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Tool Use by Chimpanzees at Ngogo, Kibale National Park, Uganda

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Abstract Chimpanzees make and use a wide variety of tools in the wild. The size and composition of their toolkits vary considerably among populations and at least to some extent within them. Chimpanzees at several well documented sites mostly use tools in extractive foraging, and extractive tool use can substantially increase their foraging efficiency. They also use tools for hygiene and for several other purposes, including attracting the attention of conspecifics, as in leaf-clipping. Some of the interpopulation variation in toolkits results from ecological variation, but differences in the efficiency of social transmission, perhaps related to differences in social tolerance, presumably also contribute. I describe tool use by chimpanzees in an unusually large community at Ngogo, in Kibale National Park, Uganda. Researchers have described some tool use for the community previously, but this is the most extensive report and is based on observations over 11 yr. The Ngogo chimpanzees have a small toolkit and use tools rarely except in leaf-clipping displays and to clean body surfaces; notably, males often use leaf napkins to wipe their penes after copulation. Extractive tool use is rare and is limited mostly to leaf-sponging and, less often, honey-fishing. Social tolerance is not low at Ngogo, but use of tools for extractive foraging, in ways documented at other field sites, may have little potential to increase foraging efficiency. Future research will undoubtedly show more tool use by females, which were underrepresented in my observations, but will probably not document much increase in the toolkit or in the use of extractive tools.

Keywords chimpanzees · extractive foraging · leaf-clipping · Ngogo · tools

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Introduction

Chimpanzees (*Pan troglodytes*) manufacture and use a wide variety of tools in the wild. McGrew (1992, 1994) listed 36 sites at which researchers had observed tool use, and others have since documented tool use at 2 new sites (McGrew *et al.* 2005; Sanz *et al.* 2004). Toolkits (different kinds of tools used for different purposes; McGrew 1992) are well documented in several populations, e.g. Gombe (McGrew 1992), Taï (Boesch and Boesch 1990; Boesch and Boesch-Achermann 2000), and Boussou (Sugiyama and Koman 1979). Chimpanzees especially use tools during extractive foraging, both to harvest otherwise inaccessible resources like pools of water in holes in tree buttresses and to improve their ability to harvest resources obtainable with their teeth and hands (Boesch and Boesch-Achermann 2000; Yamakoshi 2001). Extractive tool use can yield important nutritional gains, though it is not always the case (Yamakoshi 2001). Use of wood and stone hammers and anvils by some populations of *Pan troglodytes verus* in West Africa are notable examples of tool-mediated foraging benefits (Gunther and Boesch 1993), and extractive tool use provides similar benefits for some populations of orangutans (*Pongo pygmaeus*: van Schaik and Knott 2001) and brown capuchins (*Cebus libidinosa*: Fragaszy *et al.* 2004).

Chimpanzees also commonly use tools for hygienic purposes. For example, use of leaf napkins to wipe feces or other material from hair and to dab at wounds is widespread (McGrew 1992, 1994; Whiten *et al*. 2001). Some tool use apparently takes on social significance by drawing attention to the user. For example, in leaf-clipping, an individual holds a single leaf by the petiole, draws it horizontally between its lips, and strips the lamina from the midrib. Leaf-clipping precedes some buttress-drumming displays at Taï, whereas males at Mahale and Gombe leaf-clip when soliciting copulations from females with sexual swellings.

Chimpanzee toolkits vary remarkably across populations, along with comparable variation in the form and context of gestures, displays, grooming postures, and other aspects of behavior open to biased social transmission (McGrew 1992, 1994; Boesch and Tomasello 1998; Whiten *et al.* 2001). Variation presumably also occurs among communities within populations, though relevant data at that level are limited. As leaf-clipping indicates, contextual variation in use of particular tools also occurs. Ascertaining whether a given population uses a given tool type can depend partly on degree of habituation and the length of observation. As McGrew (1994) noted, most of the few research populations for which tool use had not been documented by the early 1990s had been subjected to only short studies and were not well habituated. Still, striking differences occur among long-term research sites where chimpanzees are well habituated. Nut-cracking with hammers and anvils is known only among West African chimpanzees (*Pan troglodytes verus*), and the diversity of tools and of manufacturing techniques, plus the extent to which tools are reused, is notably higher at Taï, where nut-cracking is common and ecologically extremely important, than at long-term research sites where chimpanzees do not crack nuts (Boesch and Boesch-Achermann 2000). Dipping for *Dorylus* spp. with pliant wands of twigs or stems occurs at Gombe, Bossou, Taï, Mt. Assirik, Mt. Nimba, Kalinzu, and Fongoli, but has not been seen at Mahale in >40 yr of research despite the fact that the ants

are common there (McGrew *et al.* 2005; Whiten *et al.* 2001; Yamakoshi and Myoma-Yamakoshi 2004).

There are several possible explanations for such variation (McGrew 1992; McGrew *et al.* 1997; Fox *et al.* 2004; Whiten *et al.* 2001). Ecological reasons might explain why chimpanzees in some populations use a certain kind of tool for resource extraction, but those in other populations do not, e.g., the relevant resources or suitable raw materials do not occur in their habitats. Alternatively, the tool type might be absent because it was never invented locally and did not spread to the population from an area where it was invented, or because social transmission of knowledge of how to manufacture and use the tool was interrupted and the knowledge lost.

Van Schaik *et al.* (1999) proposed that because the spread of knowledge about how to manufacture and use tools depends importantly on social learning, tool use should be more common, and toolkits larger, when social tolerance is high. Immature individuals then have ample opportunity to observe and to interact with a wide range of older, more experienced conspecifics, and individuals are relatively uninhibited about associating with others that have greater agonistic power. Van Schaik *et al.* (1999) used comparative data on gregariousness, association patterns, and food-sharing at different study sites to support their argument for orangutans. They also calculated tolerance indices for 5 long-term chimpanzee research sites, based on relative frequencies of meat-sharing and of collaborative hunting, amount of grooming between females, the proportion of time that individuals are solitary, the reported diversity of medicinal plant use, and relative interbirth intervals (assumed to vary inversely with the intensity of feeding competition); toolkit size was positively associated with the index.

One of the sites that van Schaik *et al.* (1999) considered was Kibale, the site of 2 long-term chimpanzee research projects, 1 (Ngogo) focused on the largest known chimpanzee community. Ngogo chimpanzees commonly hunt and share meat (Mitani and Watts 2001; Watts and Mitani 2002), and gregariousness at the site is relatively high (Pepper *et al.* 1999). The small toolkits reported for Kibale chimpanzees (McGrew 1994; van Schaik *et al.* 1999; Whiten *et al.* 2001) are thus surprising if the social tolerance hypothesis is correct. However, few published data on tool use exist for Kibale, and lists that contributed to surveys like that of Whiten *et al.* (2001) were compiled relatively early in the history of research at Ngogo. I summarize cases of tool use observed in 47 mo of fieldwork at Ngogo over 11 yr, which supplement earlier, brief accounts of tool use there (Ghiglieri 1984; Sherrow 2005). My data show that tool use is not unusually infrequent, but that most occurs in only a few contexts and that extractive tool use is rare, and also confirm that Ngogo chimpanzees have a relatively small toolkit.

Methods

Study Site and Subjects

Ngogo is in the center of Kibale National Park, which is located in western Uganda between 0° 13′ and 0° 41′ N and 30° 19′ and 30° 32′ E. The study area is about 30 km^2 and consists mostly of mature and regenerating forest transitional between lowland

and montane moist evergreen forest. It also includes smaller areas of other vegetation types, notably swamp forest dominated by *Phoenix reclinata* and *Pennisetum purpureum* grassland (Butynski 1990; Lwanga *et al.* 2000; Struhsaker 1997). Mean annual rainfall is *ca.* 1800 mm.

Ghiglieri (1984) studied chimpanzees at Ngogo in 1978–1979 and briefly in 1981, during which they were partly habituated. Research on the Ngogo chimpanzee community resumed in 1990, and observations there have been continuous since mid-1995. With 140–150 members, including 22–28 adult males, 13–15 adolescent males, >40 adult females, and ≤10 adolescent females, the Ngogo chimpanzee community is the largest ever identified. I have observed chimpanzees at Ngogo for *ca.* 10,200 h during 10 field seasons that varied from 2.5 to 10.5 mo, since May 1995. All adult males were well habituated by the end of 1995, and adolescent males have also been well habituated during most of the study time. Habituation of females and their dependent offspring has proceeded more slowly, but most were easily observable on the ground by *ca.* 2002.

Definitions and Data Collection

Most behaviors included in catalogs of chimpanzee tool use (McGrew 1992, 1994; Whiten *et al.* 2001) fall easily within Beck's (1980) classic definition of tools as detached objects that agents use to act on other objects —either animate or inanimate— to achieve some result. Physical objects, whether modified or unmodified, that chimpanzees use in foraging are clear examples: termite-fishing wands, and crumpled leaves used as sponges. Incorporation of objects into social interactions does not always fit so clearly. Leaf-clipping is a standardized catalog item and involves use of detached objects, but the objects to be affected are conspecifics and the apparent goal is to elicit their attention and perhaps to invite approaches, rather than to exert direct physical influence. Branch-waving during courtship displays seems to have the same intention as leaf-clipping, but does not involve use of detached objects. Some researchers also consider the behavior tool use (McGrew, 1994), but the designation is questionable. Nevertheless, I have included information on branch-waving here for comparative purposes.

I made observations *ad libitum* of tool use during all study periods and recorded cases of tool use by focal individuals during focal samples of adult and adolescent males and of estrous females. Leaf-grooming (McGrew 1992) is common at Ngogo (Whiten *et al.* 2001), but I did not collect quantitative data on it. I collected quantitative data on all other forms of tool use and on branch-waving. Limitations on habituation made observation of tool use unlikely in the first few months of study, but habituation was adequate for accurate data on tool use by males by late 1995. Most of my research effort has focused on male behavior (Watts 2002; Watts and Mitani 2002) and on mating strategies (Watts 1998). The observational bias toward males means that I have underestimated how often females use tools. Sexual differences in subsistence tool use are probably limited at Ngogo, given that social insects do not contribute substantially to the diet. However, my data set is inadequate to investigate whether sexual differences in the frequency, contexts, and proficiency of tool use exist (except in the case of penis-wiping), as they do at Gombe (McGrew 1979) and Taï (Boesch and Boesch 1984; Boesch and Boesch-Achermann 2000).

Results

Frequency of Tool Use and Attention-getting Displays

I recorded 317 cases of tool use other than leaf-clipping, 175 cases of leaf-clipping, and 86 cases of branch-waving (Table I). Two individuals each used 4 tools [4 cases of tool use each involved 2 different chimpanzees consecutively using the same tool]: twice they used leaf sponges that other chimpanzees had discarded and once a male used 2 honey-extraction tools that another male had made and discarded. In 4 cases, individuals used multiple tools in the same bout: adult male BT made and used 3 tools to extract honey from a beehive in a fallen tree trunk, 2 tools to extract honey on another occasion, and 4 tools to probe for and to extract either honey or larvae from a dead branch on a third occasion; adult female LE once used 2 honey extraction tools; and adolescent male WB once used 3 handfuls of leaves to dab at and wipe blood from a bite wound.

Tool types and Contexts of Use

Ngogo tools fall into 6 general categories (Table I). Chimpanzees use tools during extractive foraging, mating, play, aggression, and buttress-drumming displays, and also for hygiene and personal comfort. Leaves are the most common material for tools: individuals use handfuls of leaves to wipe hair or body surfaces, to dab at wounds, and as leaf sponges, and they use single leaves for leaf-clipping. They use sticks as probes to dip for honey and, in 3 cases, for unidentified substances inside

Table I Tool use at Ngogo: use categories, tool types, actions and contexts, and tool use by different age sex classes

Use category type	Tool	Actions	Cases Per Age-Sex Class			Juvenile	Total cases
			Adult male	Adolescent male	Adult female		
Extraction	Leaf sponge	Obtain water	9	3	2	2	16
	Stick probe	Honey dip	8		2		10
		Dip for?	2	1			3
	Stick lever	Widen hole	1				1
	Stem wand	Termite-fish			1	1	2
Hygiene	Leaf napkin	Wipe/clean hair, skin	13	4	1		18
		Dab blood	4	6	2	3	15
		Dab pus	1			1	2
		Wipe vulva			3		3
		Wipe penis	208	39			238
Comfort	Bee whisk	Clear bees	2	1			3
Aggression	Club	Hit conspecifics	1	3			4
	Missile	Aimed throwing				2	2
Attract attention	Leaf-clip	Courtship	138	19	3		160
		Buttress-drumming	12				12
		Other	2	1			3
	*Branch-wave	Courtship	69	10			79
		Threat	6	1			7

*Branch-waving arguably does not qualify as tool use, but is included for comparative purposes.

dead branches (possibly honey of stingless bees). BT once used a small stick as a lever to widen a hole in a fallen tree trunk from which he was extracting insects or insect larvae, though he extracted them with his hands and teeth. Use of sticks as clubs also occurred, and 2 times a juvenile male threw small, detached branches at a human on the ground below him. Individuals used leafy branches as whisks to clear bees from hive entrances 3 times, and fished (apparently for termites) with flexible wands made from herbaceous stems twice (Table I).

Use of tools for foraging, which includes mostly leaf-sponging, but also honey-dipping, probing for insects or larvae, and termite-fishing, accounts for only a small fraction of all tool use. The most common form of tool use in feeding is honey-dipping (≥10 cases). Most hives that the chimpanzees raid are off the ground, in hollows in tree trunks. During raids, the chimpanzees usually insert their arms into the hollows, try to grab handfuls of honeycomb quickly, and then retreat, though they sometimes repeat this and may stay next to the opening for extended periods if they are not attacked by large swarms. I have not seen tool use during arboreal raids, but have seen chimpanzees use tools to extract honey from hives in fallen tree trunks. The tools are narrow, firm *ca.* 30–40 cm sticks; the tool users scrape them against the inner walls of the hollows to try to get honey that they cannot reach with their hands, then use their mouths to remove any honey that adheres to the sticks.

The 2 cases of fishing resemble that described by Sherrow (2005). Both occurred at fallen tree trunks and the identity of the extracted food was uncertain. In the first case (June 5, 2005), 1 adult male, 1 adolescent male, 4 adult females (2 with young infants), 3 adolescent females, and 2 juveniles gathered along a large fallen tree trunk. Much of it was hollowed out, and the chimpanzees clustered in several spots to bite rotting wood from inside the hollows, apparently to extract termites. (Ngogo chimpanzees fed similarly at the same tree trunk on other occasions.) The total feeding session lasted 45 min. PE, a young adult female, fed briefly from the trunk via her teeth at the start of the session, but hesitated to approach a large hollow that appeared to be the best feeding spot, where 2 other older, larger females were feeding with adult male GA. She then moved into vegetation *ca.* 5 m to the side of the trunk and broke off a flexible herbaceous stem *ca.* 50 cm long. She stripped several leaves from the stem, carried it to the tree, climbed onto the trunk, and inserted the stem into a small hole directly above a large hollow area. She extracted the stem after a few seconds, inspected it, and reinserted it, repeating the behavior 10 times; several times she brought the stem to her mouth, and once she chewed briefly on its end to modify its form. She obtained little, if any, food; after several minutes, she discarded the tool, climbed down to the base of the trunk, and resumed biting at the inside of a hollow with her teeth.

In the second case, a juvenile female also fished briefly from a hole in a fallen tree trunk, using a 20-cm herbaceous stem from which she first stripped the leaves. She apparently did not obtain any food.

Tool use for hygiene was much more common than tool use for resource extraction. By far the most frequent form of tool use is penis-wiping (247 cases; Table I), in which a male that had just copulated detached several leaves, held them unimanually, and swept his hand once or several times from the base to the tip of his penis. The 247 cases represent 6.3% of 3782 copulations for which observations were sufficiently complete to determine whether penis-wiping occurred.

Chimpanzees use leaf napkins to dab at blood from bite wounds (15 times), to remove coagulate from vulvas (3 times), to clean feces or other material from their hair or skin (18 times), and to wipe pus from bite wounds or skin infections (2 times).

Most leaf-clipping (157 of 175 cases; Table I) is performed by males to solicit females with sexual swellings. Swollen females leaf-clipped 3 times, apparently to solicit males. Three adult males leaf-clipped 12 times before giving buttress-drumming displays; α-male BT accounted for 9 of the cases. One adult male leaf-clipped twice while sitting beneath a group of red colobus that the chimpanzees subsequently hunted. One young adolescent male leaf-clipped twice during social play. Branch-waving happened almost exclusively when males were courting females: males either were soliciting copulations from swollen females, or, in 2 cases, were apparently trying to initiate consorts; the males waved branches repeatedly and insistently in both cases, but did not persuade the females to leave others in their parties. The 1 case of branch-waving by a female involved an adult (SI) with a full sexual swelling. She was in a party with many males and had been mating with most of them, but had refused persistent attempts by adult male DO to copulate. SI had climbed a tree and sat on a bough, facing DO, which was on another bough *ca*. 5 m from her; she shook a branch at him and screamed repeatedly over a 3-min period. Males also branch-waved 6 times in apparent threats to subordinates.

Identities of Tool Users

How often Ngogo females use tools is not well known. However, notably, they use sticks to dip for honey and use leaf sponges (Table I), the most common forms of tool use for foraging. Females also use leaf napkins, and they are the only or principal tool users in the 3 reported cases of fishing for termites or insect larvae (this paper; Sherrow 2005).

Leaf-clipping is an almost exclusively male act and occurs when males solicit swollen females. All but 3 adult males leaf-clipped. The exceptions are a male that died early in the study (AR), 2 others (ST and WA) that have since died and were low-ranking and copulated infrequently, and a young adult (GRT) with a snare wound to 1 hand and that rarely copulates. Most adolescents also leaf-clip while soliciting swollen females, though we have not seen the currently youngest adolescents leaf-clipping. Adults leaf-clip more often than adolescents do (Table I); they also copulate more often. RU, an old adult male that died in September 2002, leaf-clipped particularly often (20 cases). Three females with a maximally tumescent swellings leaf-clipped at males, which approached and copulated.

Males account for all cases of branch-waving except the 1 in which an adult female threatened a male, and adult males branch-wave more often than adolescents do (Table I). Most adult males other than AR, ST, WA, GRT branch-waved. The exceptions are relatively low-ranking young adults, and failure to see them branch-wave is probably a result of sampling error, given that several adolescents branch-waved at swollen females.

I saw club use for the first time in 2006. One young adolescent male and 1 juvenile male both used sticks *ca.* 60 cm long and 1.5 cm in diameter to hit an adult female (the same individual, but on different days) on the back while she rested. The same juvenile male later hit an adult male with a stick during play and was responsible for

both cases of branch-throwing. α-male BT hit an estrous female repeatedly with a 1.5-m stem of *Aframomum* sp. during a melée in which she and many males were targets of displays and other aggression. Club use involved direct overhand motions.

Opportunities for Social Transmission

Tool users usually had audiences; this was the case for all extractive tool use. Mothers are probably the best models for social learning of tool manufacture and tool-use skills (Boesch and Boesch-Achermann 2000; McGrew 1992). Most of the observed cases of tool use by adult females involved wiping body parts with leaves, quick acts that might escape the attention of dependent offspring. Both females that used sticks to extract honey had infant or juvenile offspring that watched them, but did not use their mothers' tools or make their own. Female PE was nulliparous when she fished for insects. None of the other chimpanzees feeding from the same dead tree trunk paid close attention to her or to her tools.

In the case of fishing that Sherrow (2005) described, the female that initiated the bout elicited considerable attention and her juvenile offspring used a discarded tool. In several other of my cases, including 1 that involved a female and her juvenile offspring, tool use also attracted intense interest from onlookers, some of which used tools discarded by the makers. The cases were:

- July 13, 2000: High-ranking adult male MW used a leaf sponge to extract water from a hole in a tree buttress. Adolescent male DX watched from several meters away. When MW discarded his sponge after 3 min and left, DX retrieved it and sponged water from the same hole for 2 min. Adolescent female RUS also watched MW use his tool, but left before he finished.
- July 16, 2002: Four adult males found a beehive in a hole in a fallen tree trunk. A high-ranking male, EL, inserted his hands into the hole and extracted a large mass of honeycomb. α-male BT also extracted some honey with his hands, but EL apparently had obtained most within easy reach. When BT finished eating his honey, he inserted a stick about 30 cm long and 1.5 cm in diameter into the hole. He thrust it back and forth and from side to side vigorously, then withdrew it and ate a small amount of honey that adhered to it. He repeated this several times while EL ate his honeycomb, then discarded the tool and picked up a second stick of similar dimensions. He briefly chewed on the end of the stick, then inserted it into the hole and vigorously thrust and rotated it. EL finished most of his honey while BT was using his second tool, at which point he sat and watched BT. When BT moved aside slightly to eat some honeycomb that EL had dropped, EL picked up BT's first tool, inserted it into the hole, and extracted a small amount of honey. He repeated this several times and also used BT's second tool once before leaving the trunk. BT then made another tool from a third stick and resumed his efforts to extract honey. BS, a young, high-ranking adult male, and adolescent male BRA watched him closely. BT discarded his third tool and left the tree trunk 12 min after the honey extraction started. BS picked up BT's third tool, inspected it, and sniffed the working end, but did not insert the tool into the hole in the tree. He then left the site. BRA left the site without inspecting any of the tools.

– August 14, 2002: Adult male HA and adolescent GTZ watched adult male RU as he used a leaf sponge to extract water from a hole at the base of a tree buttress. Both approached the tree after RU left, looked at the hole, and inserted their fingers into it, but neither used the discarded leaf sponge or made another.
– August 15, 2004: Adult female CAR used a leaf sponge to extract water from a hole at the base of a tree buttress. Her juvenile daughter stood next to her and watched her closely, then picked up her mother's discarded tool when CAR left and inserted it into the same hole. She repeated this 4 times and obtained a small amount of water.

Discussion

Ngogo chimpanzees have a small toolkit, used most often for hygiene and in signals aimed at attracting the attention of conspecifics, and rarely for extractive foraging. McGrew (1994) reported only 2 habitual patterns of tool use —leaf sponge, leaf napkin— from Kibale, based on earlier data from Kanyawara and Ngogo, and commented that the list would probably lengthen as detailed observations continued. Subsequent observations through 2000 added leaf-clipping, leaf-stripping (not observed at Ngogo), and fluid dipping —use of probes to extract liquids, including honey— to the lists of habitual or customary tool use activities in Whiten *et al.* (1999) and Whiten *et al.* (2001). The lists included 10 tool types (not including branch-waving or leaf-grooming), with habitual use of probes to dip for fluid, habitual leaf-clipping, and customary or habitual use of leaves as sponges, dabs, and napkins. Sherrow (2005) added use of plant stems to fish for invertebrate prey. Observations that I report here add penis-wiping with bundles of leaves to the list of habitual behaviors, though the type of tool use (leaf napkins) that includes penis-wiping was already known from Kibale.

Thus increases in the documented technological repertoire of Kibale chimpanzees and in the number of tool types used habitually or customarily has increased only modestly since McGrew's (1994) early review despite long-term observations at Ngogo. Instead, Kibale data accord with Reynold's (2004) statement that chimpanzee populations in the northern part of the western Rift Valley escarpment, including Kibale and Budongo, have small toolkits compared to some populations of the same subspecies (*Pan troglodytes schweinfurthii*) farther to the south and to some populations of *P. t. verus*. The low diversity of extractive tool types and low frequency of extractive tool use is presumably due partly to ecological causes. Whiten *et al.* (2001) listed ecology as the probable explanation for the apparent absence of termite-fishing in Kibale, given the absence of mounds of *Macrotermes* in the forest (*cf.* Ghiglieri 1984). The inference still holds, though in modified form: insertion of flexible dipping wands into holes to extract insect prey occurs at Ngogo, but rarely, and the holes are in fallen tree trunks, not termite mounds. Researchers have thus far not identified *Macrotermes* in Ngogo chimpanzee diets, and on the few occasions when the chimpanzees eat termites, they obtain them from rotting wood, mostly with their teeth and hands (Ghiglieri 1984; Sherrow 2005). Nor have observers seen Ngogo chimpanzees eat *Dorylus*, though they are highly abundant and would apparently be

easy to harvest. Whether the chimpanzees do not recognize them as food, perhaps because investing the time and energy to harvest them would not provide adequate nutritional returns, or simply do not realize that they could use technology to harvest them and thereby avoid being bitten, is difficult to resolve (McGrew *et al.* 1997). Estimated protein intake rates from arboreal harvesting of *Campanotus* at Mahale are quite low (Yamakoshi 2001). The estimates may not extrapolate to *Dorylus*, but chimpanzees may often have better protein sources available, e.g., meat, at Ngogo (Watts and Mitani 2002).

The average returns for honey-dipping may also be low. Dipping tools may sometimes allow the chimpanzees to obtain large pieces of honeycomb otherwise beyond their reach, but I have seen tool users obtain only small amounts of honey after they or others have removed most of the comb with their hands.

Tool use would not obviously improve the efficiency with which Ngogo chimpanzees can harvest plant foods. Fruit of *Monodora myristica* and *Treculia africana*, important foods at Ngogo, require considerable effort to process. Fruits of *Monodora* have thick, hard exocarps that the chimpanzees open with their canines; whether they could significantly increase the efficiency with which they harvest nutrients from the fruits by opening them with tools is unknown. Mature *Treculia* are ≤40 cm in diameter and have a tough, but not hard, exocarp and a thick, fibrous mesocarp that surrounds a woody core. Chimpanzees bite into immature fruits and make wedges from the mesocarp, but eat only the small arils that surround the seeds of mature fruits. Getting them via the teeth and the muscles of the jaw, neck, shoulder, and arm to open the fruit and tear away the mesocarp requires considerable effort. However, material removed in the process would not be susceptible to fracture by blunt tools like the stone and wooden hammers used for nut-cracking in West Africa.

The limited toolkit at Ngogo does not seem to result from low social tolerance, contrary to what van Schaik *et al*. (1999) argued for Kibale based on data from Kanyawara. Van Schaik *et al.* (1999) did not assign values for meat-sharing, grooming between females, or collaborative hunting —3 of 6 indicators of tolerance— to Kibale. Meat-sharing is common at Ngogo (Mitani and Watts 2001). Female gregariousness is not unusually low (Pepper *et al*. 1999), grooming is common in some female dyads, and some females associate with each remarkably often (*pers. obs*.; Wakefield M., Langergraber K., *unpubl. data*). Despite infrequent subsistence tool use at Ngogo, the chimpanzees have, and use, opportunities for social transmission of techniques to make and use the tools. In the termite-fishing case that Sherrow (2005) described, 3 of the tool users were an adult female, her adolescent son, and her juvenile son. Other individuals closely attended the toolmaker/user's actions in several of the aforementioned cases, and in 3 cases used discarded tools. However, PE drew no attention when she fished in a fallen tree trunk; the other chimpanzees focused on hollow sections of the trunk below her. Only a few individuals used tools in this way or as probes to dip for honey. As Ghiglieri (1984) argued, Ngogo chimpanzees may simply have little need for extractive tools. Figs (*Ficus* spp.) are major dietary components at Ngogo and are especially important when ripe fruits from other taxa are scarce, and the chimpanzees also increase their intake of leaves when nonfig fruit abundance is low (Ghiglieri 1984; Watts *et al.* 2006). Thus the necessity hypothesis (Fox *et al.* 1999), which proposes that increased scramble competition during periods of resource scarcity forces animals with the

required cognitive abilities to exploit foods accessible only via tool use, probably does not apply at Ngogo. However, only more detailed data on foraging efficiency and food nutrient yields can show whether tool use to extract resources like honey (commonly available, as are raw materials for tools) is infrequent because transmission is inefficient, or because its benefits are too low (Whiten *et al.* 1999).

Tool use is more common for hygiene than for resource extraction. Ngogo must be added to Sonso (Budongo), Gombe, and Kanyawara (also in Kibale) as sites at which males often use leaf napkins to wipe their penes (Goodall 1986; O'Hara and Lee 2006). The percentage of copulations followed by penis-wiping was less than the figure of 9.5% reported for Sonso (though the Sonso sample is much smaller: O'Hara and Lee 2006), but greater than reported for Gombe and Kanyawara (Goodall 1986; O'Hara and Lee 2006).

Recent work at Ngogo (Wakefield, M., and Langergraber, K., *unpubl. data*) has redressed the imbalance in research effort devoted to males and females there. This work will answer questions about sexual differences in tool use there and provide much more detail on opportunities for social transmission.

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