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The Complexity of Chimpanzee Tool-Use Behaviors

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There are constant sounds of chattering, whistling, and rustling as various creatures search for food, attempt to attract mates, or avoid predators in the dense forests of the Nouabalé-Ndoki National Park. However, the rhythmic sound of a chimpanzee using a large branch to pound open a beehive is distinct from all other forest noises. Such a reverberating echo of pounding sends us racing through the underbrush to catch a glimpse of a tool-using ape. We arrive at the origin of the sound to find a young adult female lounging near a beehive surrounded by a swarm of stingless bees. She picks up a large club lying on the branch beside her, holds it as if preparing to launch it as a javelin, but instead forcefully hits its end against the beehive. She repeatedly pounds with the club before inspecting the result of her efforts. After finding that the tool possibly is too large, she carefully places it in the canopy and manufactures a shorter tool that seems easier to maneuver. She then uses the two tools alternately to hammer and lever the hive. Suddenly appearing to abandon the task, the chimpanzee climbs up into the trees' leafy canopy and returns with a slender twig deftly fashioned into a dipping probe to extract the honey. She spends the rest of the afternoon enjoying the bounty of her technological skills, while we are left to reflect on the cognitive implications of such impressive "tool kits."

Tool use involves the relating of two objects to one another, and is therefore considered more cognitively com-

plex than other types of object use. However, some types of tool use are species-specific feeding adaptations that do not require any understanding of the task. The diversity and flexibility of tool use by primates once seemed to distinguish them from other taxonomic groups, but recent research on the tool behaviors of wild corvids has challenged such broad generalizations (Hunt 1996; Hunt et al. 2006; Hunt and Gray 2003). Parker and Gibson (1977) provide criteria for distinguishing complex foraging strategies that are "context-specific" from "intelligent" tool use that is characteristic of the more advanced stages of sensorimotor intelligence. Tomasello and Call (1997) state that understanding of the dynamic relationships between objects presumably enables flexibility in applying tool-use skills across contexts, which is indicative of intelligent tool use. The technological system of chimpanzees has been lauded as being the most sophisticated form of nonhuman material intelligence observed in natural environments. Various tool behaviors of wild chimpanzees, such as nut cracking and the use of tool sets in termite fishing, have been referred to as "complex," but there have been few systematic treatments of the composition or structure of chimpanzee tool use that allow us to assess the complexity of these tasks. In this chapter we examine several traditional notions of complexity, including the number of behavioral components (elements) needed to complete the tool task, structuring of actions, and hier-

archical organization of object relations. We also provide some preliminary insights into the flexibility of different tool tasks shown by this species, which may provide some indication of their causal understanding of these tasks and the rules governing chimpanzee tool strategies.

Chimpanzee Tool Use in a Comparative Context

Among nonhuman primates, the material intelligence of chimpanzees and orangutans has been differentiated by the diversity of tools used in different contexts and relative regularity in which tools are used in comparison to their use by other taxa (van Schaik et al. 1999). Reports of tool use by New World monkeys have effectively challenged some long-standing assumptions about the phylogenetic distribution of particular features of tool-use skills. In particular, the behaviors of some wild capuchin monkey populations stand apart from the relatively rare and simple tool-use behaviors observed in other primates (Fragaszy et al. 2004; Phillips 1998; Waga 2006). Most recently, the tool-use behaviors of New Caledonian crows have further broadened our perspectives of complex tool use in other taxonomic groups. These corvids have a repertoire of several different tool behaviors (Hunt 1996), some of which differ in the complexity of their manufacturing sequences (Hunt et al. 2006; Hunt and Gray 2003). Future comparative examinations of the complexity of tool-use behaviors will provide insights into the cognitive capacities of these species. However, a necessary first step is to assess the tool technology within a species or population to determine the degree of variation in these systems and how this may inform us about ecological and social factors shaping different tool-use propensities.

Assessing Complexity of Tool Use

Sophisticated social networks and multistage food-processing techniques have been cited as complex behavior patterns that involve advanced cognitive functioning (Byrne and Byrne 1993; Byrne et al. 2001; Corp and Byrne 2002). However, there have been surprisingly few systematic treatments of complexity in wild chimpanzee tool use. Previous approaches to characterizing the complexity of particular tool tasks have included counting the number of behavioral components (elements), examining the sequential structuring of actions, and assessing the depth

and hierarchical organization of object relations. We proceed with a description of these methods before applying them to the tool-use behavior of wild chimpanzees in the Goulougo Triangle, Republic of Congo. This chimpanzee population has a large repertoire of tool-use behaviors, some of which are exhibited on a habitual or customary basis (Sanz and Morgan 2007). Through a systematic comparison of these tasks, we will assess whether the behaviors differ in their degree of complexity and what conclusions we can draw about the chimpanzees' understanding of these tasks.

Initial approaches to complexity in tool-use behaviors involved comparing the physical characteristics of tools and the modifications required in their manufacture. Oswalt (1976) proposed a method to systematically gauge the technological complexity of various hunter-gatherer populations that involved estimating the number of physically distinct structural configurations that contribute to the form of a tool. McGrew (1987) extended this analysis to wild chimpanzees, but the complexity of chimpanzee tool traditions was low on the human scale, and the variation between populations was too fine to be evaluated by Oswalt's technosystem. This is not to say that chimpanzee tools are not modified or manufactured toward a specific mental representation of a particular tool type, or even that they may not be comprised of multiple objects. Boesch and Boesch (1990) have shown that chimpanzees consistently fashion stick tools of specific lengths and diameters for particular tool-use tasks. Several stages of raw material modification may be necessary to produce a suitable ant-dipping rod at Tai (Boesch and Boesch 1990), a spear at Fongoli (Pruetz and Bertolani 2007), or a termite-fishing probe at Goulougo (Sanz and Morgan 2007; Sanz et al. 2009). Intriguingly, design complexity and number of nonrecapitulated modifications have been documented in the manufacture of tools from *Pandanus* tree leaves by New Caledonian crows to capture invertebrates (Hunt et al. 2006). The manufacture of tools with several "steps" or notches cut along the leaf edge is considered more complex than simple strip tools.

It has been suggested that estimations of behavioral complexity in natural systems can be accomplished by "repertoire counting," which involves an inventory of all the distinct components (elements) that comprise a behavior or task (Sambrook and Whiten 1997). The size of a behavioral repertoire is assumed to be positively related to

the cognitive sophistication of the organism, in which the diversity of available choices indicates a propensity for innovation and an ability to select appropriate behaviors. In general, chimpanzees have a diverse behavioral repertoire that includes many different types of tool use. This can partially be attributed to the manual dexterity of primates, which aids in the formation and manipulation of external objects (van Schaik et al. 1999). Again, this has been challenged by the “tool kits” of New Caledonian crows (Hunt 1996). Rather than labeling behaviors as complex based on the number of their behavioral components, it is more important that particular skills are explicitly linked to cognitive capabilities, such as understanding of the task. The assemblage or organizational structure of behavioral components in different settings may assist in distinguishing rigidly fixed action patterns from more flexible manifestations of tool use which show that an organism has some understanding of the task.

Most sophisticated behavior patterns are interpreted as being sequentially or hierarchically organized such that later elements require the completion of one or more previous elements. However, context-specific or fixed patterns can also involve many elements that are linearly ordered with little or no evidence of strategic flexibility or understanding of causality between external objects. Boesch and Boesch-Achermann (2000) have suggested that this flexibility is a key component in inventing and developing tool repertoires such as those of humans and chimpanzees. Flow diagrams of decision processes or alternative pathways at natural junctions can provide important insights, such as propensities to reiterate strings of elements, and abilities to substitute elements and incorporate flexible responses for coping with new situations. It is also possible to superimpose quantitative data, such as frequencies or probabilities of element transitions, onto these flow diagrams of structural organization (Tonooka 2001). This provides insights into the statistical regularity of particular element combinations, and it may also highlight essential sequences of elements that are necessary to accomplish a task (Byrne 2003). The structured use of multiple tools to achieve a goal may necessitate a higher level of hierarchical organization than tasks involving only a single tool.

The use of multiple tools to achieve a common function is relatively rare in species other than humans, but it has been observed to be habitual in some chimpanzee populations. Sugiyama (1997) compiled reports of chimpanzees using more than one tool in sequence (serial tool use)

or a combination of tools together (composite tool use) to achieve a goal. The “tree structure analysis of hierarchical cognition” developed by Matsuzawa (1996) provides a way of describing the cognitive processes involved in a series of actions or behavioral patterns. The depth of nodes in the tree structure represents complexity of action, and the number of nesting clusters indicates hierarchical levels. In tool use, the depth of nodes increases with the number of objects used. For example, termite fishing consists of a single relationship between a fishing probe (tool) and a termite (target), whereas the use of metatools, observed in nut cracking at Bossou, consists of three nested object relationships (hammer, anvil, nut). Tree-structure analysis can be applied across cognitive domains to systematically document structure and hierarchical processes within or between taxa. This approach has also been used to depict cognitive modules of symbol use (Matsuzawa 1996) and social intelligence (de Waal 2003).

Comparisons of the catalogs of tool behaviors recorded at long-term study sites have shown that repertoires differ between populations and even between adjacent groups (Boesch and Boesch 1990; McGrew 1992; Sanz and Morgan 2007; Yamakoshi 2001). We have previously reported on the technological system of the chimpanzees in the Goulougo Triangle, which includes the habitual use of multiple tool techniques that have been described as being complex (Sanz and Morgan 2007; Sanz et al. 2004). In this chapter, we systematically compare the composition and structure of different tool-use behaviors within this wild chimpanzee population. Tool behaviors directed toward different targets are likely to differ in their element composition, organizational structure, and patterning of elements. However, different tool-use tasks are also compared to investigate whether these chimpanzees have rules that govern object relations or demonstrate flexibility in employing different tool strategies in the same or different contexts. Our aim is not only to better understand the technological sophistication of these chimpanzees, but also to elucidate some of the cognitive mechanisms which have led to the emergence of these fascinating behaviors.

Approach

Study Site and Population

The Goulougo Triangle is located within the Nouabalé-Ndoki National Park, Republic of Congo. The study area

covers 380 km² of evergreen and semi-deciduous lowland forest with altitudes ranging between 330 and 600 m. The climate can be described as transitional between the Congo-equatorial and subequatorial climatic zones. The main habitats in the study area are mixed-species forest, monodominant *Gilbertiodendron* forest, and swamp. The main rainy season is from August through November, with a shorter rainy season in May.

Between February 1999 and December 2006, we spent a total of 88 months in the Goulougo Triangle habituating and studying wild chimpanzees. We conducted reconnaissance surveys in several community ranges, but the majority of our efforts were allocated to the Moto, Mopepe, and Mayele communities, which each consisted of 64 to 71 individuals (including immatures) during this period.

Data Collection

Tool behaviors were recorded ad libitum during direct observations with semi-habituated chimpanzees in the Goulougo study area. For all instances of tool behavior, we recorded the actor, behavior, type of object used, target of behavior, and outcome. We recorded digital video of tool-use behavior whenever possible. In addition, between 4 and 18 remote video-recording devices were used to conduct surveillance at termite nests of chimpanzee visitation between 2003 and 2006. (For precise details of the device used, see Sanz et al. 2004). The following tool-use behaviors were video-recorded during time spent with chimpanzees conducting direct observations or via remote video-recording devices that were installed in the forest:

HONEY GATHERING. Chimpanzees in the Goulougo Triangle have been observed to use dipping, levering, and pounding tools to gather honey from the hives of stingless bees and African honeybees (see Sanz and Morgan 2009 for a review). Inserting a probe into a bee nest to extract honey (dipping) is the most widespread tool-use strategy shown by chimpanzees in honey gathering and is seen in sites across Africa, from the Taï forest in Ivory Coast to Gombe in Tanzania (Bermejo and Illera 1999; Boesch and Boesch 1990; Boesch et al. 2009; Fay and Carroll 1994; Fowler and Sommer 2007; Hicks et al. 2005; Izawa and Itani 1966; Kajobe and Roubik 2006; Nishida and Hiraiwa 1982; Stanford et al. 2000; Tutin et al. 1995). Chiseling or lever-opening of arboreal bee nests to widen an access point to extract honey has been observed in Tanzania,

the Central African Republic, Gabon, and the Republic of Congo (Fay and Carroll 1994; Sanz and Morgan 2007; Wallauer, personal communication). Pounding or hammering of beehives with the end of a large club to break the hive structure has been observed rarely, but it seems to be exclusive to chimpanzee populations of the Congo Basin (Bermejo and Illera 1999; Boesch et al. 2009; Fay and Carroll 1994; Hicks et al. 2005; Sanz and Morgan 2007).

LEAF SPONGING. Leaf sponging involves using a mass of crushed or chewed leaves to sponge water from a tree basin. This behavior has been documented at several long-term study sites (Whiten et al. 1999, 2001), but is carefully distinguished from leaf folding by Tonooka (2001), who has compiled detailed data on the use of leaves for drinking water by wild chimpanzees in an outdoor laboratory in which the water was provisioned in a tree hollow. Reports of the natural use of leaves to drink water include the following: Gombe (Goodall 1964) and Mahale (Matsusaka et al. 2006) in Tanzania, Taï in Ivory Coast (Boesch and Boesch 1990), Bossou in Guinea (Sugiyama 1995), Lopé in Gabon (Tutin et al. 1995), Goulougo in the Republic of Congo (Sanz and Morgan 2007), Semliki in Uganda (McGrew et al. 2007), and Tongo in the Democratic Republic of Congo (Lanjouw 2002).

TERMITE FISHING AT ELEVATED NESTS. Several studies across equatorial Africa have reported that chimpanzees use fishing probes to extract termites from their earthen nests (see Sanz et al. 2004 for a review). Termite fishing typically involves inserting a flexible wand into a termite nest to extract termites that attack the invading object, but variations in this behavior have been documented between populations. For example, there are several populations of chimpanzees in central Africa that use fishing probes with a modified brush tip (Muroyama 1991; Fay and Carroll 1994; Suzuki et al. 1995; Bermejo and Illera 1999; Sanz et al. 2004, 2009). Another variation involves the use of a second tool; after unsuccessfully attempting to open termite exit holes manually, chimpanzees in the Goulougo Triangle have been observed to manufacture a perforating twig to open the exit holes on the surface of the nest (Sanz et al. 2004). The tip of the tool is pressed into the surface of the mound to clear soil from a closed exit hole. The chimpanzee then inserts a fishing probe into the cavities of the nest to extract termites. Perforating tools vary from small, straight twigs a few centimeters long

to large, unwieldy branches with leafy twigs attached (average length = 32.9 ± 19.4 cm; range = 5; 91 cm, $n = 54$).

TERMITE FISHING AT SUBTERRANEAN NESTS. Yet another task involves extracting termites from subterranean nests, which necessitates a tool kit comprised of a puncturing stick and fishing probe. Although termite nest puncturing (also referred to as digging) and fishing tool assemblages have been recovered from sites in central Africa (Sabater Pi 1974; Sugiyama 1985; Muroyama 1991; Fay and Carroll 1994; Suzuki et al. 1995; Bermejo and Illera 1999), the first full descriptions of this tool behavior have only become available from the Goualougo Triangle (Sanz et al. 2004). The chimpanzee must first gain access to the subterranean chambers of the nest by inserting the length of a stout stick into the ground, holding the midsection of the tool with both hands, and often using a foot for additional leverage. The stick tool creates a long and narrow tunnel for insertion of the fishing probe. After removing the puncturing stick, the chimpanzee inserts a brush-tipped fishing probe to extract the termites. In contrast to perforating twigs, the tools used in puncturing are uniformly straight and smooth, and are manufactured from particular tree species.

Data Analysis

Individual chimpanzees were identified from their distinct physical characteristics and these data were compiled in a population history database. Video analysis was conducted using INTERACT Version 8.04 (Mangold 2006). Video recordings were scored as tool-use bouts, sessions, and episodes (definitions adopted from Yamakoshi and Myowa-Yamakoshi 2004). An episode began when the chimpanzee manufactured a tool (or at the first moment after which they were observed with the tool) and ended when the tool was discarded or the task was abandoned. Within an episode, any number of bouts or sessions could occur. A bout began when a chimpanzee used a tool to achieve a goal, and ended when they either succeeded or failed to achieve it. A session consisted of a series of bouts by an individual towards achieving a particular goal. The chimpanzee might make several attempts to achieve the goal (widen the entrance of a beehive, create a tunnel into a subterranean termite nest), but the session continued until they attained the goal, stopped using that tool to use

another, discarded the tool, or abandoned the endeavor. For all of the following analyses, we included only recordings of individuals who were capable of the task and complete sequences of tool behaviors.

We used Matsuzawa's (1996) tree structure analysis to compare the complexity of different tool tasks. Specifically, we examined the depth of object-relationship nodes as a measure of complexity and the number of nested clusters as indicative of hierarchical levels. In addition to the overall object-relationship structures, we also present both the elements and essential actions of each tool task in a traditional flow diagram. These diagrams are the traditional way of showing the structural organization of behavioral elements and essential actions (as in Tonooka 2001). Our flow diagrams focus on the target, tool, action, and goal of each tool task.

The behavioral elements in this study were an extension of the traditional ethogram approach. We defined elements as functionally distinct behavioral units, which we assumed to have biological meaning due to their seamless execution. Natural junctions were taken into consideration when defining behavioral elements. For example, we observed that the steps involved in removing a leaf sponge from the mouth and inserting/extracting it into a water basin were very rarely disjointed. Therefore, we did not split this behavior into distinct units as was done by Tonooka (2001), who divided this action into discrete steps. Behaviors associated with tool manufacture were not included in these measures of repertoire size, but have been previously published for these tool tasks (Sanz and Morgan 2007). We defined essential actions as those that were shared by all chimpanzees who successfully completed the tool task. Behavioral elements that involved the active use of the tool were defined as tool actions.

We defined a sequence as a continuous string of at least 30 behavioral elements employed toward accomplishing a task. This number of elements was more than sufficient to achieve each of the tasks, but longer sequence lengths were preferred for robust statistical analysis. We quantified non-randomness in tool-action transitions by comparing observed first-order transition matrices with 1,000 randomly permuted matrices of the same data (custom software by R. Mundry). Matrix permutations preserve the patterning of elements within the matrix, whereas sequence permutations may alter the distribution of transitions in the matrix. However, we used sequence permutations when the

number of columns was too small to allow matrix permutations. We also calculated the Shannon-Weaver entropy index for element transitions, which provided a standardized index ranging from 0 to 1, with lower values indicating more structured relations within the matrix.

Kruskal-Wallis tests were used to test differences in repertoire sizes of behavioral elements between tool tasks. Representation of each individual was limited to a particular tool task to meet assumptions of independent data points.

Results

Our data set was comprised of 27 video-recorded episodes of leaf sponging (adult/subadult females = 10; adult/subadult males = 2; juveniles = 2), 24 recordings of honey gathering (adult/subadult females = 6, adult/subadult males = 2; juveniles = 4), 25 recordings of termite fishing at elevated nests (adult/subadult females = 5, adult/subadult males = 4; juveniles = 4), and 21 recordings of termite fishing at subterranean nests (adult/subadult females = 2, adult/subadult males = 6). A subset of these data were composed of continuously recorded episodes that could be used for sequence analysis (11 segments of leaf sponging, 24 segments of honey gathering, 33 segments of termite fishing at elevated nests, and 21 segments of termite fishing at subterranean nests).

Tree-Structure Analysis

Figure 11.1 depicts the hierarchical tree-structure analysis of tool tasks analyzed in this study. The relationships between objects ranged from level 1 to level 3 as described by Matsuzawa (1996), and the hierarchical organization differed within and between tasks. Leaf sponging is consistently a level 1 tool use that involves a leaf sponge (tool) directed toward water in a tree basin (target). Several leaf sponges could be used in a bout, but we only observed one type of tool in this context. Termite fishing at elevated termite nests most often involved a relationship between two objects—the brush-tipped fishing probe (tool) and the termites (target)—which is a level 1 tool use. However, we also observed the use of a perforating twig (tool) to open the surface of a termite nest (target) prior to termite fishing, which is a second relationship between objects in this context. The serial order of two tools to open a subterranean nest (target) with a puncturing stick (tool), and then

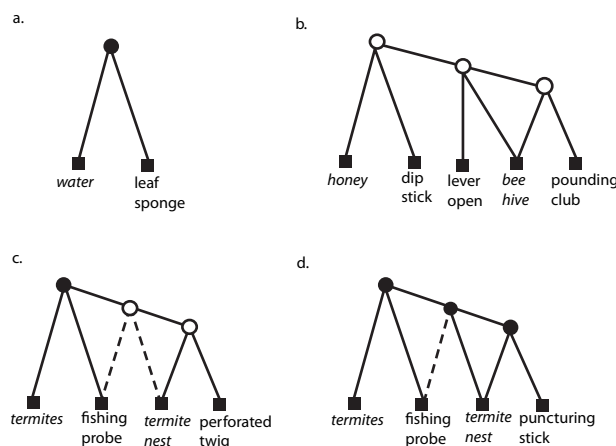


Figure 11.1 Tree-structure analysis of different tool tasks. We have adapted the notation analysis of Matsuzawa (1996) to accommodate serial tool use and multiple-function tool use. Objects are represented by solid squares, with targets italicized. A node that depicts an obligatory object relationship is represented by a solid circle. A node that represents an optional object relationship is shown as an open circle. A tool with a multiple function is connected to the target by a dotted line. Figure 11.1a depicts leaf sponging, which involves a single and consistent relationship between two objects. Figure 11.1b depicts honey gathering, which can involve multiple tools and targets but most often involves only a pounding club directed at a beehive. Figure 11.1c depicts termite fishing at an elevated termite nest, which requires the relationship between the fishing probe tool and the termites, but we have also frequently observed the use of a perforating twig to open the nest surface. A fishing probe can be used for multiple functions in this context when its orientation is reversed and the blunt end is used to clear the fishing hole. Figure 11.1d represents termite fishing at a subterranean termite nest, which requires two relationships between objects, a puncturing stick to create a tunnel into the nest, and a fishing probe to extract termites. We have also observed reversal of the fishing probe to clear the tunnel in this context.

use of a brush-tipped fishing probe (tool) to extract termites (target) was obligatory except in cases where termites were exiting their nests to forage. A third object relationship occurred in these termite fishing contexts when the reverse end of a fishing probe was used to clear debris from a termite tunnel. Three object relationships can also be detected in honey gathering, which may involve a pounding club (tool) and a lever stick (tool) to open the entrance of the beehive (target), and then also a dipstick (tool) to extract the honey (target). These episodes of multiple tool use within a task were serially ordered and temporally distinct, rather than occurring simultaneously as described in the meta-tool use of Bossou chimpanzees (Matsuzawa 1996, 2001).

Repertoire Size and Novelty of Elements

There were consistent and significant differences in the repertoire sizes of behavioral elements associated with each tool task (Kruskal-Wallis H-test, chi-square = 12.20, df = 3, $p = 0.007$). Figure 11.2 compares the average repertoire sizes of chimpanzees in different tool tasks with the relative

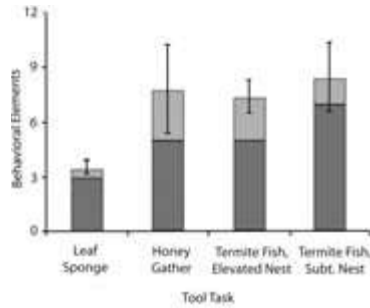


Figure 11.2 Comparison of average repertoire sizes associated with each of the tool tasks. Vertical bars indicate standard deviations. Proportions of the repertoires that consist of essential elements are highlighted in dark gray. Fewer elements and less variation are associated with leaf sponging for water than with other tool tasks. Extraction of termites from subterranean nests had the largest repertoire sizes and numbers of essential elements. The greatest variation in repertoire size was observed in honey gathering.

proportion of essential actions differentiated from additional variations in tool-use techniques. Leaf sponging was comprised of the fewest number of elements and a narrow range of associated variation (average = 3.5 ± 0.4), which indicates that this behavior may have few steps that are executed with high fidelity. Further, the majority of these behaviors were essential for achieving the task. More than twice as many elements were associated with all other tool behaviors (honey gathering = 7.8 ± 2.4 ; termite fishing at elevated nests = 7.4 ± 0.9 ; termite fishing at subterranean nests = 8.5 ± 1.9). Termite fishing at subterranean nests required two types of tool use (puncturing the nest, fishing to extract termites), and therefore was associated with the largest repertoire sizes. The number of essential elements necessary to accomplish each task was slightly lower, but the resulting depiction of task complexity was similar to that produced from estimating the entire repertoire size.

Figure 11.3 shows the overlap between the tool types and essential elements associated with each task. Leaf sponging and honey gathering did not share any tool types or elements with other tool tasks. Termite gathering at subterranean and elevated nests was differentiated by puncturing and perforating tool use. All of the fishing elements were shared between the different nest contexts—with the exception of the sweeping of termites, which was an essential behavior only at elevated nests.

Structural Organization

In addition to depicting the structural organization of behavioral elements and essential actions (figure 11.4), we

quantified transitions between tool actions and goal behaviors in observed tool sequences using the permutation method described above, which is similar to the analysis of stone tool use in nut cracking undertaken by Inoue-Nakamura and Matsuzawa (1997).

Leaf sponging required the fewest essential actions to achieve the goal. These were arranged in a simple linear structure that involved manufacture of a single tool (leaf sponge) and few associated tool actions (inserting the sponge into a basin, and then extracting it) to obtain drinking water. The consistent pattern observed in leaf-sponging sequences was seen in the fact that more than 75% of them differed from randomized data.

Termite fishing at elevated nests had a more complex structural organization of behavioral elements than leaf sponging. The chimpanzee must execute more steps by straightening the tool's fibers before inserting it into the termite nest. We also found that there were more options in this tool task than in the previous one, such as the choice of whether to gather termites directly from the tool or by sweeping a hand along its length. Despite variations observed in real sequences, all of these element transitions differed from randomly generated matrices. The transition between straightening the brush fibers to inserting them into the nest yielded a particularly strong signal, with more than 75% of observed sequences differing from randomized data.

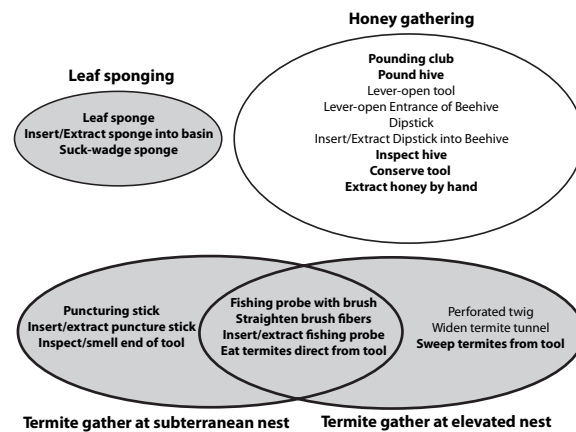


Figure 11.3 Overlap between the tool types and essential elements (in boldface) associated with each task. The region in which the oval diagrams overlap shows the elements that are shared between tool tasks. The graphical presentation is adapted from Takeshita's (2001) depiction of similarity of behavioral patterns between individuals. We found no overlap in elements of leaf sponging or honey gathering. Termite gathering at subterranean and elevated termite nests shared all the elements that were associated with fishing tool use, but diverged in their use of puncturing and perforating tools. Also, sweeping termites from the tool was an essential feeding technique only at elevated nests.

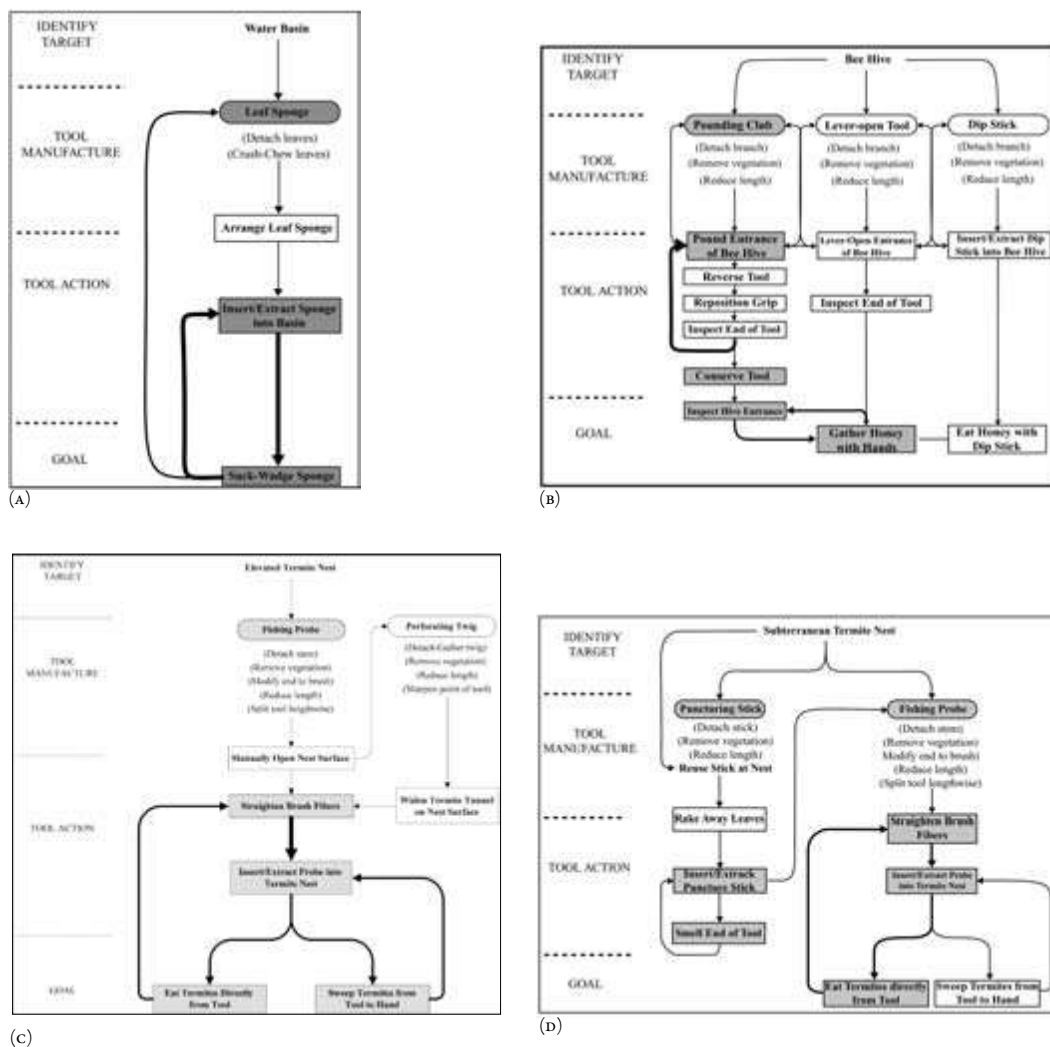


Figure 11.4 Structural configurations of the different tool-use behaviors: leaf sponging (figure 11.4a), honey gathering (figure 11.4b), termite fishing at elevated nests (figure 11.4c), and termite fishing at subterranean nests (figure 11.4d). The names of tools appear within ovals, with text in parentheses indicating steps in their manufacture or modification (Sanz and Morgan, 2007). Rectangles indicate actions toward achieving a target. Essential elements in each tool task are highlighted in gray. Transitions between tool actions and goals are quantified from first-order transition matrices. Thin lines between elements indicate observed transitions. Lines of medium thickness indicate that 50 to 75% of observed transitions differed from random permutations of the data. The thickest lines indicate that more than 75% of observed transitions differed from random permutations of the data.

Although the use of a puncturing stick is necessary to gain access to subterranean termite nests, the most salient transitions in this task were those associated with fishing. More than 50% of the observed transitions involving these elements (brush straightening, inserting the probe into a nest, gathering termites by eating them directly from the tool) differed from randomized data. In contrast to the feeding techniques shown at elevated nests, there was a stronger tendency for chimpanzees to eat termites directly from the tool rather than sweep them with their hands at the subterranean nests.

The structural complexity of honey gathering is a direct result of the increase in the number of different types

of tools. Despite the various tools and action combinations that we observed, only three observed transitions differed consistently from random patterns. Repeated pounding of the beehive was the most consistent transition observed between two elements, with more than 75% of observed transitions differing from randomized data. The cycle of inspecting the hive and gathering honey was also consistent in our observations of honey gathering.

Sequence Analysis

Tool behaviors described here differed in Shannon Weaver values (H_s) of first-order transitions (Kruskal-Wallis Test,

chi-square = 12.47; $df = 3$; $p = 0.006$). Leaf sponging was associated with the lowest H_s values (average = 0.35 ± 0.02), which indicates that patterns were defined by few elements with stable first-order transitions, in contrast to the other tool tasks which showed more variation in behavioral elements and their organization within a sequence (honey gathering = 0.45 ± 0.10 ; termite fishing, elevated = 0.56 ± 0.10 ; termite fishing, subterranean = 0.53 ± 0.05).

Discussion

We found significant differences in the composition and structural organization of different tool behaviors shown by the wild chimpanzees of the Goulougo Triangle. Not only do their tool behaviors vary in complexity, but the chimpanzees also employ different strategies to accomplish them. As expected, the tool-use behaviors were comprised of various elements necessary for tasks directed at different targets, but we also found that the sizes of element repertoires associated with each task were significantly different from each other. Viewed from the “repertoire counting” approach, this indicates that leaf sponging was a simpler task than puncturing at termite nests, which was associated with twice as many elements. However, we also found that a large number of elements could be shared between different tool-use tasks. Comparisons of the structure of these different tasks showed that the chimpanzees had the capacity to use tools in highly standardized sequential patterns (leaf sponging, termite fishing at elevated nests) and also in more flexible structural configurations (termite fishing at subterranean nests, honey gathering). Tree-structure analysis supported our finding that tool tasks differed in their complexity, and also that these chimpanzees showed flexibility in organizing them. Leaf sponging was depicted as the simplest tool task, consisting of a single relationship between tool and target. Multiple object relationships were shown in honey gathering and termite fishing at elevated and subterranean nests. Differences in the nesting of object relationships indicated that chimpanzees within this population had several strategies of multiple object use. In addition to showing that their tool behaviors varied in their degree of complexity, we found that they were capable of flexibly executing different tool-use strategies and generalizing object relationships across different contexts. Although further research is warranted, our conclusion is that the varying levels of task complexity

and flexibility in applying technological skills across different contexts demonstrates the intelligent use of tools by wild chimpanzees.

Examining Complexity in Chimpanzee Tool Behaviors

Systematic comparisons of the composition and structure of different chimpanzee tool tasks provided insights into differences that were not evident in our previous ethnographic descriptions of these behaviors (Sanz and Morgan 2007). Tool-use behaviors differed in the composition of element behaviors and sizes of specific tool-task repertoires. Within the context of unlimited choices, a selective and well-composed repertoire of behaviors associated with a particular task could indicate a chimpanzee’s degree of insight into it. However, small repertoires have also been associated with task simplicity. We found that leaf sponging had the smallest number of elements with seemingly invariant transitions. It should also be taken into consideration that this type of analysis may be sensitive to differences in defining behavioral elements which can artificially inflate or reduce levels of complexity and invalidate comparisons between studies. The relative simplicity of the leaf-sponging task is supported not only by the agreement between different measures of complexity, but also by previously published reports. It has been claimed that leaf sponging may not be a difficult tool use to innovate because it has been observed in almost all well-studied chimpanzee populations (Whiten et al. 1999, 2001) and similar behaviors have been invented by captive chimpanzees (Kitahara-Frisch and Norikoshi 1982). As shown by tree-structure analysis, this behavior consists of a single object relationship without alternative structural elements. Tonooka (2001) showed that tool use in water drinking was acquired at a relatively young age, but that social facilitation played a role in its acquisition. Juvenile chimpanzees showed more inclination to watch others during this tool behavior than did adults. There is also indication that some type of social facilitation may be responsible for the sudden increase in frequency of leaf sponging in the M group of chimpanzees at Mahale in Tanzania (Matsusaka et al. 2006). Together with analysis of the other tool tasks, these findings have prompted our current research on the relationship between task complexity and social learning.

Although repertoire sizes were larger in termite and honey-gathering contexts, we found that many of elements could be shared between the different tasks. Gener-

alization of elements across tool tasks could make learning of the tasks less cognitively demanding, but that depends on how the elements are executed within tool sequences. We found that the object relationships and element sequences in the fishing portions of the subterranean and elevated termite nest tasks were nearly identical, but that the necessity and timing of the incorporation of puncturing stick and perforating twig were extremely different. Flow diagrams of termite-gathering sequences at elevated and subterranean nests clearly illustrate the structural differences between these tool tasks (figure 11.4). Multiple tools are used in both tasks, but it is obligatory to use two tools in gathering termites only at subterranean nests. The entire length of a stout puncturing stick is inserted into the ground to create an access tunnel into the subterranean chambers of a termite nest, and then the fishing probe is used to extract the termites. Besides the obvious differences in form and function of the puncturing and perforating tools, the perforating twigs are used only occasionally to clear debris from an existing termite exit tunnel. Tree-structure analysis shows that these tasks have similar targets but involve different tools and relationships. We conclude that chimpanzees can apply termite fishing knowledge flexibly in different settings, and that they can implement these skills appropriately relative to other types of tools. Furthermore, the chimpanzees seemed to anticipate the different tasks by arriving at each nest with the appropriate tools. They often arrived at a subterranean nest with both the puncturing stick and the herbaceous fishing tools they would need. We have never observed them arriving at elevated nests with puncturing tools; rather they arrived only with fishing probes and then manufactured perforating twigs from nearby vegetation if needed.

Multiple tool use is relatively rare in nonhumans, which is another reason why the regular use of tool sets in the Goulougo is intriguing. We have observed chimpanzees using multiple tools to gather termites and open beehives to gather honey. Although tree-structure analysis shows that the depth of nodes may be similar to those in the termite-gathering tasks in this study and in the metatool use described by Matsuzawa (1996, 2001), the hierarchical structuring of object relationships in honey gathering differentiates it from the other tool-use tasks (see leaf sponging in figure 11.4a, and termite gathering in figures 11.4c and 11.4d). In contrast to the simultaneous use of multiple tools in metatool use by chimpanzees at Bossou, described by Matsuzawa (1996, 2001), the tool behaviors we observed

consisted of temporally distinct episodes of serial tool use. Although the types of object relationships varied between metatool use in nut cracking and multiple tool use in honey gathering, they had similar degrees of complexity, as evidenced by the depth of nodes produced in each case. The object relationships in the termite-gathering tasks involved the predictable use of certain tool sets in a particular context, whereas the use of tools in honey gathering seemed to be in response to the characteristics of a given bee hive. Honey gathering was also shown to be more flexible than the other tool tasks analyzed in this study, with a large element repertoire and few fixed transitions. A highly flexible tool-use strategy could be related to the highly variable physical characteristics of target beehives in the dense lowland forests of the Congo Basin. It is possible that ecological features have shaped the differences between the tool behaviors documented in this study, but direct comparisons of element repertoires, structural configurations of elements, and object relationships in different contexts may provide insight into the depth of chimpanzees' understanding in such situations.

Factors that Shape Complex Tool Use

There are several indications that technological skills similar to those described in this study exist in several chimpanzee populations in western equatorial Africa. Descriptions of tool sets used by chimpanzees to extract termites from their earthen nests have been reported from Gabon, the Republic of Congo, Cameroon, the Central African Republic, and Equatorial Guinea (Bermejo and Illera 1999; Deblauwe et al. 2006; Fay and Carroll 1994; McGrew and Rogers 1983; Muroyama 1991; Sabater Pi 1974; Suzuki et al. 1995). There is also evidence of multiple tool use in honey gathering from several sites in this region (Boesch et al. 2009; Bermejo and Illera 1999; Fay and Carroll 1994; Hicks et al. 2005). This raises the question of which specific factors could have shaped the broad and complex tool technology of these chimpanzees, and how those traditions are maintained.

Within this region of the Congo Basin we have found that there are ample ecological opportunities to use tools, and potential interspecific feeding competition that may force chimpanzees to adopt unique foraging niches. The Ndoki forests offer a relative abundance of ecological opportunities for tool use. Several species of *Macrotermes* build various types of nests, ranging from completely

subterranean nests to conspicuous towers. With a total of seven species of army ants, the assemblage of *Dorylus* in the Goulougo Triangle is the most diverse ever recorded at a chimpanzee study site (Sanz et al. 2009). Ants are harvested by chimpanzees at their bivouacs or while traveling through the forest. We have also documented the presence of at least six different bee species in the Goulougo study area, with honey gathering observed at the hives of African honeybees and three species of melipones. The presence of particular targets does not mean, however, that chimpanzees will use tools to exploit these food resources. Motivation and technological knowledge are also prerequisites. Chimpanzees reside in sympatry with western lowland gorillas (*Gorilla gorilla gorilla*) throughout much of western equatorial Africa. The high degree of dietary overlap reported between these apes at this site and several others (Morgan and Sanz 2006; Tutin and Fernandez 1985, 1993) could prompt chimpanzees to adopt innovative foraging strategies, such as tool use, that give them access to embedded food items that are not exploited as efficiently by gorillas. Gorilla densities reported from the Goulougo Triangle study area are some of the highest in this region (Morgan et al. 2006) and it is conceivable that the diverse and complex tool strategies of the chimpanzees who also inhabit that area provides a means of coping with interspecific feeding competition. At Bossou, chimpanzees were shown to use tools least frequently during periods of high fruit availability (Yamakoshi 1998). The influence of feeding competition on the frequency of chimpanzees' tool use at sites in central Africa could be assessed by comparing tool use over periods with differing degrees of dietary overlap between chimpanzees and gorillas.

Van Schaik and Pradhan (2003) have proposed a theoretical model for tool-use traditions in primates which suggests that the likelihood of an individual showing a particular tool behavior is dependent upon the probability of asocial acquisition, the probability of social learning, and the individual's opportunities for observational learning. The probability that a task is socially learned is depicted as the inverse probability of innovation, meaning that the task is acquired without social input. Asocial learning mechanisms involve individual discovery of novel information, invention of new behaviors, or elaboration on existing themes (Reader and Laland 2001). Such innovations may occur in social contexts, but they are produced without input from other individuals. Intuitively, task complexity should be inversely related to the likeli-

hood of individual invention. Preliminary analysis of social interactions that occurred during our tool sequences showed that more complex tool tasks were associated with increased attendance and facilitation. We found that more individuals were in proximity and attending to the tool user at subterranean termite nests than in other tool settings. Further, facilitation of the task by sharing of tools or targets was more common in the termite tool-use context than in leaf sponging or honey gathering.

If one is willing to accept the premise that some aspect of complex tool-use behavior is facilitated by social transmission of information, then the social networks within and between groups are also an important factor in the maintenance of these behaviors over time and space. Undisturbed social networks across several intact chimpanzee communities are likely to exist in the Congo Basin, which harbors some of the largest remaining tracts of intact forest in the world, in contrast to the devastating fragmentation of chimpanzee habitats in west Africa (Kormos et al. 2004) and the isolation of small chimpanzee populations in some areas of east Africa (Pusey et al. 2007). However, the conservation context of apes in the Congo Basin is rapidly changing with the advance of mechanized logging, mining, conversion to farmland, and human settlement (Tutin et al. 2005). Expanding human influence on wild orangutans and their behaviors prompted van Schaik (2001) to propose the fragile cultures hypothesis, which suggests that local extinction, hunting pressure, selective logging, and habitat loss affect the transmission of traditional behaviors among wild apes. It is likely that chimpanzee tool traditions would be vulnerable to similar disturbances, which underscores the importance of considering the rich behavioral diversity and social inheritance systems of our closest living relations when developing long-term conservation strategies to ensure their survival.

Implications and Future Directions

Our comparison of composition, structure, and hierarchical organization of object relationships in the tool-use behaviors of chimpanzees in the Goulougo Triangle demonstrates that there is much to be learned from the intricate complexity of these skilled behavior patterns (Byrne 2007). Most previous studies of chimpanzee tool use have defined a tool by a general description of its use, rather than analyzing the actual sequence of actions that involve its use. Our data set included repeated observa-

tions of “multiple-function” tools, with single tools having relationships with multiple targets and different functions in each of many contexts. It is also likely that recent research to identify the putative cultural variants within particular species may have masked important differences within and between populations by compiling and comparing general catalogues of behaviors (Whiten et al. 1999, 2001; Hohmann and Fruth 2003; van Schaik et al. 2003). Fascinating differences have been found in more specific treatments of some of these behaviors, however, such as the careful differentiation of leaf-folding from leaf-sponging techniques to drink water (Tonooka 2001) and locale-specific grooming patterns of wild chimpanzees (Nishida et al. 2004). Future research should be devoted to refining analysis methods for comparisons of behavior between populations or species (see chapter 13).

Several other types of research emerge from the ongoing study of chimpanzee tool technology in this population and others. Recent research has reported a significant relationship between laterality in tool manufacture and the design complexity of tools used by New Caledonian crows (Hunt et al. 2006). This would be a reasonable extension of the current study, which would also contribute to the discussion of population-wide handedness in wild chimpanzees (Lonsdorf and Hopkins 2005). Although it is not discussed in this study, we have found that chimpanzees exhibit a high degree of material selectivity for some types of tools (Sanz and Morgan 2007). Detailed investigations should be conducted to examine the basis of these raw material choices in different contexts, which may reveal new

insights into the cognitive abilities of chimpanzees in their natural habitats.

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Literature Cited

- Bermejo, M., and G. Illera. 1999. Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates* 40:619–27.
- Boesch, C., and H. Boesch. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatologica* 54:86–99.
- Boesch, C., and H. Boesch-Achermann. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford, Oxford University Press.
- Boesch, C., J. Head, and M. Robbins, M. 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution* 56:560–69.
- Byrne, R. W. 2003. Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society B* 358:529–36.
- . 2007. Culture in great apes: Using intricate complexity in feeding skills to trace the evolutionary origin of human technological prowess. *Philosophical Transactions of the Royal Society B* 362:577–85.
- Byrne, R. W., and J. M. E. Byrne. 1993. Complex leaf-gathering skills of mountain gorillas *Gorilla g. beringei*: Variability and standardization. *American Journal of Primatology* 31:241–61.
- Byrne, R. W., N. Corp, and J. M. E. Byrne. 2001. Estimating the complexity of animal behaviour: How mountain gorillas eat thistles. *Behaviour* 138:525–57.
- Corp, N., and R. W. Byrne. 2002. Leaf processing by wild chimpanzees: Physically defended leaves reveal complex manual skills. *Ethology* 108:673–96.
- De Waal, F. B. M. 2003. Social Syntax: The If-Then Structure of Social Problem Solving. In F. B. M. de Waal and P. L. Tyack, eds., *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*, 230–48. Cambridge, MA: Harvard University Press.
- Deblauwe, I., P. Guislain, J. Dupain, and L. van Elsacker. 2006. Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*)

- in the periphery of the Dja Biosphere Reserve, Southeast Cameroon. *American Journal of Primatology* 68:1191–96.
- Fay, J. M., and R. W. Carroll. 1994. Chimpanzee tool use for honey and termite extraction in central Africa. *American Journal of Primatology* 34:309–17.
- Fowler, A., and V. Sommer. 2007. Subsistence technology of Nigerian chimpanzees. *International Journal of Primatology* 28(5): 997–1023.
- Fragaszy, D., P. Izar, E. Visalberghi, E. B. Ottoni, and M. Gomes de Oliveira. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology* 64:359–66.
- Goodall, J. 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* 201:1264–66.
- Hicks, T. C., R. S. Fouts, and D. H. Fouts. 2005. Chimpanzee (*Pan troglodytes troglodytes*) tool use in the Ngotto Forest, Central African Republic. *American Journal of Primatology* 65:221–37.
- Hohmann, G., and B. Fruth. 2003. Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology* 44:563–71.
- Hunt, G. R. 1996. Manufacture and use of hook-tools by New Caledonian crows. *Nature* 379:249–51.
- Hunt, G. R., and R. D. Gray. 2003. Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society B* 270:867–74.
- Hunt, G. R., M. C. Corballis, and R. D. Gray. 2006. Design complexity and strength of laterality are correlated in New Caledonian crows' pandanus tool manufacture. *Proceedings of the Royal Society B* 273:1127–33.
- Inoue-Nakamura, N., and T. Matsuzawa. 1997. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 111:159–73.
- Izawa, I., and J. Itani. 1966. Chimpanzees in the Kasakati Basin, Tanganyika. 1. Ecological study of the rainy season. *Kyoto University African Studies* 1:73–156.
- Kajobe, R., and D. W. Roubik. 2006. Honey-making bee colony abundance and predation by apes and humans in a Uganda forest reserve. *Biotropica* 38(2): 210–18.
- Kitahara-Frisch, J., and K. Norikoshi. 1982. Spontaneous sponge-making in captive chimpanzees. *Journal of Human Evolution* 11:41–47.
- Kormos, R., C. Boesch, M. I. Bakarr, and T. M. Butynski. 2003. *West African Chimpanzees: Status and Conservation Action Plan*. Washington, DC: Conservation International.
- Lanjouw, A. 2002. Behavioural adaptations to water scarcity in Tongo chimpanzees. In C. Boesch, G. Hohmann and L. F. Marchant, eds., *Behavioural Diversity in Chimpanzees and Bonobos*, 52–60. Cambridge: Cambridge University Press.
- Lonsdorf, E. V., and W. D. Hopkins. 2005. Wild chimpanzees show population-level handedness for tool use. *Proceedings of the National Academy of Sciences* 102(35): 12634–38.
- Mangold 2006. INTERACT software, version 8.04. Arnstorf, Germany.
- Matsusaka, T., H. Nishie, M. Shimada, N. Kutsukake, K. Zamma, M. Nakamura, and T. Nishida. 2006. Tool-use for drinking water by immature chimpanzees of Mahale: Prevalence of an unessential behavior. *Primates* 47:113–22.
- Matsuzawa, T. 1996. Chimpanzee intelligence in nature and captivity: Isomorphism of symbol use and tool use. In W. C. McGrew, L. F. Marchant and T. Nishida, eds., *Great Ape Societies*. Cambridge: Cambridge University Press.
- . 2001. Primate foundations of human intelligence: A view of tool use in nonhuman primates and fossil hominids. In T. Matsuzawa, ed., *Primate Origins of Human Cognition and Behavior*, 3–25. Tokyo: Springer.
- McGrew, W. C. 1987. Tools to get food: The subsistants of Tasmanian Aborigines and Tanzanian chimpanzees compared. *Journal of Anthropological Research* 43:247–58.
- . 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew, W. C., L. F. Marchant, and K. D. Hunt. 2007. Etho-archaeology of manual laterality: Well digging by wild chimpanzees. *Folia Primatologica* 78:240–44.
- McGrew, W. C., and M. E. Rogers. 1983. Chimpanzees, tools, and termites: New record from Gabon. *American Journal of Primatology* 5:171–74.
- Morgan, D., and C. Sanz. 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goulougo Triangle, Republic of Congo. In G. Hohmann, M. Robbins, and C. Boesch, eds., *Primate Feeding Ecology in Apes and Other Primates: Ecological, Physiological, and Behavioural Aspects*, 97–122. Cambridge: Cambridge University Press.
- Morgan, D., C. Sanz, J. R. Onononga, and S. Strindberg. 2006. Ape abundance and habitat use in the Goulougo Triangle, Republic of Congo. *International Journal of Primatology* 27:147–79.
- Muroyama, Y. 1991. Chimpanzees' choice of prey between two sympatric species of *Macrotermes* in the Campo Animal Reserve. *Human Evolution* 6:143–51.
- Nishida, T., and M. Hiraiwa. 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution* 11:73–99.
- Nishida, T., J. C. Mitani, and D. P. Watts. 2004. Variable grooming behaviour in wild chimpanzees. *Folia Primatologica* 75:31–36.
- Oswalt, W. H. 1976. *An Anthropological Analysis of Food-Getting Technology*. New York: John Wiley.
- Parker, S. T., and K. R. Gibson. 1999. Object manipulation, tool use, and sensorimotor intelligence as feeding adaptations in *Cebus* monkeys and great apes. *Journal of Human Evolution* 6:623–41.
- Phillips, K. A. 1998. Tool use in wild capuchin monkeys (*Cebus albifrons trinitatis*). *American Journal of Primatology* 46:259–61.
- Pruett, J. D., and P. Bertolani. 2007. Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Current Biology* 17:11–6.
- Pusey, A.E., L. Pintea, M. Wilson, S. Kamenya, and J. Goodall. 2007. The contribution of long-term research at Gombe National Park to chimpanzee conservation. *Conservation Biology* 21:623–34.
- Reader, S. M., and K. N. Laland. 2001. Primate innovation: Sex, age and social rank differences. *International Journal of Primatology* 22:787–805.
- Sabater Pi, J. 1974. An elementary industry of the chimpanzees in the Okorobiko Mountains, Rio Muni (Republic of Equatorial Guinea), West Africa. *Primates* 15:351–64.
- Sambrook, T., and A. Whiten. 1997. On the nature of complexity in cognitive and behavioural science. *Theory and Psychology* 7:191–213.
- Sanz, C., J. Call, and D. Morgan. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biology Letters* 5:293–96.
- Sanz, C., and D. Morgan. 2007. Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *Journal of Human Evolution* 52(4): 420–33.
- . 2009. Flexible and persistent tool-using strategies in honey gathering by wild chimpanzees. *International Journal of Primatology* 30:411–27.
- Sanz, C., D. Morgan, and S. Gulick. 2004. New insights into chimpanzees, tools, and termites from the Congo basin. *American Naturalist* 164:567–81.
- Stanford, C. B., C. Gambaneza, J. B. Nkurunungi, and M. L. Goldsmith. 2000. Chimpanzees in Bwindi-impenetrable National Park, Uganda,

- use different tools to obtain different types of honey. *Primates* 4:337–41.
- Sugiyama, Y. 1985. The brush-stick of chimpanzees found in south-west Cameroon and their cultural characteristics. *Primates* 26:361–74.
- . 1995. Drinking tools of wild chimpanzees at Bossou. *American Journal of Primatology* 37:263–69.
- . 1997. Social tradition and the use of tool-composites by wild chimpanzees. *Evolutionary Anthropology* 6:23–27.
- Suzuki, S., S. Kuroda, and T. Nishihara. 1995. Tool-set for termite-fishing by chimpanzees in the Ndoki forest, Congo. *Behaviour* 132:219–34.
- Takeshita, H. 2001. Development of combinatory manipulation in chimpanzee infants (*Pan troglodytes*). *Animal Cognition* 4:335–45.
- Tomasello, M., and J. Call. 1997. *Primate Cognition*. Oxford, UK: Oxford University Press.
- Tonooka, R. 2001. Leaf-folding behavior for drinking water by wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. *Animal Cognition* 4:325–34.
- Tutin, C. E. G., and M. Fernandez. 1985. Foods consumed by sympatric populations of *Gorilla gorilla* and *Pan troglodytes* in Gabon: Some preliminary data. *International Journal of Primatology* 6:27–43.
- . 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lope Reserve, Gabon. *American Journal of Primatology* 30:195–211.
- Tutin, C. E. G., R. Ham, and D. Wrogemann. 1995. Tool-use by chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *Primates* 36(2): 181–92.
- Tutin, C. E. G., E. Stokes, C. Boesch, P. Walsh, D. Morgan, C. Sanz, S. Blake, and R. Kormos. 2005. *Regional Action Plan for the Conservation of Gorillas and Chimpanzees in Western Equatorial Africa*. Conservation International.
- Van Schaik, C. P. 2001. Fragility of traditions: The disturbance hypothesis for the loss of local traditions in orangutans. *International Journal of Primatology* 23:527–38.
- Van Schaik, C. P., M. Ancrenaz, G. Borgen, B. Galdikas, C. D. Knott, I. Singleton, A. Suzuki, S. S. Utami, and M. Merrill. 2003. Orangutan cultures and the evolution of material culture. *Science* 299:102–5.
- Van Schaik, C. P., R. O. Deaner, and M. Merrill. 1999. The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution* 36:719–41.
- Van Schaik, C. P., and G. R. Pradhan. 2003. A model for tool-use traditions in primates: Implications for the coevolution of culture and cognition. *Journal of Human Evolution* 44: 645–64.
- Waga, I. C. 2006. Spontaneous tool use by wild capuchin monkeys (*Cebus libidinosus*) in the Cerrado. *Folia Primatologica* 77:337–44.
- Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. Tutin, R. Wrangham, and C. Boesch. 1999. Cultures in chimpanzees. *Nature* 399:682–85.
- . 2001. Charting cultural variation in chimpanzees. *Behaviour* 138:1481–1516.
- Yamakoshi, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology* 106:283–95.
- . 2001. Ecology of tool use in wild chimpanzees: Toward reconstruction of early hominid evolution. In T. Matsuzawa, ed., *Primate Origins of Human Cognition and Behavior*, 537–56. Tokyo: Springer.
- Yamakoshi, G., and M. Myowa-Yamakoshi. 2004. New observations of ant-dipping techniques in wild chimpanzees at Bossou, Guinea. *Primates* 45:25–32.