New Insights into Chimpanzees, Tools, and Termites from the Congo Basin

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abstract: The tool-using behaviors of wild chimpanzees comprise the most impressive assemblages and flexible repertoires of non-human material culture. We expand knowledge of the breadth and complexity of tool use in this species by providing the first descriptions of the form and function of two distinct tool sets used by chimpanzees in preying upon termites within the forests of the Goualougo Triangle, Republic of Congo. Further, we report the first application of remote video monitoring technology to record wild chimpanzee tool-using behavior. Based on tool assemblages recovered at termite nests, we hypothesized that chimpanzees were regularly visiting two forms of termite nests and using specific tools to extract termite prey depending on the structure of the nest. Six months of continuous remote video monitoring at six termite nests confirmed that chimpanzees use a tool set to puncture and fish at subterranean termite nests and another tool set to perforate and fish at epigeal (aboveground) nests. Our findings of strict adherence to tool forms at different nest types, tool material selectivity, repeated visits to nests with reusable wood tool assemblages, and differences in material culture between communities have broad implications for our understanding of the ecological and cultural factors that shape hominoid tool use.

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Although several taxa have been observed using tools, there are few species that demonstrate habitual and complex tool-using behavior. The flexible tool-using repertoires and impressive cumulative assemblages recorded in wild chimpanzee and orangutan populations are unique and often are used in constructing referential models of early hominid technology. Some of these ape populations use stone tools, but most of their tool technology consists of perishable materials that would be invisible in the archaeological record (Boesch and Boesch 1990; McGrew 1992). Studying the behavior of wild apes enables us to overcome the constraints of material preservation and directly observe a broad spectrum of tool-using behaviors. The variation in tool-using technology shown by extant ape populations will certainly improve our understanding of the ecological and social factors shaping hominoid material culture.

Termite predation provides an excellent opportunity to examine the factors that govern chimpanzee behavioral diversity. Several termite taxa coexist with chimpanzees throughout their range, but extraction of termites from nests with tools is limited to only a subset of studied chimpanzee populations and termite species. Descriptions of termite predation have shown differences between subspecies and between even adjacent communities (Goodall 1963, 1968; McGrew et al. 1979; Nishida and Uehara 1980; Uehara 1982; McGrew and Rogers 1983; Collins and McGrew 1985, 1987; McGrew and Collins 1985). Some of these differences have been attributable to environmental variables (i.e., distribution of termite fauna), while others have been described as social traditions or cultural variants among chimpanzee groups (McGrew et al. 1979; Nishida and Uehara 1980; Uehara 1982; Collins and McGrew 1987).

Chimpanzee selection of particular termite prey species seems to be based on the frequency and duration of the termite swarming periods, accessibility, size, and palatability (Collins and McGrew 1985). Termites of the genus

Macrotermes are most commonly preyed on by chimpanzees (Collins and McGrew 1985; McGrew 1992). *Macrotermes* spp. are the largest termites found in Africa and reside in many habitat types. Their member species build different types of nests, but all have subterranean fungus gardens. For example, *Macrotermes muelleri* build large epigeal mounds (nests that protrude above the soil surface) over their underground nests, whereas *Macrotermes nobilis* build subterranean nests (nests completely below the ground; McGrew and Rogers 1983). *Macrotermes* are most often extracted from their nests with the aid of tools, whereas the mounds of *Pseudacanthotermes* and *Cubitermes* are toppled, and the termites are eaten by hand (Nishida and Uehara 1980; Uehara 1982; Newton-Fisher 1999).

Interpreting the geographical patterns of tool-using behaviors such as termite fishing between chimpanzee populations has proven difficult (McGrew et al. 1979; McGrew 1992). Although wild chimpanzees have been continuously studied for several decades at sites in East and West Africa, information from new study sites has continued to expand the diversity of their tool-using repertoire. Based on indirect evidence at several sites in central Africa, researchers have suggested that *Pan troglodytes troglodytes* use a unique tool set composed of stout sticks and slender fishing probes to extract *Macrotermes* spp. from their nests (Sabater Pi 1974; Sugiyama 1985; Muroyama 1991; Fay and Carroll 1994; Suzuki et al. 1995; Bermejo and Illera 1999). Termite mound digging sticks are thicker and more uniform than other types of tools used in termite predation in East or West Africa (McGrew et al. 1979; McGrew and Rogers 1983; Sugiyama 1985; Muroyama 1991; Fay and Carroll 1994; Suzuki et al. 1995; Bermejo and Illera 1999). Researchers hypothesized that chimpanzees used these stout sticks to drill access holes into the subterranean chambers of termite nests. Termite tunnel probing stalks, which are slender and flexible probes, were also recovered at termite nests in central Africa (McGrew and Rogers 1983; Sugiyama 1985; Fay and Carroll 1994; Suzuki et al. 1995; Bermejo and Illera 1999). It was reported that some of these herbaceous probes had frayed ends that resembled paintbrushes and may have been modifications to increase efficiency in extracting termites. Although these tools have been known for more than 2 decades from sites across central Africa, the details of tool manufacture and their specific functions in termite predation were not confirmed with direct observations.

We report the first complete descriptions of two distinct tool sets used by chimpanzees to prey on termites in the Goualougo Triangle, Republic of Congo. Tool sets are composed of at least two tool components that are used sequentially to achieve the same goal (Brewer and McGrew 1990). In contrast to early reports of chimpanzees using sticks to excavate nests, we have found that stout sticks are actually used to puncture subterranean nests, which creates access tunnels to underground termite chambers and allows insertion of a fishing probe that is used to extract the prey. Therefore, rather than referring to this technique as digging, we prefer to describe this tool use as puncturing a termite nest. Perforating twigs and fishing probes comprise another tool set that is used to access termites in epigeal nests. We also describe brush-tip fishing probe manufacture that is thus far unique to chimpanzees in central Africa. We present both ethnographic accounts of tool-using techniques and rigorous quantification of tool form to facilitate comparisons among sites. We also introduce remote video monitoring as a new method to study the behavior of wild chimpanzees with minimal human disturbance. The successful application of this remote technology has important implications for the future direction of research methodology in behavioral ecology.

Methods

Study Site and Population

The Goualougo Triangle is located within the Nouabalé-Ndoki National Park (2°05′N–16°56′N; 3°03′E–16°51′E), Republic of Congo. See figure 1 for a map of the study area. The entire study area covers 310 km^2 of lowland forest with altitudes ranging between 330 and 600 m. The climate in the study area can be described as transitional between the Congo equatorial and subequatorial climatic zones (White 1983). Rainfall is bimodal with a main rainy season from August through November and a short rainy season in May. Average monthly temperatures and rainfall were recorded at Mbeli Bai base camp, Republic of Congo (17 km from the study area). The annual rainfall averaged 1,728 ± 47 mm between 2000 and 2002 (E. Stokes, unpublished data). The average minimum and maximum temperatures during those years were 21.1°C and 26.5°C in 2000, 21.5°C and 26.8°C in 2001, and 21.9°C and 26.5°C in 2002, showing little seasonal variation (E. Stokes, unpublished data). Four forest types are recognized in the study area: monodominant *Gilbertiodendron* forest, *Gilbertiodendron* mixed species forest, mixed species forest, and swamp forest.

Sampling efforts focused on the Moto chimpanzee community, which consisted of 54 individuals: 10 adult males, 18 adult females, seven subadults, and 19 immatures. Tools from five other chimpanzee communities in the study area were also opportunistically collected. Line transect surveys of termite nest abundance in the Moto Community were conducted from May to July 2003 (J. Dzohi-Epeni, unpublished data).

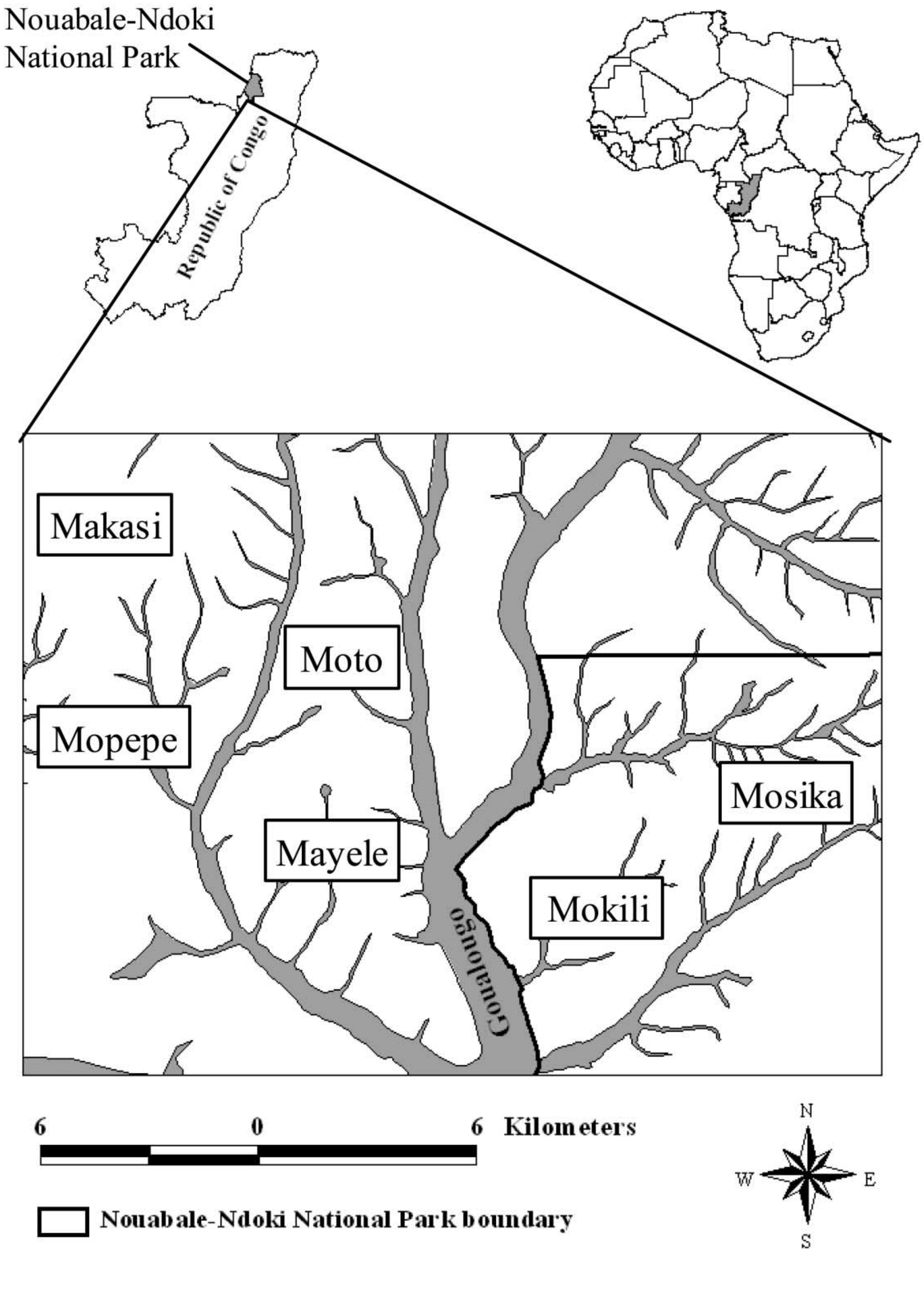

Figure 1: Map of study area showing chimpanzee communities in which tools are represented

Data Collection Protocols

Remote observations of chimpanzee tool use. Six remote monitoring/recording devices were used to conduct surveillance at termite nests for chimpanzee visitation between September 2003 and February 2004. These devices consisted of a passive infrared motion sensor, a computer program developed for this study (CHIMPCAM 1.0 and 2.0), and a digital video recorder (Sony DCR-TRV22). These components were mounted in a waterproof housing unit. The unit was securely tied 0.5–1.5 m high on a tree trunk that was 1–5 m from the termite nest. Immediately after the infrared sensor was triggered by animal movements at the nest, the CHIMPCAM computer program activated a digital video camera to record for 2 min. If the sensor detected another movement trigger within the 2 min of recording, the camera was immediately reactivated for another 2 min. This sequence was repeated until no motion was detected during a 2-min period, at which point the recorder would power down.

Scoring of tool-using behaviors. Observers scored each tape for the age-sex class of chimpanzees, individual identification, approaches with tool materials, tool type, tool manufacture, tool modification, and tool use. Operational definitions of bout, session, and episode of tool-using behaviors were based on Yamakoshi and Myowa-Yamakoshi (2004). A bout of tool use began with insertion of the tool into the nest substrate by a particular individual. It ended with the chimpanzee eating the prey or ending the sequence. A termite fishing session consisted of a series of bouts by an individual at a particular termite nest. An episode was defined by the arrival of a chimpanzee party or lone individual at a termite nest. The episode ended when all associated individuals departed.

Tool collection. Tools were collected along an established termite nest circuit (December 2001–December 2002) and ad lib. during daily reconnaissance surveys in the study area (January–June 2001, October 2001–December 2002, August–November 2003). The termite nest circuit was created by identifying and monitoring termite nests that were present along the tree phenology circuit established at the study site in 2000. The forest type and GPS point location (Garmin 12XL) were recorded for all other termite nests where chimpanzee tools were recovered. All intact tools scattered around the nest or left inserted in the nest were measured (length, diameter, length of brush tip). Herbaceous fishing probes were carried to camp for measurement, but puncturing sticks were measured at the site and identified to avoid repeat measurement during return visits. We also recorded the species of vegetation used to manufacture the tool, tool modifications (brush tip, bark peeling, removal of side branches, etc.), and approximate age of each tool.

Tool assemblages composed of different-age tools at a single nest indicated repeat visitation between circuit surveys. The materials used for fishing probes and digging sticks were homogenous within each tool type, which made it possible to operationally define tool ages and approximate tool survival time. Fresh tools were less than 3 days old and were defined as having a green stalk and flexible brush tip. Recent tools were 3 days–1 week old. Parts of the recent tool stalk were green, but the brush tip was no longer flexible and could be moldy or brown. Fishing probes remained intact for approximately 2 weeks but were categorized as old when the stalk was completely brown. Very old tools were fragile and showed deterioration. Although habitat and climate affected decay rate, the survival time of fishing probes was not more than 3 weeks. The age of puncturing sticks was more difficult to determine from appearance, but new sticks often had green bark and moist wood fibers. Recent sticks had turned brown and the ends of the tools were dry. The wood fibers of old tools were dry but intact. Very old tools were brittle and showed deterioration. Some puncturing sticks persisted and were used for more than 6 months.

Data Analysis

All statistics were conducted using SPSS 11.5 (SPSS, Chicago). The level of significance used throughout this study was $\alpha = 0.01$. The equality of variances among variables was evaluated with Levene's Test to determine whether equal variance could be assumed in subsequent statistical tests. Independent samples *t*-tests and ANOVA were used to assess differences in tool characteristics. Tukey's HSD post hoc range test was used to determine homogeneous subsets of means. A χ^2 test was used to compare observed nest visitation by adult males and females to expected values based on the community sex ratio.

Results

Termite Nests

Although several types of termite nests are found within the Goualougo Triangle study area, it seems that chimpanzees' tool use to extract termites is primarily focused on epigeal and subterranean nests of *Macrotermes* spp. The encounter rate of these preferred nests on line transect surveys in the Goualougo Triangle was 5.8 nests/km. However, only one-third of these nests had chimpanzee tools present. During reconnaissance surveys, we documented chimpanzee tool use at 98 termite nests in the Moto community, with some nests being visited several times each month. We calculated that the ratio of subterranean nests to epigeal nests exploited by chimpanzees was 1 : 4.5.

Ten termite nests within the Moto Community range were monitored for indirect evidence of visitation and tool use over 12 consecutive months. Nests were visited by chimpanzees on average 0.9 times/month, with the most frequently visited nest receiving 2.3 visits/month and the most infrequently visited nest only 0.3 visits/month. In contrast to the seasonality shown at some sites, chimpanzee termite fishing and puncturing tools were recovered from nests throughout the year.

Stout sticks and fishing probes were associated with subterranean structures that were completely flat or <1 m high. These subterranean nests are polycalic, consisting of several small chambers connected by underground tunnels. When successful in extracting termites, the chimpanzee has punctured one of the galleries, which are ~30 cm under the ground. See figure 3*A* for a diagram of the nest structure. After the nest has been disturbed, several hundred soldiers are recruited to the nest chamber to attack the intruding tool. There are no visible termite exit or entry holes on the surface of the soil above the nest because these termites construct tunnels to forage several meters from their nests, but careful inspection showed where chimpanzees had previously inserted puncturing sticks.

Nest perforation occurs on the surface of epigeal termite mounds with towers 1.8 ± 1.0 m tall ($n = 97$, range = 0.3–4.4 m) and consisting of up to 4.4 m^3 of soil. The reproductive castes are located near the center of the mound with the outside layers consisting of tunnels to the surface and galleries for food storage. See figure 3*B* for a diagram of the outer layer of an epigeal nest. The surface of the mound is often covered with visible exit and entry holes that have been sealed by workers after use. After inspecting the mound, the chimpanzee reopens these holes by hand or with the aid of a perforating twig. The fishing probe is then inserted in the outer layer of the termite mound, where soldiers arrive to defend the breach.

Remote Video Monitoring and Recording

During a 6-month sampling period (714 camera-days of termite nest surveillance), remote video monitoring devices recorded 69 chimpanzee group visits at eight nest locations. In contrast to results from tool assemblages recovered on the nest circuit (average of 0.9 visits/month), remote video monitoring showed that individual mounds received an average of 2.3 ± 1.4 group visits/month. Individual termite nests received an average of 3.8 ± 2.3 individual chimpanzees/month, with <1 chimpanzee/month visiting some nests and 10 individuals/month seen at more popular locations. The average party size visiting mounds was 1.8 ± 1.0 individuals. It is likely that actual traveling group sizes were larger but that some individuals in the party did not visit the termite nest. Adult females were the most frequent visitors to termite nests (accounting for 36% of all individuals), followed by adult males (22%). However, these rates of

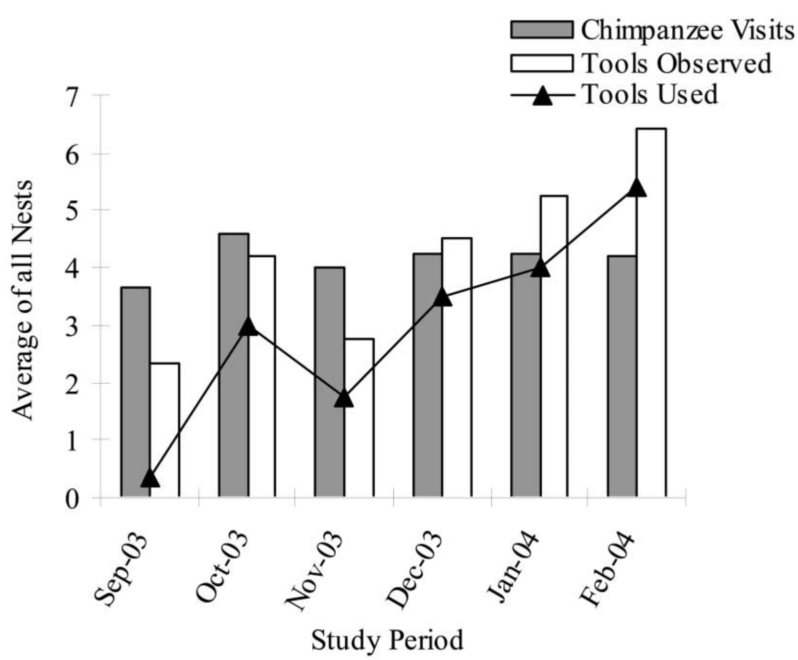

Figure 2: Average number of visits, tools, and tool use at mounds that were monitored with remote video units

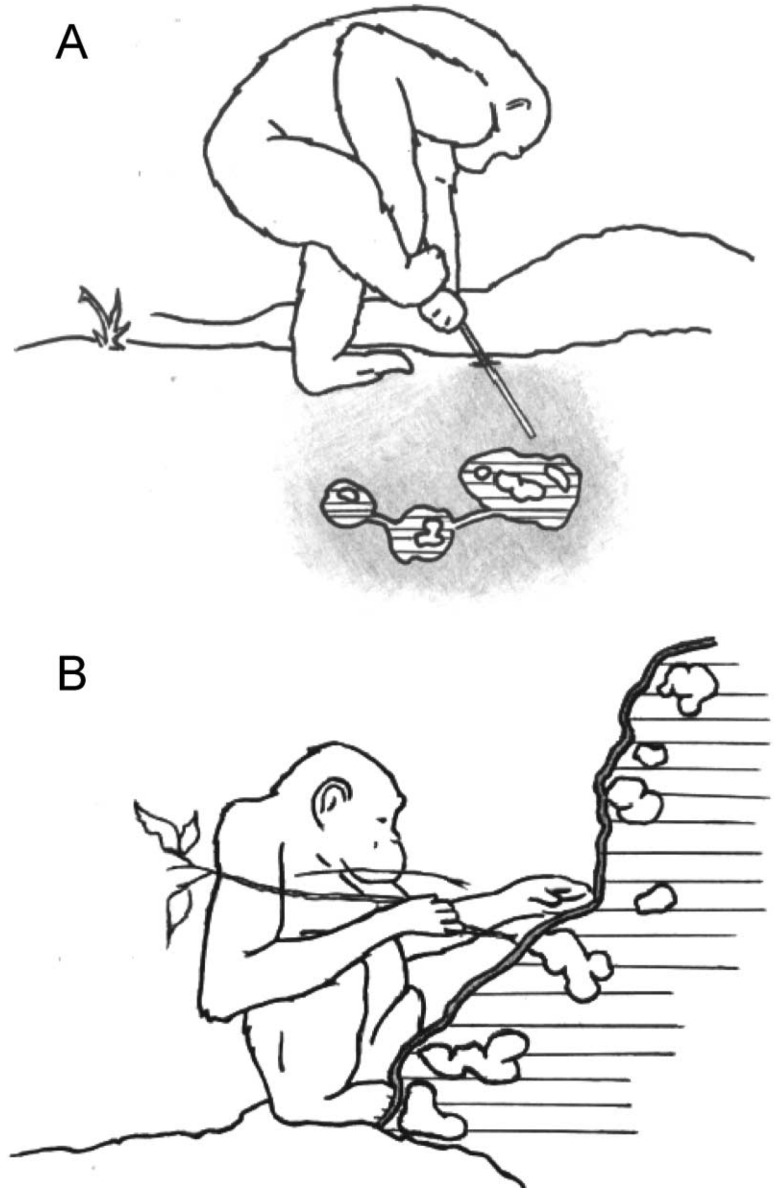

Figure 3: *A*, Adult male using a puncturing stick at a subterranean termite nest. In the cross section, the termite nest chamber and associated tunnels can be seen below the surface of the soil. *B*, Adult female using a perforating twig to open termite exit holes on the surface of an epigeal termite nest. She holds a brush-tip fishing probe in her mouth. Also notice the outer protective wall and peripheral chambers within this termite mound.

visitation did not differ from the rate expected by the female-biased sex ratio ($X^2 = 0.73$, $df = 1$, NS).

We were able to individually identify 82% of the chimpanzees who were recorded visiting termite nests. The remaining individuals were unidentified because views of their distinguishing features were obstructed. Twenty-nine of the 54 chimpanzees in the Moto community were represented in this sample. With these visual capture and recapture data, we confirmed that individual chimpanzees were repeatedly visiting nests within the Moto community range. The average number of visits by known individuals was 3.4 ± 2.3 visits during the 6-month study period, with some individuals sighted on eight occasions.

Tool use was observed during more than half of these visits, with the frequency increasing as chimpanzees be-

Video 1: Still photograph from remote video (available in the online edition of the *American Naturalist)* shows chimpanzees approaching termite nest. This is the first time that this adult female chimpanzee and her infant see the remote video camera. Although distracted from her task by the camera, the adult female has arrived at the termite nest location to extract termites with her set of tools: a fishing probe, carried in her mouth, and a stout stick in her hand to puncture the underground termite nest.

came habituated to the remote video units. Figure 2 shows the average number of visits, tools, and tool use at termite nests with remote video units over the study period. We interpret this increasing trend in the number of tools used relative to the number of chimpanzee visits and tools observed at mounds to indicate habituation to the camera units rather than seasonality in termite predation. During initial visits, chimpanzees would arrive with tools but depart after noticing the camera. The number of tools observed and used later surpasses the number of chimpanzees

Video 2: Still photograph from remote video of puncturing tool sequence (available in the online edition of the *American Naturalist)*. In this sequence, a young adult male of the Moto chimpanzee community uses a puncturing tool set at a subterranean termite nest. First he rakes surface debris away from the location where he will insert the puncturing stick. He pushes the stick into the ground, which creates a tunnel into the subterranean termite nest. He then inserts a fishing probe into the nest and extracts termites clinging to the end of the tool.

visiting nests, indicating that individuals were extending their visits and using several tools during the same visit. The average duration of visits also increased over the study period. The average visit lasted less than 1 min during the first month that cameras were at mounds. The average duration of visits subsequently increased to 12 min, with contacts lasting up to 41 min in the last 2 months of the sampling period.

Descriptive Accounts of Chimpanzee Tool Transport, Techniques, and Brush-Stem Manufacture

Tool transport. Remote cameras recorded chimpanzees arriving at termite nests carrying puncturing and/or fishing tools on 45 occasions. All tools were transported by adults and were appropriate for the type of termite nest being approached. Video 1 (in the online edition of the *American Naturalist*) shows an adult female carrying a fishing probe arriving at a subterranean nest. A chimpanzee arrived carrying both a stout stick and a fishing probe on seven occasions. All were arrivals at subterranean nests, which necessitate puncturing before fishing. Chimpanzees were never observed to arrive with only a puncturing stick at either a subterranean or an epigeal nest; a puncturing stick alone would not be effective at subterranean nests or appropriate at mounds where perforating twigs and probes are used. Chimpanzees arrived at termite nests carrying only fishing probes on 38 occasions; 82% of these arrivals were to epigeal mounds and 18% were to subterranean mounds at which wooden puncturing tools were already present. Direct observations showed that fishing probes were newly manufactured each day but that they were sometimes transported and reused at multiple nests. In contrast, 69% of chimpanzees who were observed puncturing termite nests reused sticks scattered around subterranean nests from previous chimpanzee visits rather than transporting new sticks to the nest for each session.

Puncturing subterranean termite nests. Forty-one observations were made of chimpanzees puncturing termite nests with stout sticks. See video 2 (in the online edition of the *American Naturalist*) for remote video footage of an adult male puncturing a subterranean termite nest. To locate a suitable site, the chimpanzee visually scans the surface of the soil and may even walk to several old fishing hole locations to inspect them. The chimpanzee then rakes away the leaf litter and surface debris with one hand. Standing above the target insertion point, the chimpanzee points the end of the stout, smooth stick at the location that has been cleared of leaves and begins to push the tool into the ground with both hands grasping the midsection of the tool (see fig. 3*A*). Often they will use one foot to grasp the tool while their body weight is shifted over the tool to press it farther into the ground. After reaching the desired depth, the tool is removed by pulling upward with both hands while the chimpanzee stands bipedally. The end of the tool or insertion point is then often smelled or visually inspected. It is possible to detect whether a termite nest has been punctured by changes in substrate matrix as the tool is inserted or the smell of termites killed by the puncturing stick. During 13 episodes, chimpanzees accessed termite nests and proceeded to insert a slender fishing probe with a brush tip into the tunnel to extract termites. If a nest was not punctured or termites had fled to other nest chambers, the puncturing process was repeated.

Perforating epigeal nests. Our remote video recordings revealed a new chimpanzee tool set consisting of perforating twigs and fishing probes in this chimpanzee population. See video 3 (in the online edition of the *American Naturalist*) for remote video footage of an adult female perforating and fishing at an epigeal nest. Chimpanzees were observed on 20 occasions using a perforating twig to reopen termite exit/entry holes on the surface of epigeal nests after unsuccessfully attempting to open the holes by hand. Perforating twig tools are held with a precision grip as the tip is pressed into the surface of the mound (see fig. 3*B*). The end of the tool is used to push through the soil replaced by termites to seal the nest. The soil barrier is <1 cm thick and relatively soft in contrast to the cemented structure of the nest. After the hole has been opened and cleared of debris by hand or with the tip of the twig, the chimpanzee inserts a brush-tipped fishing probe into the cavities of the nest to extract termites. Chimpanzees were observed perforating several areas on the mound during the same visit, and the same holes were often reopened during repeat visitation.

Brush-tip fishing probe manufacture and use. Chimpanzees typically make three modifications to a fishing probe before using the tool for extracting termites: the length of the stalk is modified (when selected from the herb stand or later) by removing a stalk segment, the broad leaf is removed from one end of the stem, and the other end is fashioned into a "brush tip." Chimpanzees were observed to make brush-stem modifications to 95% of the herbaceous fishing probes that were manufactured at termite nests; 22 observations of brush-stem manufacture were made with remote cameras. After taking a single stem from the stand, the chimpanzee removes the leaf from the distal end of the tool with his/her mouth. One end of the tool is then pulled sideways through partially closed teeth (most often their molars) several times to fray the end of the herb into a brush tip. Some individuals were also observed biting the end of the tool with their incisors to pull apart the fibers.

The brush tip is very flexible, so there is a specific technique for inserting this tool into the termite mound.

Video 3: Still photograph from remote video (available in the online edition of the *American Naturalist*) that shows a chimpanzee using a perforating tool set at elevated nest. A new chimpanzee tool set consisting of perforating twigs and fishing probes was revealed in our remote video recordings. Perforating twigs are more variable in form than other tools used in termite predation by this population, so it was only after watching the video sequences that the tool use in nest perforation was identified. In this sequence, an adult female of the Moto chimpanzee community presses the end of a perforating twig into the surface of an elevated termite nest to open the termite tunnels, and she then inserts a fishing probe into the nest to extract termites.

Chimpanzees first wet the brush tip with saliva and then quickly pull the brush through their hands or mouth to further straighten and compact the fibers before inserting the brush into the mound. This brush straightening is performed almost every time that the tool is inserted into the mound, and tools not successfully threaded into the mound are straightened again before insertion.

The brush-tipped fishing probe is withdrawn from the nest in one swift motion, sometimes with the tool stalk resting on the opposite arm for support. Chimpanzees remove termites from the end of the probe by two methods: "direct mouthing," picking termites directly from the brush fibers with their lips, or "pull through," picking termites from the sides of their fists after having swept a closed hand up the length of the tool to gather termites onto their hands (for description of these behaviors with ants, see McGrew 1974 and Yamakoshi and Myowa-Yamakoshi 2004). The chimpanzees were also observed "mopping" insects with the back of their hands and wrists. These insects were then picked from the hair on their arms with their lips (for original description of this behavior at Gombe, see van Lawick-Goodall 1968).

Tool Characteristics

A total of 332 puncturing sticks and 852 fishing probes were recovered during nest circuit surveys and ad lib. data collection in six chimpanzee community ranges. Because perforating tools were identified within the latter portion of this study, the sample is limited to 19 tools from two communities. These tools are compared with tools used in termite predation at other chimpanzee study sites in table 1.

Puncturing sticks. Puncturing sticks had an average length of 40.6 ± 14.2 cm ($n = 332$, range = 11–95 cm) and average diameter of 9.6 ± 2.3 mm ($n = 315$, range = 1–18 mm). Ninety-eight percent of these tools were manufactured from *Thomandersia hensii* with all leafy material removed. Tertiary branches are not usually found along the stalk of this tree species, but 47% of puncturing sticks were inadvertently peeled of bark from repeated insertion into the nest. Both ends of these tools may be used in puncturing subterranean nests.

Fishing probes. Although similar to puncturing sticks with an average length of 43.1 ± 12.9 cm ($n = 852$, range = 11–104 cm), fishing probes were half as thick with an average diameter of 4.5 ± 1.3 mm ($n = 848$, range = 1–11 mm). In contrast to the woody puncturing sticks, fishing probes were always made from flexible herbaceous materials. Ninety-six percent of fishing probes were manufactured from *Sarcophrynium* spp., and the remaining 4% were made from *Haumania danckelmaniana*, *Ataenidia conferta*, *Megaphrynium* sp., and unidentified herb species accounting for seven tools. Most commonly,

Table 1: Tools used in termite predation at several chimpanzee study sites

	Termite nest puncture				Termite fish				
	N	Length (cm)	*N*	Diameter (mm)	*N*	Length (cm)	*N*	Diameter (mm)	References
Pan troglodytes schweinfurthii:									
Gombe, Tanzania					145	30.7	32	4	McGrew et al. 1979
Mahale, Tanzania					97	54.6			Uehara 1982
Pan troglodytes troglodytes:									
Goualougo, Republic of Congo	332	40.6 ± 14.2	315	9.6 ± 2.3	852	43.1 ± 12.9	848	4.5 ± 1.3	This study
Guga, Republic of Congo	66	52.7 ± 15.1	35	10.9 ± 2.8	42	50.8 ± 9.5			Suzuki et al. 1995
Lossi, Republic of Congo	169	56.6 ± 12.9	159	9.8 ± 2.3	107	54.3 ± 11.6	78	3.9 ± .9	Bermejo and Illera 1999
Bai Hokou, Central African Republic	74	58.7 ± 18.3	72	12.3 ± 3.5	62	50.5 ± 17.5	41	4.1 ± 1.1	Fay and Carroll 1994
Campo, Cameroon	110	46.8 ± 8.3	111	9.9 ± 1.6	4	30.5			Sugiyama 1985
Campo, Cameroon	81	44.5 ± 9.2	81	9.0 ± 1.6	16	44.4 ± 5.0	16	4.0	Muroyama 1991
Okorobiko, Cameroon	46	49.7	46	11	…	…	…	…	Jones and Sabater Pi 1969; Sabater Pi 1974; McGrew et al. 1979
Belinga, Gabon	2	68, 76	2	14, 18	23	37.8	23	3–4	McGrew and Rogers 1983
Pan troglodytes verus:									
Assirik, Senegal					173	32.5	12	2.5	Jones and Sabater Pi 1969; Sabater Pi 1974; McGrew et al. 1979

Table 2: Comparison of tool characteristics across communities

	Termite nest puncture			Termite fish			Brush tip	
Community	*N*	Length (cm)	Diameter (mm)	*N*	Length (cm)	Diameter (mm)	*N*	Brush (cm)
Moto	163	42.5 ± 14.5	9.4 ± 2.3	707	43.1 ± 12.9	4.5 ± 1.3	586	11.9 ± 5.1
Mopepe	52	34.5 ± 11.1	9.8 ± 2.4	56	46.4 ± 12.7	4.5 ± 1.4	20	11.5 ± 4.7
Mayele	33	37.4 ± 9.6	10.1 ± 2.8	34	46.8 ± 10.6	5.0 ± 1.2	28	17.0 ± 6.2
Mosika	41	51.8 ± 15.7	1.0 ± 2.4	…	…	…	…	…
Mokili	47	34.1 ± 9.2	9.9 ± 2.1	…	…	…	…	…
Makasi	…	…	…	48	37.4 ± 12.3	4.5 ± 1.1	45	9.9 ± 4.8
Total	336	40.7 ± 14.1	9.6 ± 2.3	845	43.1 ± 12.9	4.5 ± 1.3	679	11.9 ± 5.3
ANOVA		$F = 14.5$, df = 4, $P < .01$	$F = 1.1$, df = 4, $P < .01$		$F = 5.4$, df = 3, $P < .01$	$F = 1.4$, df = 3, $P < .01$		$F = 11.4$, df = 3, $P < .01$

tools consisted of an herb stalk with the leaf removed and one end intentionally modified into a brush tip. Brush tips were found on 81% of all fishing probes, but remote video footage has shown that only probes with brush tips were used to extract termites. Therefore it is likely that discarded tools without brush tips collected at nests had not been used. The average length of brush tips was 11.9 ± 5.3 cm ($n = 684$, range = 0.3–45.4 cm), which accounted for approximately 29% of the tool length ($n = 684$, SD = 12.5%). Only the brush end of these tools is inserted into the termite nest. However, the brush tip represents only a portion of the functional tool length because part of the stalk is also inserted into the mound.

Perforating twigs. Perforating twigs had an average length of 47.0 ± 23.0 cm ($n = 19$, range = 5–91 cm) and average diameter of 5.4 ± 1.1 mm ($n = 19$, range = 3–8 mm). The form of these tools varied greatly from small straight twig segments only a few centimeters long to large unwieldy branches with several leafy twigs attached. In contrast to the specific tool materials used for fishing probes and puncturing sticks, perforating twigs were made from materials in close proximity to the nest, regardless of species. Only one end of these tools was used to perforate the nest, most likely because the other end had intact vegetation. Some tools were found with their end branches removed, but many were unmodified. The wood fibers at the end of these twigs were occasionally frayed from the motion of pressing the stick into the nest surface and clearing soil from the hole. We did not observe chimpanzees intentionally modifying the tools to fray the end as with the brush-tip fishing probe; rather, this seemed to be the result of repeated insertion into the nest. These tools were never used for gathering termites, but after a hole on the mound surface had been opened, a brush-tip fishing probe was used to extract termites from the nest. The same perforating tool was often reused several times within one bout of termite fishing but not during subsequent visits.

Comparison of tool types. The length and diameter of tools with different functions in termite predation used by chimpanzees in the Goualougo Triangle are shown in table A1 in the online edition of the *American Naturalist.* There were significant differences in the lengths and diameters of these tool types ($ANOVA_{length}$, $F = 5.3$, df = 2, $P < .01$; $ANOVA_{diameter}$, $F = 745.4$, df = 2, $P < .01$). The distribution of tool lengths overlapped, with perforating twigs showing the largest degree of variation. More distinct distributions were seen among tool diameters, with puncturing sticks being thicker than probes and twigs.

Comparisons Within and Between Communities

Differences in tools within the Moto community. Cumulatively, we collected tool assemblages with at least 10 tools from 14 epigeal mounds and three subterranean nests in the Moto community. Tables A2 and A3 in the online edition of the *American Naturalist* show the physical characteristics of fishing probes and puncturing sticks recovered at repeatedly visited nests. There were no significant differences in tool characteristics among the assemblages recovered from each of these nests in the same community (puncturing sticks: $ANOVA_{length}$, $F = 0.6$, df = 2, NS; $ANOVA_{diameter}$, $F = 0.3$, df = 2, NS; fishing probes: $ANOVA_{length}$, $F = 1.4$, df = 13, NS; $ANOVA_{diameter}$, $F = 0.8$, df = 13, NS; $ANOVA_{brush}$, $F = 1.5$, df = 13, NS).

Differences in tools between communities in the Goualougo Triangle. Table 2 compares termite tool characteristics across communities. Puncturing stick length (ANOVA, $F = 14.5$, df = 4, $P < .01$), fishing probe length (ANOVA, $F = 5.4$, df = 3, $P < .01$), and brush-tip length (ANOVA, $F = 11.4$, df = 3, $P < .01$) differed between communities within the Goualougo Triangle, but tool diameters were similar (puncturing stick: $\mathrm{ANOVA}_{\mathrm{diameter}}$, $F = 1.1$, df = 4, NS; fishing probe: $\mathrm{ANOVA}_{\mathrm{diameter}}$, $F = 1.4$, df = 3, NS). All the puncturing stick lengths from each community formed a homogeneous subset, except the Mosika community, which showed longer tools than the others. Two subsets within the communities with regard to fishing probe length were noted: one used longer probes and one used shorter probes. Members of the Mayele community used longer brush tips than all other communities sampled.

Discussion

We have provided conclusive evidence that chimpanzees in central Africa are using different tool technologies to prey upon termites than populations in East and West Africa, which contributes to the increasingly complex material culture shown by this species. Chimpanzees in the Goualougo Triangle employed different tool sets to access termites in subterranean and epigeal nest structures of *Macrotermes* spp. With the aid of a remote video monitoring system, we observed chimpanzees in the Goualougo Triangle arriving at nests with appropriate tool materials, manufacturing brush-tipped fishing probes, using puncturing sticks in combination with fishing probes to access subterranean termite nests, and using perforating twigs to open the surface of epigeal termite mounds before extracting termites with probes.

Chimpanzees have been observed using fishing probes at many study sites across Africa, but the puncturing or perforation of termite nests has been limited to the range of the central subspecies. Based on the distribution of different termite tool technologies shown by chimpanzees, McGrew et al. (1979) proposed three distinct inventions of termite fishing. They suggested that probing technology originated separately in the forest-woodland-grasslands of both East and West Africa and that perforating (synonymous with digging, but in this article referred to as puncturing) technology arose within the forests of the central chimpanzee. McGrew et al. (1979) suggested four ways that these hypotheses could be disproved: first, if an isolated population showed these technologies; second, if two studied populations were contiguous and only one showed a particular termite tool technology; third, if a mixed forest-woodland-grassland population showed perforating (puncturing) behavior or a forest-dwelling population showed fishing behavior; or fourth, if a single population used both techniques. In this report, we have presented the tool technologies customarily used by the chimpanzees in the Goualougo Triangle in preying on termites, and these tool use practices clearly support the third and fourth challenges to McGrew et al.'s (1979) assertion of separate origins of termite probe and perforating (puncturing) customs.

Tool sets are composed of more than one type of tool, which requires that an individual understand the associative role of each tool to perform a specific task (Sugiyama 1997). Although multiple tool use in wild chimpanzees is rare, we have clearly differentiated two tool sets that are frequently used by chimpanzees in the Goualougo Triangle when preying on termites. Nest visitation by at least half of the Moto community, similar assemblages collected in other communities within the study area, and tool sets recovered at other sites in this region suggest that these types of sequential tool use are customary in this population (Fay and Carroll 1994; Suzuki et al. 1995; Bermejo and Illera 1999). In this report, we also provide quantitative data of differences in tool characteristics between adjacent chimpanzee communities. However, attributing these variations to ecological constraints or social customs will require detailed comparative research on termite fauna and tool materials between sites.

Large variation in termite consumption has been reported between sites, but it is evident that these social insects are an important aspect of chimpanzee feeding ecology for some communities. At Gombe, adults may allocate more than 10% of their day to termite fishing in particular months, and termites were the fifth most common food item for females (McGrew et al. 1979; Pandolfi et al., unpublished manuscript cited in Pandolfi et al. 2003). Sex differences in termite fishing are apparent at Gombe (McGrew 1979, 1992). Adult females with dependents were the most frequent visitors to termite nests at Goualougo. However, the sex differences in nest visitation were not significant when the population sex ratio was taken into account. Termite nests were regularly visited throughout the year at this site and two other sites in central Africa (Okorobiko: Sabater Pi 1979; Guga: Suzuki et al. 1995). Termites are also eaten throughout the year at Gombe, but peaks were reported at the beginning of the rainy season (McGrew et al. 1979). Mahale and Assirik showed similarly high frequencies of termite fishing in the rainy season (McGrew et al. 1979; Uehara 1982). Continued long-term monitoring and quantification of sex differences and ecological variables are needed to determine the factors associated with frequency of termite predation at this site.

Tool Characteristics

There were distinct differences in the form of stick tools used for different functions. Chimpanzees consistently fashioned tools made of specific materials that had uniform lengths and diameters suitable for distinct tasks in termite predation (table A1 in the online edition of the

American Naturalist). Further, the tool kit used by chimpanzees in central Africa for extracting termites from their nests differs from kits used in East and West Africa, as earlier reported by McGrew et al. (1979).

Chimpanzees in the Goualougo were specifically selecting *Thomandersia hensii* for penetrating subterranean termite nests. Similar preferences for specific tool materials in termite predation have also been observed in Bai Houkou and Assirik (McBeath and McGrew 1982; Fay and Carroll 1994). We attempted to dig into termite nests with several other tree species of the same length and diameter, but none created a tunnel into the nest that allowed fishing. Although it is one of the most common tree species in the Ndoki forests, *T. hensii* are not always located in close proximity to nest sites. By retracing the travel path of chimpanzees, we were often able to find the location where raw materials for tools had been gathered, which showed that they had been specifically selected and transported to specific nests. Several *Thomandersia* trees that were sources of puncturing stick materials were tens of meters from the termite nest, not visible from the tool-using location, and visited by chimpanzees on several occasions for gathering raw materials for tool making.

Chimpanzees were also selective for materials used to manufacture fishing probes. Rather than selecting materials within arm's reach of the termite nest as described by McGrew et al. (1979) in Gombe and Assirik, 96% of fishing probes in Goualougo were made from *Sarcophrynium* spp. stalks. McGrew and Collins (1985) reported that tool material choice was dependent upon seasonal availability of vegetation around the nest. However, the majority of termite fishing probes in this region are made from the smooth, flexible stalk of *Marantaceae* plants that are abundant and available throughout the year in this area (Fay and Carroll 1994; Bermejo and Illera 1999). Chimpanzees showed much greater variation in perforating twig material choice than the other types of tools used in termite predation. The tool task and flexibility in functional tool form allow chimpanzees to fashion perforating twigs as needed from vegetation surrounding the nest rather than to select specific materials and transport them to the nest in preparation for the termite extraction task.

Chimpanzee use and reuse of perishable tool materials provide valuable insights into hominoid tool-using patterns. Fishing probes were carried between nests on the same day but were never seen to be cached at tool sites. Wooden puncturing tools were cached at tool sites and reused by subsequent visitors to the nest. This difference in tool reuse could be due to differences in material substrates. Herbaceous fishing probes are not functional after only a few days, whereas stout puncturing sticks remain viable tools for several months.

Past researchers have suggested that puncturing sticks left inserted in nest matrix may function as plugs to access holes that would be reopened during subsequent visits (Fay and Carroll 1994; Suzuki et al. 1995). However, we found no evidence that fishing holes were regularly plugged and then reused. Chimpanzees often removed tools that were inserted in the mound matrix without fishing in that particular tunnel. We have also recovered what Sugiyama (1985) described as "brush sticks," but these did not seem to have a particular function in termite predation. Rather, it seems that the sticks' appearance (puncturing sticks with frayed ends) was a by-product of the sticks' removal from the tree source. Bermejo and Illera (1999) also suggest that the fraying at the end of sticks was caused by breaking the tree stem with a back-and-forth movement. Rather than serving as an important component in the termite extraction process, these ends quickly become blunted with repeated insertion into the mound. Our assertion that the brushes on puncturing sticks are not important in puncturing or fishing for termites is further supported by Sugiyama's (1985) and our observations that all these tools that were found inserted into nest matrix had the "brush" end in the air.

Although the brush tip was certainly an important feature of fishing probes in this population as shown by its prevalence in several communities, further research will be needed to determine the improved efficiency yielded by this secondary modification. Understanding of the utility and potential to generalize the function of this type of tool was demonstrated when a young chimpanzee used her brush-tip fishing probe to gather termites that were marching on the ground near a nest. Interestingly, the form and modifications of termite fishing probes were similar to those used in ant predation at this site. Further investigation is needed to determine the relationship between tool forms and tasks in social insect predation.

Comparisons Within and Between Communities

Evidence of both termite fishing and puncturing was found in all communities surveyed within the Goualougo Triangle. Tool homogeneity was shown within puncturing stick and fishing probe assemblages in the Moto community range. However, we did find evidence of subtle intercommunity differences in tool characteristics that were not easily attributable to environmental factors. Different communities showed slight variation of the tool theme that was shared by all communities within the study area. For example, puncturing sticks in the Mosika community were significantly longer than those recovered in other communities, whereas the fishing probes of the Makasi community were shorter than others. Finally, brush tips of fishing probes in the Mayele community were longer than brush tips made in all other communities. We are not yet able to exclude the possibility that ecological conditions vary between these adjacent communities such as those associated with patterns of termite predation at Mahale, but the communities in the Goualougo share continuous forests composed of the same subhabitat types, which makes ecological differences unlikely (Nishida and Uehara 1980). It is also possible that these differences in tool characteristics have arisen and evolved as traditions among adjacent communities, similar to the subcultural differences observed in other populations (McGrew et al. 2001; Boesch 2003).

The results of this study prompt further research into the relationship between termites and tool-using behaviors of chimpanzees. The next phase of our research in the Goualougo Triangle will involve long-term remote monitoring of termite nests in several chimpanzee communities to compare technological traditions within the region. The Sangha River Trinational protected area in northern Congo provides one of the last opportunities to document the natural differences in material culture among several intact social groups and processes of technological diffusion within a wild ape population. These results of this study emphasize the importance of continuing to protect the remaining forests of the Congo Basin, their ape inhabitants, and the unique and largely undocumented cultures that reside within them.

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