

Savanna Chimpanzees, *Pan troglodytes verus*, Hunt with Tools

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Summary

Although tool use is known to occur in species ranging from naked mole rats [1] to owls [2], chimpanzees are the most accomplished tool users [3–5]. The modification and use of tools during hunting, however, is still considered to be a uniquely human trait among primates. Here, we report the first account of habitual tool use during vertebrate hunting by nonhumans. At the Fongoli site in Senegal, we observed ten different chimpanzees use tools to hunt prosimian prey in 22 bouts. This includes immature chimpanzees and females, members of age-sex classes not normally characterized by extensive hunting behavior. Chimpanzees made 26 different tools, and we were able to recover and analyze 12 of these. Tool construction entailed up to five steps, including trimming the tool tip to a point. Tools were used in the manner of a spear, rather than a probe or rousing tool. This new information on chimpanzee tool use has important implications for the evolution of tool use and construction for hunting in the earliest hominids, especially given our observations that females and immature chimpanzees exhibited this behavior more frequently than adult males.

Results and Discussion

Chimpanzees (*Pan* sp.), our closest living relatives, have been observed to use tools in over 25 different contexts across all populations that have been studied [4]. Most notably, chimpanzees use tools to acquire social insects and to pound open hard nuts with a hammer and anvil [3, 4]. Generally, ape tool use in the wild occurs within a foraging context and is largely restricted to processing vegetable matter or invertebrates [3, 4]. However, at a new site in the mosaic savanna habitat of southeastern Senegal, we observed chimpanzees (*Pan troglodytes verus*) of the Fongoli community fashion tools in attempts to extract lesser bushbabies (*Galago senegalensis*) from cavities in hollow branches or tree trunks. Only one other instance of such tool-assisted hunting has been reported for wild chimpanzees. In that case, an

adolescent female at Mahale, Tanzania used a branch to rouse a squirrel from a hollow branch [6].

The observed hunts were recorded between March 2005 and July 2006. Bushbabies are small (weighing about 200 g [7]), nocturnal prosimians that sleep in hollow cavities or other shelters during the day [8]. Consumption of prosimian prey is itself rare for chimpanzees [4]. At most long-term study sites, red colobus monkeys (*Piliocolobus* sp.), which are absent from this dry site, are the most common prey recorded for chimpanzees [9].

In only one of the 22 recorded cases was the chimpanzee successful in finding and acquiring prey, but the observed tool making and associated hunting behavior was systematic and consistent. A common definition of tool use requires “the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user ... is responsible for the proper and effective orientation of the tool” ([5], p. 10). We analyzed specific modifications made during the process and divided the behaviors into a stepwise progression of tool manufacture and use, which indicates “crafting” by Fongoli chimpanzees, a behavior previously attributed only to humans and other sophisticated tool users such as crows [10] (Figure 1). In fact, termite-fishing and ant-dipping behaviors by chimpanzees should also be considered examples of “crafting” given the similar number of steps involved in making and refining these types of tools [4, 10]. Although each step observed in hunting with tools by Fongoli chimpanzees has been recorded for chimpanzees at other study sites in different tool-using contexts, the combination of these steps within a hunting context is unique, having been observed in only a few isolated cases [6, 11]. The number of steps completed during this task by Fongoli chimpanzees is similar to what has been observed during foraging on difficult-to-process plant foods by wild gorillas (*Gorilla gorilla beringei*) [12] and ex-captive orangutans (*Pongo pygmaeus*) [13] and is considered hierarchical in organization [12, 13]. The sequence of steps is hierarchically organized, with some steps that can be occasionally omitted and others that can be repeated. This structure is similar to what has been described as a branching tree [12], demonstrating the flexibility involved in an otherwise standardized process.

In most cases, Fongoli chimpanzees completed four or more steps of tool manufacture and use during hunting. In all cases but one, chimpanzees broke off living branches to make their tool. In every case, individuals trimmed side branches and leaves from the main branch/tool. In many cases, chimpanzees further trimmed both the proximal and distal ends and sometimes stripped the entire tool of bark (n = 8). Trimming off the smaller distal end appears to effectively strengthen the tool. In only one case was an individual observed to break a tool while using it. Individuals also

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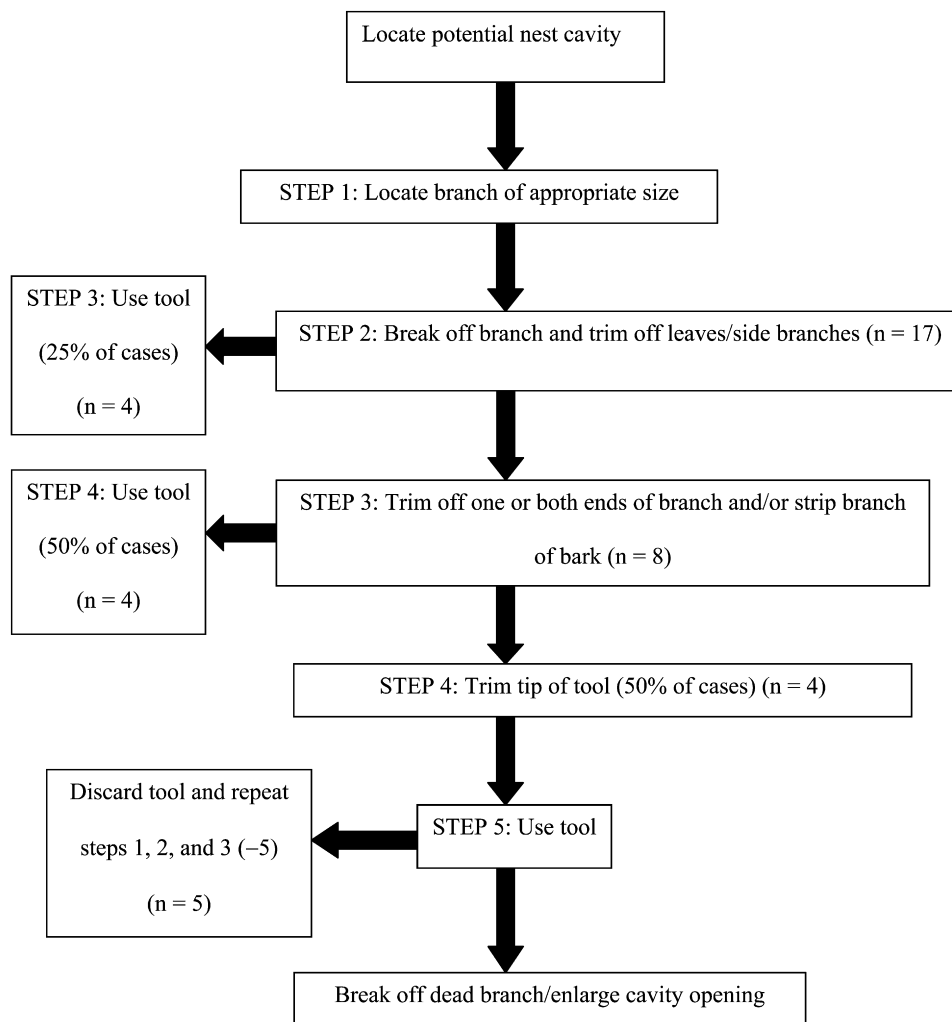


Figure 1. Steps Involved in Making Tools for Hunting by Fongoli Chimpanzees

sharpened the tip of the tool with their incisors ($n = 4$, Figure 2), sometimes using multiple bites to trim the tool end to a point. The function of this trimming appears to differ from similar behavior seen in other tool-using contexts, where it is usually done to obtain items that are within a small space (e.g., to extract the kernel from within a nut after it has been pounded open) and cannot be reached otherwise [14, 15]. The average diameter of cavities chimpanzees exploited with tools was estimated to be 11 cm (9–12 cm, $n = 7$), large enough for a chimpanzee to insert its arm up to the shoulder. However, tools did not function simply as an extension of the arm. Tools, but not hands and arms, were first forcefully inserted into cavities. In this way, tools functioned as spears.

Chimpanzees forcibly “jabbed” (sensu Marlowe [16]) tools into hollow trunks or branches multiple times and smelled and/or licked them upon extraction. In only two of 22 cases was tool use playful (in the case of the infant male) or exploratory in nature (“investigatory probe” [3]). In all other cases, chimpanzees were judged to use such force in inserting the tool that prey within the cavity could have been injured. In all observed cases, chimpanzees used one hand in a “power grip” [17] to

jab the tool downward multiple times into the cavity. In the single instance in which a chimpanzee was observed to extract a bushbaby, it was unknown whether the prey was alive or dead after the use of the tool, but it made no attempts to escape, nor did it utter any vocalization. In that case, the chimpanzee ultimately broke off the terminal end of the hollow branch by moving several meters up the large (>10 cm diameter) branch and jumping on the branch until it broke off. She then climbed down, reached into the cavity, and pulled out the bushbaby. This same behavioral sequence was also seen in two other cases. The opening of cavities after using a tool, especially after the chimpanzee has moved some distance from the cavity opening to do so, suggests that the tool is used to immobilize prey rather than for extraction. Bushbabies move rapidly, using a vertical clinging and leaping form of locomotion [7], and opening a nest cavity before immobilizing this prey would presumably result in frequent escape. Given these lines of evidence, the tools used by Fongoli chimpanzees can better be described as spearing as opposed to rousing tools [6].

Individuals observed fashioning or using hunting tools included one adult female, one adult male, three adolescent females, two adolescent males, one juvenile



Figure 2. Tip of Hunting Tool Sharpened with Teeth

Tool length approximately 70 cm.

female, one juvenile male, and one infant male. Multiple immatures were associated with tool-assisted hunting several times. One adolescent female was observed fashioning such tools a total of five times and was successful in removing and eating a bushbaby once, for a success rate of 0.20, similar to solitary male chimpanzee hunters at Tai, Ivory Coast (17% success rate [14]) but less successful than single hunters' success rates at Gombe, Tanzania during red colobus hunts (30%–40% [18]). In addition to the aforementioned case in which an adolescent female acquired a bushbaby with a tool, two other individuals were seen eating bushbabies, but the method of procuring the prey was not seen. An adult male was observed eating a bushbaby but was not observed to share meat with any other individuals, although several chimpanzees approached him and briefly watched him consume the prey. The adult female was seen to eat the largest portion of a bushbaby while her juvenile daughter fed on meat, presumably of this same bushbaby. The adolescent female who captured a bushbaby consumed her prey without sharing, although she was surrounded by a number of adult males. Extensive meat sharing, as characterizes monkey eating at other sites [14], was not observed in this context but had been seen in the same individual adult male chimpanzees with green monkey (*Chlorocebus aethiops*) prey at this same site just ten days previous. Sharing meat among chimpanzees correlates with coordination during hunts in most cases [14], although this view is disputed [19]. Regardless, given the small size of bushbaby prey and the lack of necessity for coordinated hunting in order to secure them, it is not surprising that more meat sharing does not occur.

Behavioral studies at Fongoli focus on the 11 adult males in this community of 35 chimpanzees, yet most of our observations of tool-assisted hunting are of females and immature individuals, underscoring its importance in these sex-age classes. This is in stark contrast to chimpanzee hunting behavior in general, a predominantly male activity [9, 14, 18, 20]. Immature chimpanzees at Fongoli appear to exploit a niche relatively ignored by adult males. This supports the proposal that individuals whose access to preferred resources such as meat is limited by social or physical factors respond by developing alternative means with which to

acquire them [6]. Social factors have also been proposed to explain why female but not male bottlenose dolphins use tools [21]. Our findings at Fongoli may support the hypothesis that female hominids play a role in the evolution of the earliest tool technology [16, 22], and we suggest that these technologies included hunting-related behavior, in addition to gathering-related activities.

The multiple steps taken by Fongoli chimpanzees in making tools to dispatch mammalian prey involve the kind of foresight and intellectual complexity that most likely typified early human relatives, e.g., Australopithecines. The observed utility of materials that do not fossilize further indicates that our assessment of the cognitive capacity of relatively small-brained hominids is most likely underestimated, as has been suggested elsewhere [23, 24]. The oldest known weapons of organic material are 400,000-year-old wooden spears [25], approximately 2 million years younger than the earliest evidence for stone-tool use by hominids [26]. Although we have long known that chimpanzees are efficient tool users [27], the observation of such behavior in a hunting context has significant implications for the way we have traditionally viewed hominid hunting. The suggestion that the earliest tool technology likely consisted of pounding or throwing rocks and hitting and jabbing sticks at about 6 million years ago [16] is supported by our findings.

Savanna chimpanzees, although little studied, can provide insight into behaviors characteristic of our own lineage given similarities with early Plio-Pleistocene hominid environments [28–34]. Chimpanzees at Fongoli inhabit a diverse and mosaic savanna environment, characterized by woodland, grassland, and small patches of gallery forest [35]. Early hominids inhabited increasingly open-canopy environments, and the selective pressures associated with such an environment may also operate on living savanna chimpanzees. The combination of hunting and tool use at Fongoli, behaviors long considered hallmarks of our own species, makes this population especially intriguing. The observation that individuals hunting with tools include females and immature chimpanzees suggests that we should rethink traditional explanations for the evolution of such behavior in our own lineage. Learning more about the

Table 1. Observations of Hunting Behavior with Tools by Fongoli Chimpanzees

Date	Subject	Age-Sex Class	Time of Day	Steps Completed (minimum)	Duration	# Tools Used	Tool Length (cm)	Base Width (mm)	Tip Width (mm)	Height of Cavity
Mar. 16, 2005	YO	Adult male	18:10	3	>7 min	1	50 ^a			7.0 m
May 17, 2005	TM	Adolescent female	07:50	3	3 min	1	100 ^a			2.5 m
May 21, 2005	TI	Adolescent female	17:03	?	>2 min	1	70 ^a			4.0 m
Sep. 6, 2005	JM	Juvenile male	09:40	?		1				
Sep. 29, 2005	JJ	Infant male	13:30	?	13 min	1				
Sep. 29, 2005	JM	Juvenile male	13:40	?	1 min	1				
Oct. 29, 2005	TM	Adolescent female	13:10	?	2 min	1				4.0 m
Dec. 28, 2005	NI	Adolescent female	10:52	?	>2 min	1	60 ^a			1.5 m
Dec. 28, 2005	TM	Adolescent female	10:54	?	1 min	1	40 ^a			1.5 m
Jun. 13, 2006	NI	Adolescent female	10:05	3		1	70	5	2	7.0 m
Jun. 15, 2006	FA	Adult female	08:30	3	5 min	1	75	5.5	1	3.0 m
Jun. 15, 2006	NI	Adolescent female	18:00	4	10 min	2	77.5	19	4.5, <1 ^b	6.0 m
Jun. 19, 2006	NI	Adolescent female	14:20	3		1	45	6	3	6.0 m
Jun. 20, 2006	TI	Adolescent female	07:44	2		1				10.0 m
Jun. 20, 2006	JM	Juvenile male	07:57	4		1	71	19	4.5	10.0 m
Jul. 3, 2006	DV	Adolescent male	17:20	3		1	45	6.5	3	2.75 m
Jul. 4, 2006	BO	Adolescent male	13:40	5	8 min	4	40, 42.5, 50.5	4.5, 3.5, 8.5	1, 2, 5	10.1 m
Jul. 6, 2006	DV	Adolescent male	08:24	5	4 min	1	70 ^a			9.5 m, 20.0 m
Jul. 8, 2006	NI	Adolescent female	07:05	5		1				8.5 m
Jul. 9, 2006	NE	Juvenile female	07:59	4	11 min	1	45	9.5	2	8.5 m
Jul. 13, 2006	TM	Adolescent female	18:45	4	1 min	2	75	16.5	4.5	4.5 m
Jul. 13, 2006	TM	Adolescent female	19:00	4		1	120	16	6	2.5 m

^aEstimated length only; not used in analyses.

^bTip width before and after trimming with teeth.

unique behaviors of chimpanzees in such an environment, before they disappear, can provide important clues about the challenges facing our earliest ancestors.

Experimental Procedures

Research was conducted at the Fongoli study site in southeastern Senegal (12°40'N, 12°13'W). The site can be described as a mosaic savanna habitat, composed mostly of woodland and grassland with small patches of gallery forest (approximately 2% of home range) [35]. Rainfall in the region occurs during a single wet season, from June through September, and averages 800–1100 mm per year [36]. Temperature averages 28.5°C [35]. The Fongoli community has one of the largest home ranges of any chimpanzee community studied thus far. The community range is estimated to be at least 63 km² [35].

The Fongoli community of chimpanzees has been studied since April 2001, with adult males becoming habituated to the presence of human observers in 2005, so that systematic behavioral data could be collected. Adult females are still wary of human observers, and all adult females were not identified until January 2006. The study period was March 2005–August 2006, with most observations made during June and July 2006. The community is composed of 35 individuals. Following Baldwin's [37] age categories, with slight modification, adults were estimated to be >13 yr of age, adolescents were 9–13 yr of age, juveniles 5–9 yr, and infants less than 4 yr of age. The Fongoli community consisted of 20 males, including 11 adults, three adolescents, four juveniles, and two infants. Fifteen females, including eight adults, four adolescents, one juvenile, and two infants, reside within the community.

Adult males serve as focal subjects in a long-term study of the ranging and feeding ecology of chimpanzees in one of the driest and most open habitats chimpanzees live in today. However, because more than just the focal subject can be observed during focal-subject follows, we also took into account the presence of other individuals in parties in calculating expected values of hunting behavior (see below).

When chimpanzees were observed searching trees for cavities or making tools in order to hunt for bushbabies, or when the sound of tools being jabbed into hollow cavities was heard, observers approached the area and recorded all details of the hunt that could

be observed. In approximately half of all instances, the entire hunting bout was not seen. However, except for one case, observers were able to reach the hunting chimpanzee in time to see details of tool use. We define a hunting bout as the total amount of time the chimpanzee was observed making and using tools. Bouts therefore included tool preparation and use and could include multiple instances of tool use by the same chimpanzee. Bouts ended when tools were discarded. The observations of chimpanzee tool use at Fongoli are summarized in Table 1.

Tool length averaged 63 cm (40–120 cm). The basal width of the 12 recovered tools averaged 10.0 mm (3.5–19 mm), and the tip averaged 3.2 mm (1–5 mm). Multiple hollows in a single tree were explored on three occasions. Sometimes, multiple tools were used in a single cavity (n = 4). Tools were often made from the tree in which the hollow was found (n = 7), although at least two individuals made their tool before ascending the tree. In one case, bushbaby hair was found adhered to a recovered tool, indicating that either the chimpanzee was unsuccessful in acquiring its prey or that the nest cavity had been abandoned. Although detailed data on handedness during tool use were not collected, two individuals were observed to only use their left hand in thrusting the tool, but at least one individual was also seen using both his right and left hands separately to thrust the tool into hollow cavities.

We used data on party composition collected during 17 months, from March 2005 through August 2006, to come up with expected values regarding age-sex class hunting behavior. Data on the proportion of parties (here defined as all individuals present in a day [38]) that adult males accounted for compared to all other individuals were averaged according to month. More than 2500 hr were spent in contact with Fongoli chimpanzees on 272 days, and daily party size averaged 15.4 individuals (n = 17 months). Overall average male presence was 46%, and females and immature chimpanzees accounted for 54% of all individuals. When we used these values to calculate expected hunting observations, males hunted significantly less than expected, whereas other individuals hunted significantly more than expected ($\chi^2 = 14.947$, df = 1, p < 0.01).

We also specifically examined the 19 days between 13 June and 13 July, 2006, when the majority of hunting behavior was observed. This allows us to more reliably consider the number of females in a party, given that not all females were identified before 2006. During this time, when 13 of the 22 observations of hunting with tools were recorded, the Fongoli community generally moved as one large

group across its range. Mean number of individuals in this large party per day ($n = 19$) was 30.5 (range: 23–34). A total of 227 contact hours were spent with chimpanzees. During this time, adult males accounted for 36% of party composition, and female and immature chimpanzees accounted for 64% of party composition. When we used these proportions to calculate an expected value for hunting rate, the low proportion of hunting with tools by males at Fongoli compared to the proportion of observations of females and immature chimpanzees using tools to hunt is significantly less than expected ($\chi^2 = 7.4$, $df = 1$, $p < 0.05$). Female and immature hunting was significantly greater than expected on the basis of their representation in the party. These values do not take into account the focus on males as subjects of observation as opposed to females and immature chimpanzees, only their presence in the group, and this supports further the observed difference between adult-male versus other chimpanzees' tool-assisted hunting behavior.

Supplemental Data

Supplemental Data include three movies and are available with this article online at: <http://www.current-biology.com/cgi/content/full/17/5/DC1/>.

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