, which placed them apart from all other animals (Oakley, 1956). Since then, researchers have imposed chimpanzees (*Pan troglodytes*) into this special category, as their tool use abilities have been shown to be universal and very flexible (e.g., Goodall, 1970; Boesch and Boesch, 1990; McGrew, 1992; Whiten et al., 1999; Sanz and Morgan, 2007). The ubiquity of chimpanzee tool use has convinced most anthropologists that chimpanzees are part of this tool user category (Ambrose, 2001). Nevertheless, new criteria have frequently been proposed to qualify the differences between the two species. The classic criterion is that only humans modify natural objects to fashion tools (Leakey, 1961): a claim that was contradicted in the early 1960's from observations of spontaneous use of sticks by the Gombe chimpanzees when fishing for termites (Goodall, 1964). Next, it was proposed that only humans possess tool kits comprised of different tool types, of which

each fulfills a different function (Oakley, 1956), however, the growing list of tool types used by the chimpanzee populations in Gombe, Mahale, Tai, Bossou, and Goulougo, all of whom were observed using between 15 to 25 different types of tools, have modified this claim (Sugiyama and Koman, 1979; Boesch and Boesch, 1990; Sanz et al., 2004). Another major claim was that only humans are dependent on tools for their survival (Trinkaus, 1992), but a more complete analysis has shown that, in some chimpanzee populations, the quantity of food that was acquired with tools is very important during some periods of the year (Boesch, 1996; Yamakoshi, 1998). Another proposition was that only humans fashion tools following arbitrary cultural rules rather than in a purely adaptive way (Klein, 2000). However, population differences in tool use, such as for ant dipping, were also shown to be cultural rather than adaptive (Boesch, 1996; Moebius et al., 2008). It has been proposed that only humans use tools to access underground food (Hatley and Kappelman, 1980; Wrangham et al., 1999; Laden and Wrangham, 2005), which is thought to be indicative of some higher cognitive abilities. However, new observations have documented underground food extraction with tools in different chimpanzee populations (Lanjouw, 2002; Sanz et al., 2004; Hernandez-Aguilar et al., 2007). Additionally, it was proposed that only

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humans use tools to hunt (Leakey, 1961), but recent observations from Fongoli chimpanzees complemented those from Gombe and Tai and help weaken this claim (Plooj, 1978; Boesch and Boesch-Achermann, 2000; Pruetz and Bertolani, 2007). Finally, it has been suggested that humans are the only species to combine many tools to attain one goal, as well as use one tool for more than one purpose (Oakley, 1956). Only one type of tool is used in most cases of chimpanzee tool use, and tools are not often used for multiple purposes, but recently some evidence suggests that tool sets (i.e., different tool types that need to be used one after the other in order to reach one goal) might be regularly used by chimpanzees of Central Africa (Suzuki et al., 1995; Bermejo and Illero, 1999; Sanz et al., 2004). Combined, these studies suggest that much of what has been proposed as qualitative differences between these two species might instead be quantitative differences.

Because tool use is now recognized in chimpanzees, adopting an integrated framework to describe the details and technological complexities observed in chimpanzees might help us in understanding the similarities and differences between chimpanzee and human tool-using skills. In addition, the identification of qualitative differences in tool-using abilities may enable us to detect which cognitive and technical skills were likely to have been important in human evolution (McGrew, 1992; Byrne, 2004). Oswalt (1976) was one of the first to propose a single framework to describe the complexity of material culture in different human civilizations, adopting a hierarchical and dichotomous taxonomy that allowed quantitative comparisons between forms and cultures. Semenov (1964) pioneered a detailed analysis of macro- and micro-traces on stones and bones to understand their functions and the way of life for the people that employed those tools. At the same time, the “chaîne opératoire” framework was applied in archaeology to detail the dynamic interactions between the object and the technological activities (Leroi-Gourhan, 1964; Lemonnier, 1983; Bar-Yosef et al., 1992; Roche et al., 1999). Such approaches have been applied to tool use in non-human primates with the aim of making comparisons between species (McGrew, 1987; Westergaard, 1994; Pruetz and Bertolani, 2007; Carvalho et al., 2008). Tool complexity has been described in terms of technounits (Oswalt, 1976), sequences or order (Wynn and McGrew, 1998; Carvalho et al., 2008), or hierarchical organization (Byrne, 2004).

To better understand the similarities and differences in tool use behavior between humans and chimpanzees, we present evidence of tool use in a newly studied population of chimpanzees in Loango National Park, Gabon. Within this population, we have documented extensive use of tool sets of up to five different tools to extract honey from hives of different species of bees, including some with underground nests. By analyzing the complexity of this extractive technology using a chaîne opératoire or operational sequence approach, which lists all possible sequential steps required from the selection of the raw material to the fulfillment of the goal, will allow us to make comparisons with observations of tool use in other chimpanzees and with tool use in Early and Middle Stone Age hominins.

Methods

Study site and habituation

Loango National Park is located on the coast of Gabon, between the border with Congo and the capital city of Libreville, and was officially declared a national park in 2002. Our study site is in the southwest section of the park between the Atlantic Ocean and a large lagoon. The site consists of several vegetation types including coastal forest, swamps, dry forest, and mangroves.

The project started in February 2005 with the aim of habituating both chimpanzees and gorillas, with two teams of 2 to 3 observers

typically patrolling an area of about 80 km² to search for traces of the apes and to try to contact them. The habituation of the apes in this area is still in its infancy; consequently, most direct observations are opportunistic and of short duration, depending upon the situation in which the animals are contacted (e.g., for the two first years of study, the average contact duration with chimpanzees was 8.7 minutes, $N = 245$ in year 1 and $N = 218$ in year 2). In addition, the animals are often frightened by, or are interested in, our presence, and therefore unaltered observations of their behaviour are not yet possible.

Tool collection and analysis

During patrol, teams (which included the authors, research assistants, and local field assistants) would collect all encountered tools that were believed to have been used by chimpanzees. The vast majority of tools were associated with honey extraction. We have not yet been able to confirm the use of tools for termite eating by the Loango chimpanzees, as shown in Goualogo chimpanzees (Sanz and Morgan, 2007), but we could confirm that nut cracking with hammers is absent, despite the abundant presence of both *Coula edulis* and *Panda oleosa* nuts (Boesch, pers. obs.). Most of the tools were found in association with obvious signs of chimpanzee activity next to or under a beehive, and covered by honey if fresh (or smelling strongly of honey). Only tools associated with such signs were collected. The teams revisited sites where tools were found by large hives, as chimpanzees would come back to a beehive as many as 5 times to extract more honey. Between February 2005 and September 2007, we collected 614 potential tools from 45 sites and stored them at our camp for later analysis. In the majority of the instances involving tree nests, chimpanzees would extract honey from nests located at least 20 m above the ground, and the tools they used were collected after they had already departed. Therefore, it was impossible to identify with confidence the individual tools used by chimpanzees for different purposes from the many different tools found on the ground. Hence, we used an archaeological approach, whereby we used a clear morphological definition of tools (Table 1a and b) allowing for the classification of the collected tools into different types, and avoiding problems of inter-observer reliability. In doing so, we assumed that our morphological types corresponded to different functions, but we could confirm this only in the few cases where direct observations were possible (see below). We set clear required criteria for an object to be classified under one of the six tool types. Those criteria include only objective physical properties that can be determined from impact signs on the sticks collected. From personal experience, we noticed that a stick broken forcefully and quickly from its substrate will break neatly, whereas a stick broken more progressively will exhibit fibers that separate as the stick is progressively bent, producing something like a frayed end. To fulfill our criteria, a blunt end results from the pounding or hitting against a hard surface, bending the wood fibers strongly at the end of the stick (Fig. 1a). Similarly, we considered an end to be frayed when, despite use, the fibers remained extended and open (which would not happen if it was pounded). Goualogo chimpanzees have been described to intentionally produce a frayed end with their teeth (Sanz and Morgan, 2007). However, since we did not have direct observations to confirm this, we did not imply such an intentional modification.

Furthermore, to prevent biased or subjectivity in tool classifications, we applied a “triple blind procedure.” Following the procedure used by Mercader et al. (2007), we implemented this procedure to independently assess if the tools we collected were, in fact, tools and showed signs that could be classified as tools with confidence: we required a tool to show signs of modification and wear. Three observers (CB, JH, and MR) independently determined

Table 1a
Definition of tools and tool functions used by chimpanzees for honey extraction in Loango National Park.

Name	Definition	Equivalent names
Tool	Stick found under a beehive presenting at least one modification and clear signs of wear from being used.	
Pounder	Thick stick used to break open the protection of the beehive entrance so as to permit access. After use, the tool possesses at least one distinct blunt end.	Pounding stick (1, 2) Hammer club (3)
Enlarger	Stick used to perforate and enlarge the different compartments within the hive. After use, the tool presents at least one distinct blunt end and traces of levering sometimes on the side.	Prying stick (2, 4) Dip stick (2, 5)
Collector	Stick used to dip or scoop the honey out of the beehive. After use, the tool presents distinct signs of wear at one frayed end.	Bee probe (6), Fluid dip (7) Fishing probes (8, 4)
Perforator	Stick used to perforate through the ground to locate the honey chamber and to dig into the soil. After use, the tool presents at least one distinct blunt end with soil on it.	Punctuating stick (1, 5, 8) Digging stick (2) Perforating stick (4)
Swabber	Strips of bark used to dip and “spoon” the honey out of the opened beehive.	

1 = Sanz et al. (2004), 2 = Fay and Carroll (1994), 3 = Hicks et al. (2005), 4 = Bermejo and Illero (1999), 5 = Sanz and Morgan (2007), 6 = Fowler and Sommer (2007), 7 = Sanz and Morgan (2009), 8 = Deblauwe et al. (2006).

the type of modifications (stripped of leaves, stripped of bark, end cut), as well as the type of wear (blunt or frayed end) for each of the potential tools. Furthermore, we tried to determine the possible function of the tool (Table 1a and b, Fig. 1a–c). We required unanimity between the three observers for a potential tool to be considered a tool, or in order to determine its function. This procedure is conservative, because items thought to be tools when collected, but did not show any signs of wear or modification, were discarded from further analysis and their function was assigned only if all three observers agreed. In this double selection process, 178 of the 614 (29%) items collected in the forest were discarded during the triple blind test procedure. Of those considered as tools ($N = 436$), we did not reach unanimity about the function for only 55 tools (12%) and these were therefore considered to have an “unknown” function.

Bees and beehives in Loango National Park

The chimpanzees in Loango were found to use tools mainly for extracting honey from hives of different species of bees. The most

Table 1b
Operational criteria for inferring function of tools used by chimpanzees for honey extraction in Loango National Park.

Name	Size Diameter	Modification			Wear		
		Length Reduction	Removal of		Blunt end	Frayed end	Soil
			Leaves	Bark			
Pounder	>3.1 cm	f	f	f	+	–	–
Enlarger	<3 cm	+	f	f	+	–	–
Collector	<3 cm	+	f	f	–	+	–
Enlarger/ Collector	<3 cm	+	f	f	+	+	–
Swabber		+	f	+	–	–	–
Perforator	<3 cm	+	f	f	+	–	+

Length reduction is observed when, after breaking off a stick, the other end is cut to reduce its length.

+ = required to be present; – = required to be absent; f = facultative (as it can be seen, but is not used as a criterion in the classification of tools).

common hives were those of honeybees (*Apis mellifera*), large sweat bees or Melipone bees (*Meliponula bocandei* and *Meliplebeia nebulata*) located in trees, and small sweat bees (*Meliplebeia lendliana*) found in ground nests. It was difficult to characterize beehives in trees, as they could be located very high off the ground. Honeybees generally make their nests in large tree trunks with a rather small opening, and many bees constantly guard the nest entrance. African honeybees can be extremely aggressive and would attack any aggressor in a swarm. We were therefore unable to confirm if chimpanzees prefer to attack nests with a larger entrance and/or with less aggressive defenders.

We found three intact tree nests of large sweat bees in fallen trees and dissected them (Fig. 2a and d). The entrance of the nest was either a small hole in the branch or tree trunk, or a larger hole that was partially closed by the bees with hard dried wax through which only a small entrance was seen and used by the bees. The arboreal nests had an internal diameter of about 30 cm and an internal length of as much as 1 m. Such nests are normally found in large branches of tall trees. Many bee nests are situated in branches with a very small entrance, or just a tiny fold of the bark, and cannot be accessed by the chimpanzees, while those attacked by the chimpanzees possess larger entrances or are in large branches that break off. The internal structure was difficult to judge, but from the three we opened, we observed that wax chambers structured the interior of the nests so that honey was not directly accessible even after breaking open the main entrance (Fig. 2b and c).

The entrance to ground nests is typically a very small and fragile tube made of wax and resin (Fig. 2e). These can descend as far as 100 cm deep underground, where small *Meliplebeia* bees construct one chamber that is rarely located directly vertical beneath the tube entrance (Fig. 2f). As these tubes follow an irregular and circumvented route to the underground chambers, we believe that chimpanzees would typically need to perforate the ground with sticks to find out where those chambers are, and we regularly found many tools left behind that were still inserted in the ground. The sticks selected to perforate the ground are very straight (Fig. 1c). When perforated, the thin wax layer surrounding the chamber breaks into an open space where the honeycombs are located. This action alerts the bees, and their buzzing can be heard from the surface. Personal tests confirmed that perforating the ground with a stick enables one to locate underground chambers.

Statistical analysis

The morphological characteristics, length, diameter, and number of modifications of the five types of tools for the three different bee nests were compared using the Kruskal-Wallis test. Due to repeated testing, we required a $p < 0.01$ to be considered as significant.

Results

Direct observations of tool use by chimpanzees

Habituation of chimpanzees takes five years on average, so that it is not surprising that our direct observations of tool use are limited (Goodall, 1986; Boesch and Boesch-Achermann, 2000). However, we did make some clear observations of tool use in chimpanzees for the purpose of honey extraction. On July 6th, 2005, a group of 9 chimpanzees was seen gathered around a large sweat bee nest located approximately 40 m high in a tree. J.H. and an assistant heard a heavy pounding sound and saw a large pounder fall to the ground as they arrived, most likely after the nest opening was enlarged. The chimpanzees stayed for 79 minutes before becoming aware of the presence of the observers,

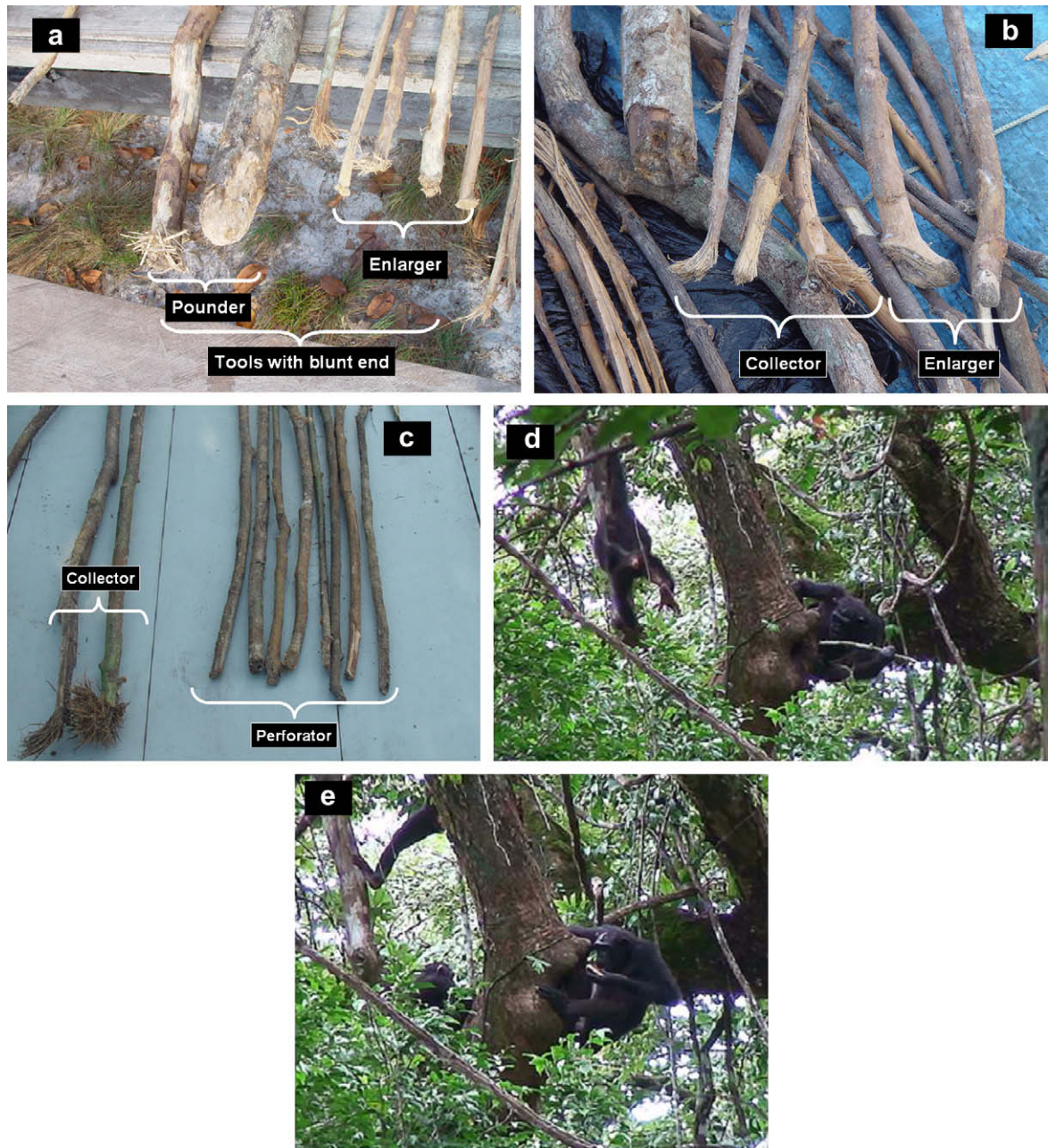


Figure 1. Illustrations of some of the different tool types used by chimpanzees in Loango National Park, Gabon, to extract honey from 3 different types of bee nests: a) Group of tools including pounders (right pounder diameter = 4.8 cm) and enlargers; b) Closer view of three collectors (left) and two enlargers (right) (left enlarger diameter = 2.0 cm); c) Ground nest tools showing two collectors (right collector diameter = 1.9 cm) and some perforators with their special straight line shape; d) A female chimpanzee using an enlarger in an *Apis* tree nest and, e) then taking a piece of comb with her hand.

after which they quickly departed. Four individuals were observed making new tools by breaking branches from a tree, modifying them, and then inserting them into the tree hole to extract honey. Once inserted, the chimpanzees were seen to rapidly and forcefully rotate them inside the hole, suggesting that they were first breaking up the internal chambers (with the enlarger) before “dipping” for the honey. One adult male was observed to first remove the bark of a *Garcinia* sp. branch with its teeth and then put one end of the stick in its mouth and chew on it, as if to fray it before using it to extract honey. A short while later, an adult female with two juvenile offspring approached the nest entrance and let her juvenile offspring lick the end of the first stick, while she used the second one to extract more honey. In another instance, on the 23rd

of July 2005, C.B. and an assistant were attracted to a site by a loud pounding sound, at which two adult males were seen to use tools to extract honey for 13 minutes from a big fallen branch. The first chimpanzee used a large broken shrub with leaves and branches still intact, and tried to push it into the hole. He then broke the shrub, rejected the end with the leaves, and shoved the newly modified tool into the hole and performed sweeping semi-circular motions before removing it and putting it into his mouth. He then pulled the tool through his mouth to remove the honey, and reinserted it into the hole. The second male used a ready-made tool lying on the ground. In eight other instances, we saw twelve chimpanzees using tools to extract honey from both honeybee and sweat bee nests in trees or in fallen branches.



Figure 2. Illustrations of the three types of bee nests exploited by the chimpanzees in Loango National Park, Gabon: a) A large sweat bee (*Meliponula* sp.) tree nest in a fallen branch with the pile of tools used by chimpanzees found on the ground; b) Close-up of the intact nest entrance of a *Melipone* tree nest showing the cross-shaped wax entrance; c) Close-up of the entrance once the hard wax is removed, showing the softer wax layer containing the honey; d) Tree nest of honeybees (*Apis mellifera*) with a pounder still inserted in the nest entrance; e) Entrance to a ground nest of small sweat bees (*Meliplebeia lendliana*) visible only thanks to a small yellow wax tunnel and, f) Close up of one chamber containing the honey of an underground sweat bee nest.

Loïc Mackaga made a detailed observation of chimpanzee tool use at an arboreal honeybee nest in October 2008. An adult male chimpanzee was observed to first break the entrance of the nest with a large pounder and then remove honeycombs with his hand. Two adult females, up to 5 m away from the hive, made tools and used them to enlarge the nest and remove pieces of honeycomb from its wall. Once successful, they let the tool fall down and removed the comb with their hands (Fig. 1d and e). One of the females made a second tool to allow her to break off more of the comb. Two juveniles and another adult female then came to remove honey and pieces of comb without using tools.

Number and type of tools used for extracting honey

More tools were used on average at the tree nests of *Melipone* bees than at both *Apis* bee nests or *Melipone* ground nests (Table 2). We revisited some of the large *Melipone* nests up to 4 times and each time we found fresh tools under the nest. One of the large nests had 125 potential tools lying on the ground under the tree following 4 visits by the chimpanzees. *Apis* nests were also found in trees, seemed to possess smaller entrances, and fewer tools were used to extract their honey. *Melipone* ground nests were much more difficult to detect, and we had the impression that sometimes

Table 2

Measurements, with standard deviations in brackets, for the different tool types used by the Loango chimpanzees to extract honey from the three different nest types.

Nest species	Tool type	Sample size	Diameter	Length	Number of modifications
<i>Apis</i> nest	Pounder	6	4.2 cm (2.20)	88.8 cm (20.6)	0.66 (1.15)
	Collector	6	1.1 cm (0.34)	95.7 cm (43.0)	1.66 (1.96)
	Enlarger	5	1.0 cm (0.16)	64.9 cm (16.3)	4.20 (1.30)
Melipone tree nest	Pounder	32	3.7 cm (1.23)	77.4 cm (32.7)	1.92 (1.26)
	Collector	178	1.9 cm (6.59)	67.7 cm (31.6)	3.44 (1.55)
	Enlarger	75	1.2 cm (0.41)	77.5 cm (24.8)	4.34 (1.05)
	Collector/Enlarger	22	1.2 cm (0.27)	74.1 cm (18.7)	5.09 (0.81)
	Swabber ^a	55			
Melipone ground nest	Perforator	10	1.1 cm (0.24)	69.3 cm (24.0)	3.37 (0.61)
	Collector	26	1.1 cm (0.31)	48.1 cm (23.1)	2.95 (0.85)

^a Swabbers are bark strips that are dried and have rapidly lost their original shape making reliable measurements of length and diameter impossible.

tools were used to search for the underground chambers, but that this quest was not always successful, which could explain the lower number of tools used.

The difference in the number of tools resulted not only from the fact that they used more tools for *Melipone* tree nests but also that they used more types of tools (Fig. 3). Tool sets (i.e., different types of tools used chronologically to access a single food source) seemed to be used for all three types of beehives (Fig. 3). In addition, tool sets were larger for *Melipone* tree nests, including as many as 5 types of tools, than for the other two types of nests, with three types of tools used at *Apis* nests and 2 types at *Melipone* ground nests (Table 2). Chimpanzees were seemingly using 5 types of tools in a sequential order to access the honey within *Melipone* tree nests: first, a pounder was used to break open the nest entrance, then enlargers created an opening to access the different chambers within the nest, and finally, collectors were used to remove the honey. Additionally, at two nests, swabbers (elongated strips of bark) were also used as collectors. Finally, some tools presented obvious wear at both ends, with one end of the tool being blunt and the other having been frayed, indicating that they had been used for two functions, such as an enlarger as well as a collector. For *Apis* nests, only three different types of tools were found in the tool set: pounders, enlargers, and collectors. It is possible that painful bee stings limit the amount of time chimpanzees can stay at nests, which would in turn limit the number of tools they use. Two types of tools were found at *Melipone* ground nests, including one that was unique to this type of nest:

perforators, which were most likely used to vertically penetrate the ground around the nest entrance and locate the underground honey resources. Tests conducted at nest sites, and the inspection of nests previously exploited by chimpanzees, indicated that the perforators must be inserted into the ground to a depth of 20–90 cm to locate the precise position of the single underground chamber. No signs of the chambers are visible on the ground level (Fig. 1d). Furthermore, we never found a pounder at these ground nests, since dried wax was not blocking the entrance of the nest and no pounding was required to access them.

Tool size and functions

Different tool types within each tool set were characterized by different lengths and diameters, as measured with a ruler at the wear end for diameter (Table 2, Fig. 4a and b). Generally, tools used for the same function were rather homogenous in size, as the length and diameter did not differ between nest types (comparisons of each tool type for each of the three nest types using Kruskal-Wallis tests found no significant difference in diameter, length, and modification number). The only exception was that the collectors were longer for *Melipone* tree nests than for *Apis* tree nests, and the shortest for *Melipone* ground nests ($p < 0.001$). However, tools used for different functions also looked different. Pounders used to break open nests are thicker (comparisons of pounders to other tool types across the three nest types using Kruskal-Wallis tests: $p < 0.001$ for diameter). We defined pounders as being thicker, and this result is only a confirmation of the initial impression that led us to define pounders in the first place. In contrast, tool length is similar for each tool type regardless of nest type ($p > 0.05$), as they all are used for the function of accessing the honey and, therefore, the length seems more determined by the depth of the nest in which the honey is found, rather than by the function of the tool.

Tool making and number of modifications

Tools with different functions were also modified in different ways (Table 2, Fig. 5). Generally, enlargers were modified in more ways than the other tool types (Kruskal-Wallis tests: $p < 0.001$, for the number of modifications). Pounders showed the least signs of modifications (Kruskal-Wallis test: $p < 0.001$, for number of modifications). In addition, the type of bee nest also influenced the number of modifications made to a tool: collectors for *Melipone* tree nests had more signs of modification than collectors used for the other two nest types ($p < 0.001$).

Discussion

Tool sets, which have been proposed to be uniquely important in human tool use, have rarely been observed in wild chimpanzee

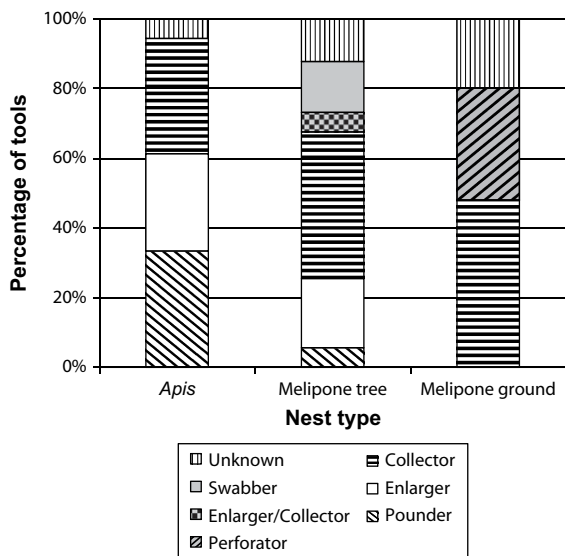


Figure 3. Tool sets in chimpanzees of the Loango National Park, Gabon, used to extract honey from three different types of nests. Tool sets included 3 to 5 different tool types. Grey-marked tool types were found only for one specific type of nest.

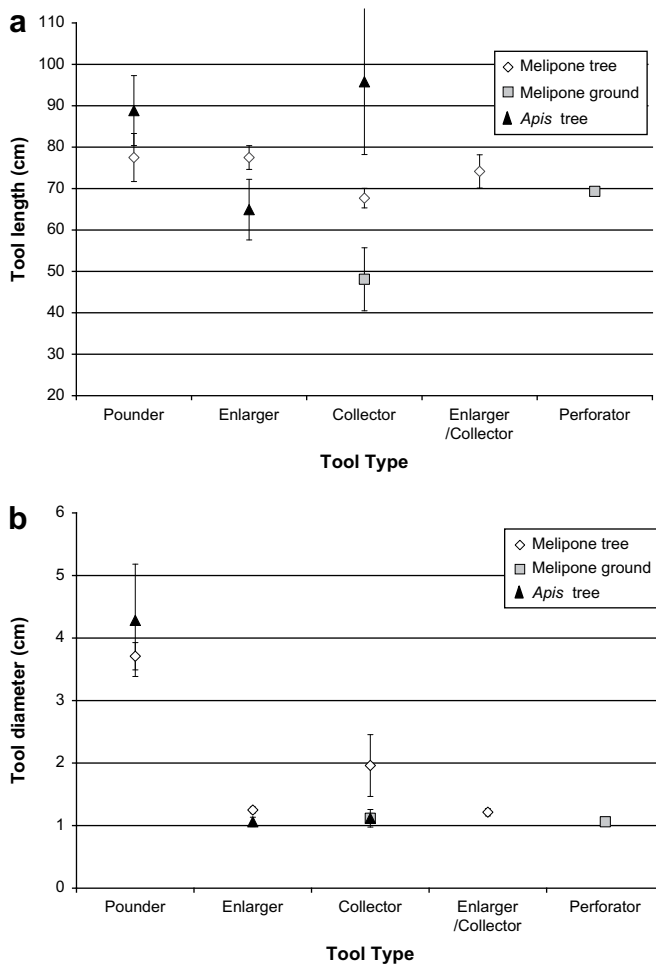


Figure 4. Tool length (a) and diameter (b) of 5 different tool types used for the three bee nests by chimpanzees in Loango National Park.

populations until recently. One notable exception involved Tāi chimpanzees, who were observed using hammers to break the nuts of *Panda oleosa*, *Parinari excelsa*, or *Detarium senegalense*, and were often seen inserting a stick in order to extract pieces of kernel from inside the shells (Boesch and Boesch, 1990). Furthermore, a reintroduced group of chimpanzees in Liberia was also observed using similar sets of sticks to occasionally break open beehives (Hannah

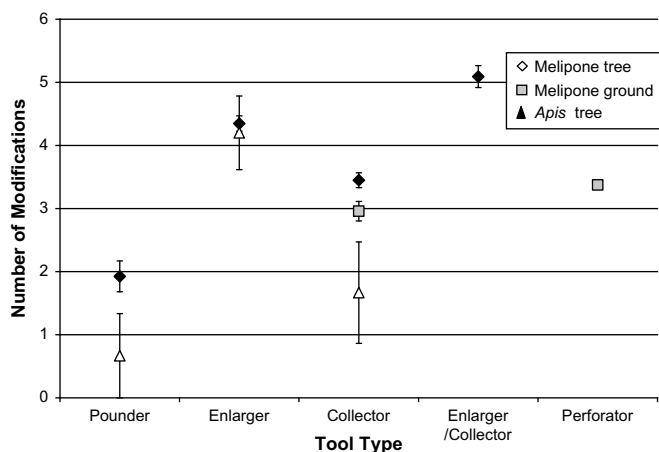


Figure 5. Number of modifications done to 5 different tool types used for three nest species by chimpanzees of the Loango National Park.

and McGrew, 1987). In recent years, data from central African chimpanzees have shown the prevalence of tool sets for honey extraction and termite fishing (Bai Hokou: Fay and Carroll, 1994; Lossi: Bermejo and Illero, 1999; Goulougo: Sanz et al., 2004; Sanz and Morgan, 2007; Ngotto: Hicks et al., 2005; Dja Biosphere Reserve: Deblauwe et al., 2006). The tool sets found in Loango confirm that Central African chimpanzees use tool sets more systematically than chimpanzees from other African regions. More tools have been found under bee nests in Loango than in Goulougo, but this difference could be explained by possible differences in nest structure: one of the two *Melipone* bee species raided in Loango is not the same as the two exploited by the chimpanzees in Goulougo (Sanz and Morgan, 2009). Specifically, Loango chimpanzees did not conduct raids on mason bees that construct their nests on tree trunks, which most likely require fewer tools than when raiding lodger bees that use deep tree cavities. Chimpanzees demonstrate an elaborate flexibility in their tool use and can readily use complex tool sets whenever necessary.

Such tool sets are used to extract honey from both tree hives and underground hives. Gathering honey from underground hives, similar to underground termite fishing in Goulougo, is special in the sense that chimpanzees cannot see where the resource is hidden and use the first tool, the perforator, as an exploratory tool to “feel” where the resource is located underground. In both cases, external indirect signs of food sources are visible (e.g., large termite mounds or small fragile *Melipone*-made tubes), but the nest itself is not visible and its exact location cannot be inferred. Therefore, chimpanzees have to investigate the soil in order to locate food that can be, in the case of *Melipone* underground nests, as much as 1 m deep and 70 cm lateral to the visible tube. Locating the underground chamber can take a human between 20 to 40 minutes (Boesch, pers. obs.). The successful locating of honey is apparent from honey sticking to the ends of perforators. To extract honey, a tunnel needs to be dug sideways so as to reach the underground chamber and prevent soil from getting mixed with the honey once the membrane of the chamber is broken (in general, the intact upper membrane of the chamber in the emptied hole can be felt). We think that such tunnels are dug with the help of perforators to loosen the soil. These tunnels are sometimes barely large enough to let a human arm through, and therefore indicate that chimpanzees know exactly where they are aiming. This cannot be done by simply following the bee tube, as it is much too fragile to resist the tool-assisted digging process. Thus, an elaborate understanding of unseen nest structure, combined with a clear appreciation that tools permit the location of unseen resources, and a precise three-dimensional sense of geometry for reaching the honey chamber from the correct angle, is demonstrated by the chimpanzees when extracting underground honey. It has been proposed that an elaborate understanding of causal relationships between external objects is required for flexible tool use to evolve (Boesch and Boesch-Achermann, 2000), and the fact that such exploratory tools are only seen in chimpanzees and humans supports this proposition.

Multiple function tools, in which both ends have been used for two different functions, have previously been proposed to be a uniquely human invention. Their use has now been confirmed in Loango chimpanzees for the purpose of gathering sweat bee honey. Obvious wear signs are still recognizable on both ends of 10% of the collected tools, even months after their use, indicating different functions for each end (see Sanz and Morgan [2007] for a similar case in Goulougo chimpanzees). In the absence of direct observations, it is too early to determine how chimpanzees used these tools specifically, but it is important to note that this type of tool use is not known from other chimpanzee populations in East and West Africa.

The sequential organization of the techniques requires many steps to be performed to have the appropriate tools ready in the correct order to extract the honey (Fig. 6a,b). Not only are different actions and modifications necessary to produce tools or results, but those tools are then combined in a precise order to achieve the goal. Different sequences can be produced, for example, using only two tools and a hand for extracting honey from tree nests (Fig. 6a), or using three or four tools. In other words, different sequential routes can be taken, either with two tools or with three or four tools, to extract honey from tree nests. In addition, parts of sequences can be repeated, e.g., collectors, or enlargers and collectors, can be refashioned after having been used previously for honey eating. All of this is done high up in the trees, often while suspending in acrobatic positions, because nest entrances are frequently oriented downwards or located away from convenient suspensory branches (Fig. 1d, see also Sanz et al. [2004] for pictures), tools are often discarded once honey can be reached, and, if needed again, tools have to be remade. This explains why we found an average of 18 tools under such tree nests. A similar sequential analysis for ground bee nests revealed that the operational sequence is less complex, as a maximum of two different types of tools was used but only one was actually mandatory (Fig. 6b).

Thus, we observed Loango chimpanzees following a hierarchical sequence of steps embedded within a sequential organization of tool use, when extracting honey from beehives. A similar operational sequence approach revealed lower levels of complexity in chimpanzees, both for nut cracking (Boesch and Boesch-Acher- mann, 2000; Carvalho et al., 2008), and for hunting tools (Pruetz and Bertolani, 2007), as these are basically linear sequences. The same will probably be true if applied to termite fishing or dipping, as seen in Gombe chimpanzee (McGrew, 1987). However, an operational sequence analysis of thistle-eating techniques in mountain gorillas revealed a non-linear sequence, and was therefore proposed to be of greater complexity than chimpanzee tool use (Byrne, 2004). However, since the non-linearity results from alternative routes used to achieve the same goal, and since only one of them will be used at a time, this sequence is less complex than the case of mandatory tool sets where different parallel sequences need to be performed to reach a goal, as is the case for honey extraction.

Central African forests are especially rich in many different species of bees, and this may have led to the use of these specialized tool sets by Central African chimpanzees for honey extraction (see also Sanz and Morgan, 2009). The forests of West Africa have many bees as well, but Tai chimpanzees were seen to concentrate mainly on honey from *Apis* tree nests, often using only their hands; tools were rarely used, perhaps because entrances in trees are often large enough to allow direct access (Boesch and Boesch, 1990). This confirms that tools are routinely used to access underground resources by some chimpanzee populations (see also Sanz et al., 2004; Hernandez-Aguilar et al., 2007). Therefore, as in the use of hammers to crack nuts, chimpanzees are significantly increasing the food sources they can exploit within a given habitat. Humans have been proposed to be unique in shaping the resources they can extract from their environment through technology (Wrangham et al., 1999; Ambrose, 2001; Laland et al., 2007). Chimpanzees clearly show a similar propensity with these unique tool use techniques. In addition, chimpanzees can also routinely use the same tools for multiple functions, which illustrates another facet of their flexibility in complex tool use.

Some of the sequential actions we observed in honey gathering by chimpanzees are reminiscent of what has been proposed for early hominin tool use during the Early and Middle Stone Age (Wynn and McGrew, 1998; Roche et al., 1999; Henshilwood et al., 2001; Goren-Inbar et al., 2002; Wynn, 2002). This includes: an

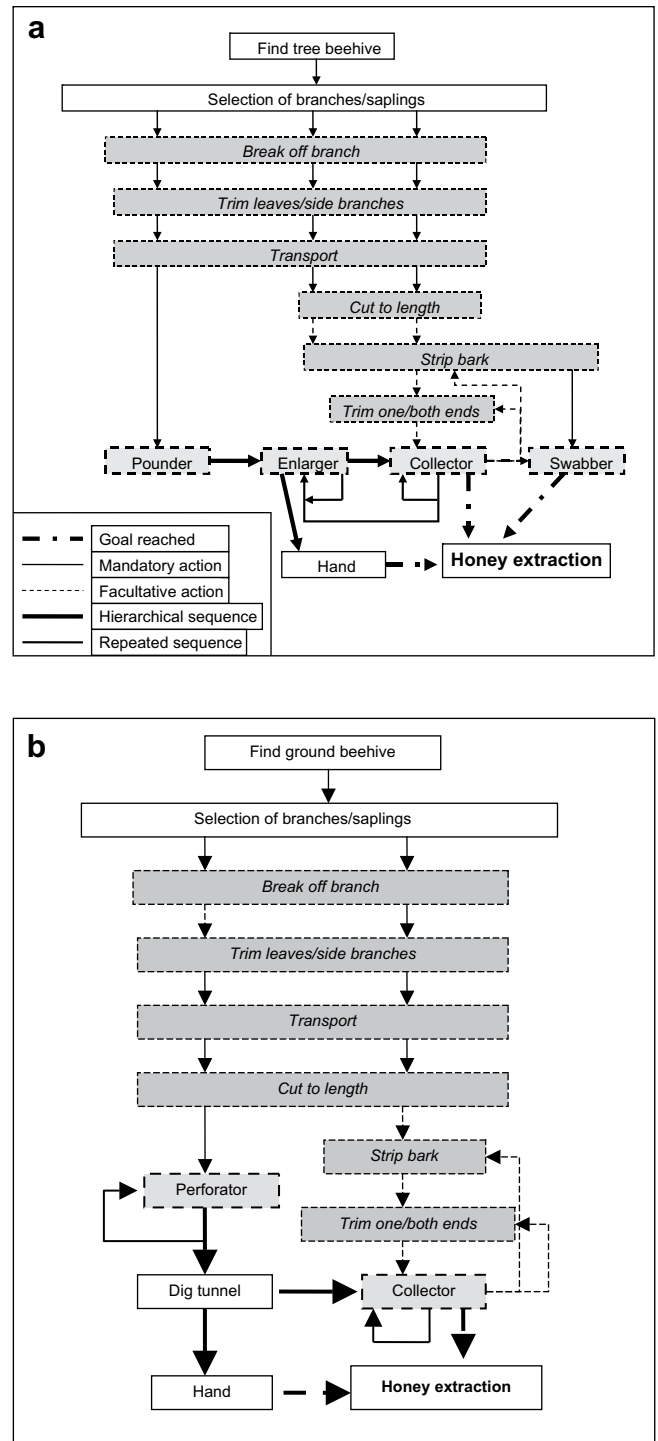


Figure 6. Schematic diagram of the operational sequence structure representing the possibilities of the sequential use of tools for honey extraction in Loango chimpanzees, a) for *Melipone* bee tree nests, and b) for *Melipone* bee ground nests. Thick arrows present the obligatorily sequential order between tools to obtain honey from an intact beehive. Normal arrows present additional tools, actions, or the reuse of tools that can occur when extracting honey from a beehive. Thin arrows present actions required (solid arrows) or facultative ones (dashed arrows), on the raw material in order for it to become a tool. Tools are in a dashed light gray box, actions on raw material are in a thin dashed dark gray box, and actions are in a box. The tool type “enlarger/collector” is not represented in Fig. 6a, as they simply are sticks for which each end represents two tools.

appreciation of the quality of the raw material, sometimes before even being at the food source; material selectivity; transport of raw material and tools; reduction and shaping of raw material before use (reduction in length, removal of lateral branches and leaves, and intentional shaping of brush in some cases); retouching during usage; a notion of order when using sequential tools; a notion of geometry; uniformity of tool forms; and an important cultural component in tool use (e.g., Loango chimpanzees live in a forest full of *Coula edulis* and *Panda oleaso* nuts, but do not crack them open with tools as Tai chimpanzees do in Côte d'Ivoire). However, the repeated reduction (up to 30) of one stone core in the Middle Stone Age indicates an elaborate débitage scheme that has not been found in chimpanzees. Another difference is that the use of tool sets as seen as in chimpanzees, has now to be found in that period of human evolution, while the use of tools to make other tools (e.g., stone knapping by Early and Middle Stone Age hominins), has not yet been observed in chimpanzees.

There is no direct evidence of tool manufacture and tool use before 2.5 Ma (Ambrose, 2001). Does that mean our ancestors at that time period did not use tools? If we assume that brain size is related to tool use, then we should expect to find plenty of evidence for tool use in *Australopithecus*. However, direct evidence of tool use is restricted to the occurrence of bone tools or inferred indirectly from the presence of isotopes showing evidence of protein consumption (d'Errico et al., 2001). If, however, we consider our evidence from chimpanzees, we need to take into account the environmental conditions experienced by our ancestors. Nuts, termites, and beehives need to be available in order for individuals to use tools to feed on them. However, to exploit those resources, an understanding of external object causality is required, as both edible parts, the nut and the honey, are not always directly visible. Boesch and Boesch-Achermann (2000) proposed that it is through hunting that this cognitive ability (the basis for flexible tool use) is acquired. While tool use *per se* has been observed in many birds and mammal species, flexible and complex tool use distinguishes humans and chimpanzees from all other animal species (Boesch and Boesch-Achermann, 2000). The fact that our early ancestors lived in more forested regions than previously thought (Rayner et al., 1993) suggests that they might have hunted on small mammals, like chimpanzees, and this practice may have opened the way to flexible and complex tool use.

The divide originally proposed between human and chimpanzee tool use continues to narrow as we discover new ways that tools are used in chimpanzee populations. Similarities in tool use between these two species lie in the fact that tools are used to reach some specific resource. It seems to be the presence of resources, combined with an understanding of how to reach them, that determines how tools are used. It is interesting that, for both humans and chimpanzees, honey, which is a rich and abundant food source in the tropical forest, seems to be an important resource in eliciting complex tool use (Bahuchet, 1985; Bailey, 1991; Hill and Hurtado, 1996). Important differences still remain, as tools used by humans have a much larger scope of function, which makes humans so dependent upon tools. But the fact remains that the dependence on tools in some human populations is much less important than in others (McGrew, 1987), suggesting that the key differences between both species in this domain might be more one of quantity rather than quality. The Savanna Model proposed that leaving the forest stimulated the acquisition of human-like behavior in our ancestors, however, tool use by chimpanzees is more frequent and diverse in forest dwelling populations rather than in the savanna (see also Boesch and Boesch, 1990; Sanz and Morgan, 2007), and thus specific ecological challenges seem more powerful in explaining the presence of different tool sets in chimpanzees. We anticipate that more tool use and tool use abilities will

be discovered in chimpanzees, as more populations living in different habitats will be studied. Hence, we need to learn more about chimpanzee tool use to resolve questions of what is specific about human tool use.

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