



Flexible and Persistent Tool-using Strategies in Honey-gathering by Wild Chimpanzees

Crickette M. Sanz · David B. Morgan

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Abstract Several populations of wild chimpanzees use tools to raid bee nests, but preliminary observations of chimpanzees in the Congo Basin indicate that they may have developed sophisticated technical solutions to gather honey that differ from those of apes in other regions. Despite the lack of habituated groups within the range of the central subspecies, there have been several reports of different types of tools used by chimpanzees to open beehives and gather honey. Researchers have observed some of these behaviors (honey dipping) in populations of western and eastern chimpanzees, whereas others (hive pounding) may be limited to this region. Toward evaluating hypotheses of regional tool using patterns, we provide the first repeated direct observations and systematic documentation of tool use in honey-gathering by a population of *Pan troglodytes troglodytes*. Between 2002 and 2006, we observed 40 episodes of tool use in honey-gathering by chimpanzees in the Goulougo Triangle, Republic of Congo. Pounding was the most common and successful strategy to open beehives. Chimpanzees at this site used several tools in a single tool-using episode and could also attribute multiple functions to a single tool. They exhibited flexibility in responses toward progress in opening a hive and hierarchical structuring of tool sequences. Our results support suggestions of regional tool using traditions in honey-gathering, which could be shaped by variation in bee ecology across the chimpanzee range. Further, we suggest that these chimpanzees may have an enhanced propensity to use tool sets that could be related to other aspects of their tool repertoire. Clearly, there is still much to be learned about the behavioral diversity of chimpanzees residing within the Congo Basin.

C. M. Sanz (✉)

Department of Primatology, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany
e-mail: sanz@eva.mpg.de

D. B. Morgan

Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, IL 60614, USA

D. B. Morgan

Wildlife Conservation Society, Brazzaville, Republic of Congo

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Introduction

The tool-using skills of chimpanzees are distinguished from those of other nonhumans by a combination of factors, including the use of ≥ 2 types of tools to achieve a goal and flexibility in adapting tool strategies to new circumstances. Several populations of wild chimpanzees use tools to raid bee nests, but preliminary observations of chimpanzees in the Congo Basin indicate that these apes may have developed sophisticated technical solutions to gather honey that differ from those of apes in other regions. Differences in tool using strategies may reflect responses to different bee taxa, functional tactics for coping with target beehives, or socially transmitted traditions that differ between groups of chimpanzees (McGrew 1992). We attempt to precisely identify differences in tool-using strategies among populations by compiling reports from across the species range. This provides an informative context for presenting the first full descriptions of tool-using behaviors in honey-gathering by a population of the central subspecies of chimpanzee (*Pan troglodytes troglodytes*).

Chimpanzees typically gather the honey of African honey (Apini) and stingless (Meliponini) bee species that is stored in wax or resin vessels within the nest, but they also dip for the honey of carpenter bees (*Xylocopa* sp.) at some sites in West Africa (Table I). Nests of *Apis* may contain several kilograms of honey, whereas stingless bees rarely store >1 kg (Roubik 1989). Bees have developed effective means of protecting their hives that most often involve the fortification and concealment of their nests. Different bee species show particular nesting habits, but there is also variation in nest building within species (Roubik 1989). Bee nests of Apidae are most often built in tree hollows or other preexisting cavities (Roubik 1989). Other bees may find lodging underground, in the forest canopy, or within the nests of other insects such as ants or termites. Certain bees also restrict or close the nest entrance when an intruder is detected. Another form of nest defense is to pursue or sting the intruder. *Apis* and Meliponini both have alarm pheromones that mark the hive raider so as to direct their conspecifics to the threat. The task of the honey-gathering chimpanzee is to overcome the defensive strategies of the bees themselves, breach the protective structure of the hive, and extract the honey and larvae.

Previous reports of chimpanzee tool use in honey-gathering describe several different tools and associated behaviors (Table II), which together are referred to here as tool strategies. Inserting a probe into a beehive to extract honey (dipping) is the most widespread tactic used by chimpanzees in honey-gathering (Ivory Coast: Boesch and Boesch 1990; Guinea: Ohashi 2006; Central African Republic: Fay and Carroll 1994; Gabon: Boesch *et al.* in press; Tutin *et al.* 1995; Republic of Congo: Bermejo and Illera 1999; Sanz and Morgan 2007; Tanzania: Izawa and Itani 1966; Uganda: Nishida and Hiraiwa 1982, Stanford *et al.* 2000, Watts 2008, Wrangham and Muller, *pers. comm.*). Chimpanzees may also manually detach an entire hive or a branch segment that contains a bee nest, and then use a dipping tool to extract the honey (Ohashi 2006). As reported from populations in Nigeria,

Table 1 Bee taxa associated with reports of chimpanzee tool use in honey-gathering

	<i>P. t. vel.</i>			<i>P. t. verus</i>			<i>P. t. troglodytes</i>				<i>P. t. schweinfurthii</i>							
	GA	BS	TA	AS	BE	HK	ND	NG	LN	LP	GT	LS	GO	KS	MK	BW	KZ	KA
<i>Apis</i> sp.																		
<i>Apis mellifera</i>	b		d	+	-			p	d, p, l	d, l	d, p, l	d, p, l	g, w		d	d?		b, d
Meliponini	d, g	d	d		d, g	g	-	b, l	d, p, l	d, l	d, p, l	d, p, l		d	d	d?		
<i>Hypotrignona gribovii</i>	d, g				d, p		p											
<i>Hypotrignona ruspalii</i>	d, g																	
<i>Meliponula beccarii</i>																		
<i>Meliponula bocandei</i>																		
<i>Meliponula ferruginea</i> ^a	d, g							d, p, l, s										
<i>Meliponula nebulata</i>																		
<i>Meliponula lendliana</i>										d, l	d, l							
<i>Meliplebeia tanganyikae</i>								d, g										
<i>Xylocopa</i> sp.		d	b, k												d			g

This table format was adopted from McGrew (1992).

Gray shading indicates report of bee presence at that site.

Bee specimens were collected at Goaloungo (by C. Sanz and D. Morgan) and Loango (by C. Boesch, M. Robbins, and J. Head) with the intention of identifying all Melipone bees at these sites. More systematic and coordinated sampling of bee taxa across field sites could provide additional insights about the influence of ecological factors on tool use in honey-gathering. Revised taxonomic classifications and corrections by D. Roubik.

b = probe, d = dip, g = dig, k = bee kill, p = pound, l = lever, s = swab, w = whisk, + = tool use reported; -, tool use not reported for that particular bee taxa.

GA = Gashaka, Nigeria (Fowler and Sommer 2007); BS = Bossou, Guinea (Humle, pers. comm.); TA = Tai, Ivory Coast (Boesch, pers. comm.); AS = Assirik, Senegal (McGrew 1992); BE = La Belgique (near Dja), Cameroon (Deblauwe 2006); HK = Bai Hokou, C.A.R. (Fay and Carroll 1994); ND = Ndakan, C.A.R. (Fay and Carroll 1994); NG = Ngotto, C.A.R. (Hicks et al. 2005); LN = Loango, Gabon (Boesch et al. in press; Boesch, pers. comm.); LP = Lopé, Gabon (Tutin et al. 1995); GT = Goualougo Triangle, R.O.C. (this study); LS = Lossi, R.O.C. (Bermejo and Illera 1999); GO = Gombe, Tanzania (Wrangham 1975); KS = Kasakati, Tanzania (Izawa and Itani 1966); MK = Mahale-K, Tanzania (Nishida and Uehara 1983); BW = Bwindi, Uganda (Kajobe and Roubik 2006); KZ = Kahuzi Biega, Uganda (Yamagiwa et al. 1988); KA = Kanyawara, Uganda (Wrangham and Muller, pers. comm.).

Note: Bee taxa were not listed in the reports of tool use for Ngogo, but this site is located in Kibale National Park near the Kanyawara site.

^a *Meliponula erythra* = *M. (A.) ferruginea*.

Table II Tool use by wild chimpanzees in honey-gathering

Chimpanzee subspecies	Type of beehive	Research site behavior	Tool form	Length (cm)	Diameter (cm)	n	Reference
<i>Pan troglodytes verus</i>							
Bossou, Guinea		Dip ^a					Ohashi 2006
Tai Forest, Ivory Coast	Arb, Fln, Sbt	Fish ^a (dip)	Twig	28.1	0.8	42	Boesch and Boesch 1990
Tai Forest, Ivory Coast	Fln	Bee kill ^a	Twig	29	0.7	3	Boesch and Boesch 1990
Tai Forest, Ivory Coast	Fln	Probe nest ^a	Stem, Twig	14.8	0.5	7	Boesch and Boesch, 1990
Assirik, Senegal	Arb	Dip?	Stick	93.3±47.7	0.7±0.4	8	Bermejo <i>et al.</i> 1989
<i>Pan troglodytes vellerosus</i>							
Gashaka, Nigeria	Sbt	Dig	Stick	29.6±6.4	0.8±2.0	9	Fowler and Sommer 2007
Gashaka, Nigeria	Sbt	Probe	Stick	35.3±19.3	0.6±4.0	172	Fowler and Sommer 2007
Gashaka, Nigeria	Arb	Brush stick (dip)	Stick	46.1±13.6	0.9±2.4	9	Fowler and Sommer 2007
<i>Pan troglodytes troglodytes</i>							
La Belgique (near Dja), Cameroon	Sbt	Dig	Stick	69.7±13.7	1.4±0.3	13	Deblauwe 2006
Forest near Yaoundé, Cameroon	Sbt	Dip	Twig				Merfield and Miller 1956
Bai Hokou, C.A.R.	Fln	Pry/ram (lever/pound) ^a	Club	20	7	1	Fay and Carroll 1994
Bai Hokou, C.A.R.	Sbt	Dig	Stick	40	3.5	1	Fay and Carroll 1994
Bai Hokou, C.A.R.	Arb	Pound, ^a dip ^a	Club				Fay and Carroll 1994
Ndakan, C.A.R.	Arb	Pound ^a	Club	30–40	10	1	Fay and Carroll 1994
Ngotto Forest, C.A.R.	Sbt, Fln	Dig, pry (dig, lever)	Stick	58.1		56	Hicks <i>et al.</i> 2005
Ngotto Forest, C.A.R.	Arb	Hammer (pound)	Club	35.6, 88.9	2.4	2	Hicks <i>et al.</i> 2005
Lopé, Gabon	Arb, Fln	Lever ^a , dip ^a	Stick	78.5±26.9	1.6±0.5	95	Tutin <i>et al.</i> 1995
Lopé, Gabon	Arb, Fln	Lever, dip ^a	Stick	62.8±28.5	1.5±0.7	14	Tutin <i>et al.</i> 1995
Lopé, Gabon	Arb, Fln	Lever, dip	Stick	47.5±15.6	1.0±0.4	4	Tutin <i>et al.</i> 1995
Loango, Gabon	Arb	Pound	Club	80.0	3.4	18	Boesch <i>et al.</i> in press
Loango, Gabon	Arb	Enlarge (lever)	Stick	76.3	1.2	66	Boesch <i>et al.</i> in press
Loango, Gabon	Sbt	Perforate (dig)	Stick				Boesch <i>et al.</i> in press
Loango, Gabon	Arb, Sbt	Collect (dip) ^a	Stick, twig	68.9	1.1	136	Boesch <i>et al.</i> in press
Loango, Gabon	Arb	Swab	Bark strip				Boesch <i>et al.</i> in press

Goulougo, R.O.C.	Arb	Pound ^a	Club	62.7±22.4	2.8±0.7	27	Sanz and Morgan 2007
Goulougo, R.O.C.	Arb	Lever-open ^a	Stick	83.2	2.0	1	Sanz and Morgan 2007
Goulougo, R.O.C.	Arb	Dip ^a	Stick	43.2, 44.7	0.6, 1.3	2	Sanz and Morgan 2007
Goulougo, R.O.C.	Arb	Whisk ^a	Twig			1	Sanz and Morgan 2007
Lossi, R.O.C.	Arb	Chisel (pound) ^a	Club	70, 40–50	4, 7	2	Bernejo and Illera 1999
Lossi, R.O.C.	Arb	Bodkin (lever) ^a	Stick	70, 40–50	4, 7	2	Bernejo and Illera 1999
Lossi, R.O.C.	Arb	Dip ^a	Stick	60		1	Bernejo and Illera 1999
<i>Pan troglodytes schweinfurthii</i>							
Ituri, D.R.C.		Pound	Club				Hart, pers comm. in McGrew, 1992
Kahuzi-Biega, D.R.C.	Sbt	Dig	Stick	31.2, 43.4	0.8, 1.1	2	Yamagiwa et al. 1988
Gombe, Tanzania	Sbt	Dig/pry ^a	Stick				Goodall 1986
Gombe, Tanzania		Brush (whisk) ^a	Leaves				Goodall 1986 (p. 542)
Gombe, Tanzania		Lever-open	Stick				Wallauer pers comm.
Kasakati, Tanzania	Arb	Dip ^a	Stick				Izawa and Itani 1966
Mahale-K, Tanzania		Dip ^a	Stick				Nishida and Hiraiwa 1982
Bwindi, Uganda	Arb	Dip?	Stick	60	1.6	9	Stanford et al. 2000
Bwindi, Uganda	Arb	Dip?	Stick	27	0.5	12	Stanford et al. 2000
Bwindi, Uganda	Arb	Dip?	Stick	33.8	0.7	10	Kajobe and Roubik 2006
Kanyawara, Uganda		Dip ^a	Stick				Wrangham and Muller pers comm.
Kanyawara, Uganda		Probe ^a	Stick				Wrangham and Muller pers comm.
Ngogo, Uganda		Dip ^a	Stick	30	1.5	1	Watts 2008
Ngogo, Uganda		Whisk ^a	Twig				Watts 2008

The authors assigned tool behaviors in parentheses based on descriptive accounts. Arb = arboreal nest, Sbt = subterranean nest, Flin = fallen tree.

^a Scientists at site reported direct observations of tool actions.

Table III Tool behaviors observed in honey-gathering by wild chimpanzees

Behavior	Definition in honey gathering context	Localities of known observations
Hive pound	Chimpanzee uses end of a stout branch to hit the entrance of beehive to gain access to honey. The function of this tool is to weaken or break the area near the entrance of the hive to provide a larger access point. The pounding action often causes the end of the club to become blunt and smooth.	Bai Hokou, C.A.R. (Fay and Carroll 1994); Ndakan, C.A.R. (Fay and Carroll 1994); Ngotto Forest, C.A.R. (Hicks <i>et al.</i> 2005); Loango, Gabon (Boesch <i>et al.</i> in press); Goualougo, R.O.C. (Sanz and Morgan 2007); Lossi, R.O.C. (Bermejo and Illera 1999)
Honey pound		
Honey hammer		
Fluid dip	Chimpanzee inserts twig or stick into entrance of hive. The stick is extracted and honey is transferred to the mouth. The function of this tool is to collect honey from the hive. Some populations have been reported to use frayed dip sticks, but dip sticks may also become frayed as a byproduct of repeated dipping into the hive.	Tai, Ivory Coast (Boesch and Boesch 1990); Bossou, Guinea (Ohashi 2006); Bai Hokou, C.A.R. (Fay and Carroll 1994); Loango, Gabon (Boesch <i>et al.</i> in press); Lopé, Gabon (Tutin <i>et al.</i> 1995); Goualougo, R.O.C. (Sanz and Morgan 2007); Lossi, R.O.C. (Bermejo and Illera 1999); Kasakati, Tanzania (Izawa and Itani 1966); Mahale-K, Tanzania (Nishida and Hiraawa 1982); Bwindi, Uganda (Stanford <i>et al.</i> 2000); Kanyawara, Uganda (Wrangham and Muller <i>pers. comm.</i>); Ngogo, Uganda (Watts 2008)
Honey fish		
Collector ^a		
Probe	“A chimpanzee, in order to get access to the grubs and the honey, first tests for the presence of adults by probing the nest entrance with a stick” (Boesch and Boesch 1990, p. 89). Chimpanzee holds one end of a twig or stick tool and pushes the other end either into the hive entrance or on the area near the hive entrance. This action may be repeated several times, and the chimpanzee may visually examine or smell the end of the tool between probing. Tool function seems to be determining the presence of bees, verifying access into the hive, or testing the structural integrity of the nest.	Tai, Ivory Coast (Boesch and Boesch 1990); Gashaka, Nigeria; (Fowler and Sommer 2007); Kanyawara, Uganda; (Wrangham and Muller <i>pers. comm.</i>)
Investigatory probe ^b		
Lever-open	Chimpanzee inserts stick tool into hive entrance and then moves the tool vigorously within the nest. Insertion of the tool into the nest and pressing against the sides of the hive structure may provide leverage to widen access to the inner chambers of the hive or break the inner structures of the hive. The sides or ends of the tool may show wear from friction with the hive entrance or inner nest chambers.	Loango, Gabon (Boesch <i>et al.</i> in press); Ngotto Forest, C.A.R. (Hicks <i>et al.</i> 2005); Lopé, Gabon (Tutin <i>et al.</i> 1995); Goualougo, R.O.C. (Sanz and Morgan 2007); Lossi Forest, R.O.C. (Bermejo and Illera 1999); Gombe, Tanzania (Wallauer, <i>pers. comm.</i>)
Lever		
Bodkin		
Pry		
Enlarger ^a		
Push with foot	Chimpanzee places end of tool at hive entrance, and a foot on the other end of the tool to apply force on the hive entrance. The function of this tool is to weaken or break the area near the entrance of the hive.	Goualougo, R.O.C. (this study)

Flail/club	Chimpanzee hits side of stick or club against hive entrance. Sides of tool show wear. Rather than focusing specifically on the hive entrance, these forceful blows with the side of the club may serve to weaken the structure of the area around the hive as well as the hive entrance.	Goualougo, R.O.C. (this study)
Press and hold	Chimpanzee holds midsection of tool and places end of tool at the hive entrance, and pushes for several seconds. In addition to possibly weakening the hive structure, pressing and holding for several seconds may also provide information about the structural integrity of the hive.	Goualougo, R.O.C. (this study)
Rotate/twist	Chimpanzee places end of tool at hive entrance and then rotates tool as if drilling into the nest. Tool stays in contact with nest while rotated. The function of this tool is to provide a larger access point into the hive.	Goualougo, R.O.C. (this study)
Whisk/swat Brush	Chimpanzee uses leaves or leafy twig to dispel insects that mob the hive attacker. The tool is vigorously whisked or swatted at insects near the entrance of the hive or around the body of the tool user.	Goualougo, R.O.C. (Sanz and Morgan 2007); Gombe, Tanzania (Goodall 1986); Ngogo, Uganda (Watts 2008)
Dig/pry Perforator ^a	Chimpanzee uses a stick tool to access a subterranean beehive. Tools are used to pry soil from entrance or dig into earth. The function of the tool may be to locate the exact location of the underground hive, provide an access point to the hive, or perforate the hive structure itself to access to honey.	La Belgique, Cameroon (Deblauwe 2006); Loango, Gabon (Boesch <i>et al.</i> in press); Ngotto Forest, C.A.R. (Hicks <i>et al.</i> 2005); Kahuzi Biega, D.R.C. (Yamagiwa <i>et al.</i> 1988); Gombe, Tanzania (Goodall 1986)
Bee-killing tool	"If present, adult bees block the entrance with their abdomens, ready to sting. The chimpanzee then disables them with the stick to make them fall out and eats them rapidly. Afterwards, the chimpanzee opens the branch with its teeth to obtain the grubs and the honey." (Boesch and Boesch, 1990, p. 89)	Tai, Ivory Coast (Boesch and Boesch 1990)
Swabber^a	Long strips of bark are used to collect honey from a beehive.	Loango, Gabon (Boesch <i>et al.</i> in press)

Definitions include both behavioral observations of tool actions and the probable function of the tool based on the outcome of the tool action. When information is available, we also include comments about potential wear patterns on the tool resulting from this behavior. The authors have grouped terms from the literature that are likely to represent the same behavior.

^aBoesch *et al.* (in press) determined the function of tools recovered at tool sites based on the size, thickness, and types of wear on the tool. C. Boesch *et al.* (*pers. comm.*) related the tool types they have recovered (pounder, collector, enlarger, perforator, swabber) in Loango, Gabon to the definitions of tool using behaviors defined in this table.

^bBeehive probing is likely to be identified at most sites as investigatory probing that is not limited to the honey-gathering context. Goodall (1968) defined investigatory probe as "probe use to examine location (usually hole/recess), then sniffed." Investigatory probe is considered a universal behavior across long-term chimpanzee study sites (Whiten *et al.* 2001).

Cameroon, Central African Republic, and Tanzania, it is less common for chimpanzees to use a tool to dig or pry open subterranean hives (Deblauwe 2006; Fay and Carroll 1994; Fowler and Sommer 2007; Goodall 1986; Hicks *et al.* 2005). Researchers have observed chimpanzees using a tool as a lever to widen the access point to extract honey in Tanzania, Central African Republic, Gabon, and Republic of Congo (Bermejo and Illera 1999; Fay and Carroll 1994; Hicks *et al.* 2005; Sanz and Morgan 2007; Tutin *et al.* 1995; Wallauer, *pers. comm.*). Researchers have rarely observed pounding or hammering of beehives with the end of a large club to break the hive, but it seems exclusive to chimpanzee populations of the Congo Basin (Central African Republic: Fay and Carroll 1994, Hicks *et al.* 2005; Republic of Congo: Bermejo and Illera 1999; Sanz and Morgan 2007). Based on the geographical distribution of particular behaviors (Fig. 1), Hicks *et al.* (2005) hypothesized that there are regional honey-gathering traditions among wild chimpanzees. However, it is important to define tool-using behaviors more precisely so that observers can accurately identify similarities and differences between sites (Table III).

Although there are several published reports spanning >50 yr, the available information on the honey-gathering by wild chimpanzees in central Africa has been limited to recovered tool assemblages or fleeting observations of unhabituated apes. We examined if previous suggestions of regional tool traditions in honey-gathering are supported by direct observations of chimpanzees in central Africa. We analyzed video recordings of honey-gathering to define tool behaviors more precisely in this context and examine the plausibility of regional patterns of tool use. We also summarize information on the taxonomic composition of bee species to investigate if characteristics of the target hives may be shaping the honey-gathering strategies of wild chimpanzees across sites.

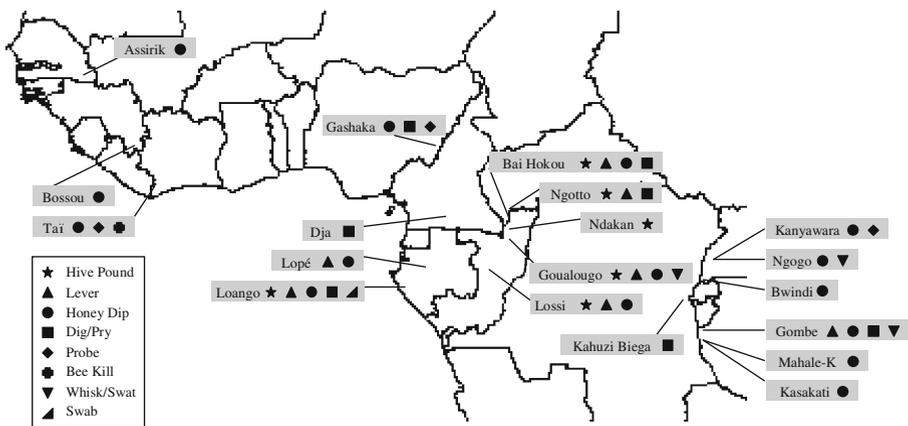


Fig. 1 Location of sites where chimpanzees use tools to gather honey. Symbols indicate the types of tool use at each site.

Methods

Study Site

The Goualougo Triangle is located in the southern portion of the Nouabalé-Ndoki National Park, Republic of Congo. The study area covers 380 km² of evergreen and semideciduous lowland forest, with altitudes ranging between 330 and 600 m. The climate is transitional between the Congo-equatorial and subequatorial climatic zones. Rainfall is bimodal, with a main rainy season from August through November and a short rainy season in May.

Study Population

Between February 1999 and December 2006, we spent 88 mo in the Goualougo Triangle habituating and studying wild chimpanzees. We conducted reconnaissance surveys in several community ranges, but the majority of this time was concentrated on the semihabituated Moto community, which consists of 70 individuals, including immatures.

Data Collection

We documented chimpanzee tool-using behaviors via direct observation. For all instances of tool using behavior, we recorded the actor, type of object used, target of object, actions, context or goal of the tool-using behavior, and the outcome, which we used to define tool function. We recorded digital video of tool-using behaviors, duration of honey-gathering episodes, other chimpanzees present, and collected tools whenever possible. We recorded the location of each tool site, species of targeted beehive, materials used to make the tool, length, diameter, and any modifications to the raw materials. Tool measurements are reported in Sanz and Morgan (2007).

We also collected information about the height, size of the hive entrance, and other physical defenses of the target beehive. We adopted Roubik's (1989) classification of bee nesting biology, which includes digger bees, lodger bees, and mason bees. Digger bees excavate nests in the ground or other substrate. Lodger bees modify preexisting cavities. Mason bees construct nests that are not enclosed in a substrate.

Video Data Analysis

We archived data from digital video cassettes on external hard drive devices and converted them to MPEG files for review. We conducted video analysis using INTERACT Version 8.04 (Mangold 2006). We scored video recordings as tool-using episodes and bouts (Yamakoshi and Myowa-Yamakoshi 2004). An episode begins when the chimpanzee manufactures a tool or the first moment after which they are observed with the tool and ends when the tool is discarded or the task is abandoned. A bout begins when a chimpanzee uses a tool toward achieving a goal and ends when he/she attains the goal, begins using another tool, discards the tool, or pauses use of the tool for >5 s.

Using an ethogram of tool behaviors compiled from reports of honey-gathering at other sites (Table II), we scored tool using actions within video recorded episodes of honey-gathering. If we did not find an observed behavior on the list of existing

definitions, then we operationally defined the novel behavior. We calculated Cohen's κ to assess point-by-point agreement for tool actions (pound, dip, lever-open, push with foot, flail/club, press and hold, rotate/twist, whisk/swat) between Sanz and an undergraduate student assistant. We scored tool actions as events, and the interval width for accuracy was 5 frames. Interobserver reliability between 2 coders was $\kappa=0.84$ ($n=23$ episodes), which is considered excellent (Fleiss 1981).

Elements are defined as functionally distinct behavioral units (Byrne and Byrne 1993; Byrne *et al.* 2001). To illustrate examples of multiple tool use, we graphed sequences of behavioral elements (including tool actions) as they occurred in honey-gathering episodes. Sanz and Morgan (*in press*) define the essential elements and structures of several tool-using behaviors observed in the Goulougo Triangle chimpanzee population.

Results

Between 2002 and 2006, we observed 40 episodes of chimpanzees using tools to gather honey. We video recorded 30 of these episodes, representing 12 different individuals and subsequently analyzed them in greater detail. Chimpanzees in Goulougo most often used tools to open and raid arboreal *Meliponini* hives, but also targeted beehives located in fallen trees and subterranean hives. We often located beehives in areas that were difficult to access (Fig. 2), such as tree hollows, under the bark of living and rotting trees, and embedded in arboreal ant nests. The most common defenses of the bees were the structure of the hive and mobbing of the nest invader. Attempted beehive raids took place throughout the year in Goulougo, with no apparent seasonal trends. There were slightly higher frequencies of honey-gathering in April and from August to September, which coincides with environmental cues such as minimum temperature in the dry season which trigger flowering events that influence honey production by bees.

The average duration of honey-gathering observations was 19 min ($n=26$, which include the full episode), with successful episodes lasting 31 min on average and unsuccessful episodes <5 min on average. Chimpanzees were successful in obtaining honey in half (52%) of our video-recorded observations. It was clear that they expended significant effort to open the hive and attain relatively small amounts of honey. The average number of tool using bouts in a successful honey-gathering episode was 14 ± 15.7 ($n=14$ episodes), compared to only 2.67 ± 2.74 in 12 unsuccessful attempts. The ratio of tool actions to goals for honey-gathering chimpanzees showed that an average of 6 tool actions ($n=6$, average= 6.10 ± 8.15 , range= $0.23-22.8$) were required for every taste of honey. The total number of tool actions ranged from 1 to >1000 beehive pounding actions in a single episode.

In total, we observed 8 distinct types of tool actions during video recordings of honey-gathering (Table III). Beehive pounding was the most common tool tactic, accounting for 94% of all tool actions and shown by 11 individuals (adults/subadults=6, juveniles=5). Fluid dipping accounted for 2.1% of tool actions and was exhibited by 5 individuals (adults/subadults=3, juveniles=2). Lever-opening comprised 1.8% of tool actions, and was shown by 7 individuals (adults/subadults=4, juveniles=3). Five individuals (adults/subadults=3, juvenile =2) exhibited a press-and-hold action, but this behavior comprised only 0.3% of tool actions. Two juveniles flailed and clubbed

the bee nest with the side of a branch, consisting of 0.4% of tool actions. Push with foot, rotate/twist, and whisk insects were exhibited by a single juvenile, and comprised 1.1%, 0.2%, and 0.04% of tool actions, respectively.

Most honey-gathering episodes in Goulougo involved 1 or 2 tools, but up to 5 tools were used by a single individual during a successful honey-gathering episode (Fig. 2). Although limited samples sizes prevented us from making a statistical assessment, successful tool-using episodes typically involved more tools (average=2.14, $n=14$) than unsuccessful honey-gathering episodes (average=1.54, $n=12$). Subjects did not use multiple tools simultaneously, but one after another in a serial fashion. We observed them using the same tool repeatedly during different bouts, or alternately with other tools. Most of the tools had a single function, but we also observed that a single object could be associated with several different tool-using functions (Fig. 3). Chimpanzees also frequently conserved pounding tools between bouts. Tools were placed in the canopy or held (in the foot, hand, mouth, groin pocket, or neck pocket) while the chimpanzee inspected the hive or between bouts of tool use. In Fig. 3a, we present a tool-using episode in which a chimpanzee first used a large pounding club that was eventually placed on an adjacent branch while she manufactured a smaller pounding club. After several bouts of pounding with the second club, she retrieved and reused her first tool. The female then subsequently manufactured a dipping probe to extract honey after succeeding to open the hive. This sequence of behaviors provide evidence of hierarchical structuring of tool use, with the opening task preceding the extraction task.

Comparing Observations Across Sites

The greatest diversity of tool-using behaviors in honey-gathering has been exhibited by the central subspecies of chimpanzee. In addition, pounding is almost exclusively observed within the *Pan troglodytes troglodytes* range, with the single exception reported from Ituri, Democratic Republic of Congo. In contrast, fluid dipping is the most commonly reported tool-using behavior in honey-gathering across sites and has been observed in all chimpanzee subspecies. The other most common tool-using



Fig. 2 Images of chimpanzees using tools to pound beehives. On the right, an adult female uses a large club to pound open a hive of *Meliponini* attached to the bark of a large tree. The left image shows a subadult female pounding the rotten bark of a dead tree to access a hive of *Meliponini*.

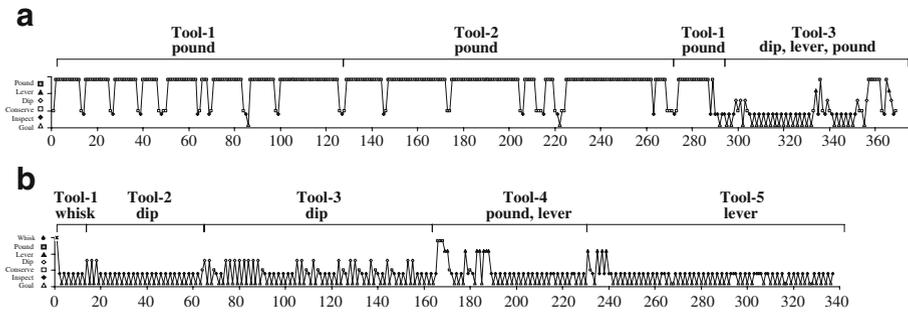


Fig. 3 Honey-gathering episodes including serial tool use of wild chimpanzees in the Goulougo Triangle, Republic of Congo. The y-axis summarizes behavioral elements (whisk, pound, lever, dip, conserve tool, inspect hive, and reach goal) important in achieving the honey-gathering task (Sanz and Morgan, *in press*) and the x-axis shows the progression of behavioral elements as the chimpanzee foraged for honey. **(a)** A tool-using episode of an adult female that used multiple tools to open a hive and then extract honey. The first 2 tools were stout branches used to pound the hive, while the third was a slender dipping probe fashioned from a twig. The first part of the episode was dominated by pounding actions that are separated by inspection of the hive. There were only 2 times that the chimpanzee consumed a small amount of honey. After the hive was opened with the reuse of the first tool, the chimpanzee manufactured a third tool to extract honey. **(b)** A tool using sequence of a juvenile male that first whisked away bees and then used another tool to dip for honey. The chimpanzee discarded the dipping tool and then gathered honey with his fingers, but subsequently manufactured another dipping tool. The chimpanzee then manufactured a fourth tool to pound and lever the hive entrance. The final tool was used as a lever to open the hive, after which the chimpanzee resumed eating honey.

behaviors are probing, prying/digging, and lever-opening. Researchers have attributed multiple functions to chimpanzee tools at several sites, including Lossi and Goulougo in Republic of Congo (Lossi: Bermejo and Illera 1999; Goulougo: this study) and Loango in Gabon (Boesch *et al.* *in press*).

To examine whether tool dimensions differed between tool functions, we compiled the diameter and length of tools reported from different sites. We excluded tools associated with multiple functions from this comparison. Tools used to pound and lever-open were consistently larger than tools used to dig, dip, and probe. Pounding (4.64 ± 3.59 cm, $n=48$) and lever-opening (3.40 ± 3.14 cm, $n=68$) tools had a larger diameter than tools used to dig (1.67 ± 1.25 cm, $n=25$), dip (0.98 ± 0.37 cm, $n=286$), and probe (0.54 ± 0.08 cm, $n=179$). Tools used to pound (59.99 ± 18.60 cm, $n=48$) and lever-open (59.83 ± 34.67 cm, $n=68$) were longer than tools used to dig (44.15 ± 17.59 cm, $n=25$), dip (49.93 ± 20.54 cm, $n=286$), and probe (25.05 ± 14.50 cm, $n=179$). However, one should interpret these results with caution because we found evidence that terms were not used consistently to define tool behaviors across sites.

Discussion

We provide the first repeated direct observation and systematic documentation of chimpanzee tool use in honey-gathering in the Congo Basin. Researchers have observed some of these behaviors (dip) in other populations of chimpanzees, whereas others (pound/hammer) may be limited to this region. In addition, some tool

behaviors may have been misidentified across sites owing to the lack of precise definitions of tool actions or functions. However, pounding of beehives is a distinctive behavior, with tools that surpass the size of any other honey-gathering tools used by wild chimpanzees (Table I). We confirm that pounding of beehives is habitual, defined as “seen repeatedly in several individuals, consistent with some degree of social transmission” by Whiten *et al.* (1999, p. 1488) among the population of wild chimpanzees in the southern portion of the Nouabalé-Ndoki National Park. Chimpanzees showed a high degree of persistence, as indicated by duration of tool using episodes and number of actions toward raiding beehives. Pounding was the most successful technique to open a hive, but chimpanzees exhibited flexible strategies and insightful problem solving in honey-gathering. We made repeated observations of sequential use of ≥ 2 types of tools, which is a behavior pattern that is rarely observed in other wild ape populations (Fox *et al.* 1999; Sugiyama 1997). Although tools may initially be manufactured for a specific function, we also found that chimpanzees were capable of using a tool for multiple functions. Such complex and flexible tool using behavior has not previously been reported for chimpanzees in West or East Africa, suggesting that their may be specific factors affecting their promulgation throughout this region.

Bees of *Apis* sp. and Meliponini occur throughout the range of all studied chimpanzee populations. It is plausible that bee ecology or hive structures vary across the chimpanzee range, but we had the impression that each hive was structurally unique and presented a challenge to the chimpanzee targeting it. This may be due to the prevalence of mason and lodger bees that opportunistically exploit substrates to encase their hives. Such varied targets may necessitate the tool user to possess multiple tactics that can be flexibly implemented or hierarchically structured relative to the conditions of each hive encountered.

Brewer and McGrew (1990) defined the use of a tool set as the consecutive use of >1 type of tool for a single task. Chimpanzees in the Goulougo Triangle used multiple tools in serial order, and showed hierarchical organization of tool-using behaviors with opening tools and actions preceding those to extract honey. Brewer and McGrew (1990) reported a clear instance of serial tool use by a young female chimpanzee that used several tools to open a hive and extract honey. During their long-term field research on gorillas in Republic of Congo, Bermejo and Illera (1999) observed a chimpanzee using the opposite ends of a single tool as a chisel and a bodkin to open a beehive. Chimpanzees in the Goulougo Triangle regularly use tool sets in other foraging contexts (Sanz *et al.* 2004), which could increase their overall technical competence or increase the likelihood of generalizing skills between tasks. In particular, these chimpanzees seemed to have developed the technological skills of using certain tools to overcome the defenses of their prey, and then another tool to gather/extract the item. For example, a perforating twig is used to open the exit tunnels of termites on the outer surface of elevated termite nests, which provides access for an herbaceous fishing probe used to extract the termites from the inner chambers of the nest. These chimpanzees also forage for termites in subterranean nests, which requires creating a tunnel into the nest with a stout puncturing stick, and then using a fishing probe to extract the termites. We have recently documented another tool set that is used by chimpanzees in the Goulougo Triangle to forage on army ants.

Chimpanzees in central Africa reside in sympatry with western lowland gorillas throughout most of their range. There is a high degree of dietary overlap between these species (Morgan and Sanz 2006), which may have prompted the development of advanced tool behaviors in these chimpanzees. Tool use in foraging contexts has been suggested to provide increased access to resources that results in a net energy gain for the tool user. Gunther and Boesch (1993) found a nutritional return of 9 times the energy output of nut-cracking behaviors. However, there are several indications that honey-gathering is not a particularly beneficial foraging strategy. First, rewards for honey-gathering were variable and ranged from only a few drops of honey to several handfuls of comb. Even if bee larvae were consumed, the nutritional return of gathering wild honey, which is composed of 69–80% sugar (Roubik 1989), is not likely to provide remarkable nutritional returns for the amount of energy expended. Second, a high degree of effort was expended to open beehives and attempts were not always successful. The success rate for honey-gathering in Goulougo was only 52% for the episodes we observed, with an average of 6 tool actions required for each taste of honey. Third, there is an element of risk inherent in this tool activity, which often occurs in the high canopy. Chimpanzees suspend themselves at precarious angles to access beehives, and a juvenile fell to the ground while gathering honey on the side of a large tree. Finally, overcoming the defenses of the beehives is technically challenging and there could be costs associated with individually inventing effective tool behaviors. For example, we observed younger individuals frequently engaging in tool practice, using a detached object in an appropriate fashion toward a location that did not contain honey or the hive was impossible to open. Based on the widespread observations of hive pounding and hammering in this region, there is likely to be some social facilitation of tool techniques. We observed tool transfer and sharing of tool sites between individuals, which is similar to a previous report of chimpanzees in the Tai forest sharing a honey dipping tool (Boesch and Boesch 2000, p. 193).

Based on our literature review and field research on this topic, we identified several steps that could advance the understanding of chimpanzee tool-using behavior in honey-gathering. As demonstrated by recent reviews of chimpanzee tool use in army ant predation (Schöning *et al.* 2007), more systematic and coordinated sampling of bee taxa across field sites is likely to provide important information about ecological factors influencing tool use in honey-gathering. Our aim in compiling a list of tool behaviors observed in honey-gathering (Table III) was to provide an ethogram for future observations that we hope will assist in standardizing the identification of behaviors between sites. We strongly advocate that scientists record video footage of tool-using behaviors because this provides the means to review each tool using episode for detailed information that can aid in identifying or defining specific behaviors, measure interobserver reliability in identifying tool behaviors, and share the observations with other scientists. Several scientists have discussed the possibility of creating a video ethogram of tool-using behaviors for their individual site or as a collaborative effort among several sites, which would be an important resource that could greatly improve the quality of comparisons across sites.

The rich behavioral diversity and technological traditions of wild chimpanzees has important, but often overlooked conservation value. Each wild chimpanzee

population has a distinct repertoire of tool using behaviors, and the preservation of these technological traditions should be another consideration for long-term conservation strategies (McGrew 2004). Conservation initiatives on behalf of great apes have focused on mitigating negative human impacts on ape density or distribution, but it is important to determine whether human disturbances are affecting the traditional behaviors of wild apes. Expanding human influence on wild orangutans and their behaviors prompted van Schaik (2001) to propose “The Disturbance Hypothesis for the Loss of Local Traditions in Orangutans,” which suggests that local extinction, hunting pressure, logging, and habitat loss may disrupt the transmission processes of traditional behaviors among wild apes. Initial studies of chimpanzees in the Congo Basin have expanded our understanding of the behavioral diversity of this species, and future research promises even more discoveries that will be possible only if we ensure the long-term preservation of these great apes and their habitats.

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