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ORIGINAL ARTICLE

Rikako Tonooka

Leaf-folding behavior for drinking water by wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea

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Abstract The use of leaves for drinking water by wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea, was observed intensively. The natural hollow of a tree, used by chimpanzees, was filled up with fresh water every morning. Seventy episodes of leaf-using behavior by 14 chimpanzees were directly observed and video-recorded. The chimpanzees at Bossou most frequently (70.3%) used a particular kind of leaf, *Hybophrynium braunianum* as tool material. The chimpanzees folded one or more leaves in the mouth. This technique, "leaf folding", was observed more frequently (57.9 %) than "leaf sponge" or "leaf spoon". Chimpanzees began to perform this behavior at about 2.5 years old. Infant chimpanzees showed more frequent observations of others (especially their mothers) using leaves before trying to drink water with leaves. Both observation and trial and error might be necessary for the acquisition of this tool-use behavior.

Key words Tool use · Water drinking · Leaf selection · Technique · Wild chimpanzees (*Pan troglodytes verus*)

Introduction

The ability to use tools has been considered one of the major characteristics of the human species. However, tool-using behavior is not restricted to humans or even to primates (Beck 1980). Tool use in nonhuman animals is of great interest to comparative psychologists for many reasons. First, tool use requires a highly flexible ability in object manipulation and object combination (Fragaszy and Adams-Curtis 1991; Torigoe 1985; Vauclair 1984). Second, cognitive abilities, such as understanding of causal relationships, might be required to use tools (Limongelli et al. 1995; Nagell et al. 1993; Tomasello et al. 1987; Visalberghi and Limongelli 1994). A third reason is the learning processes required for the acquisition of tool use. If a specific tool-using behavior is acquired, how does the animal learn it? In other words, what kinds of learning processes are involved in the acquisition of novel tool use? Recent studies of tool-use behavior in captive nonhuman primates mainly focus on this third question (Kitahara-Frisch and Norikoshi 1982; Nagell et al. 1993; Sumita et al. 1985; Tomasello et al. 1987).

Nonhuman primates, especially chimpanzees, are particularly suitable subjects for this topic. They show various and complex types of tool-using behavior in their natural habitat (Beck 1980; Boesch and Boesch 1990; Goodall 1986; McGrew 1992), such as ant dipping, termite fishing, nut cracking, honey dipping, drinking water with leaves, and so on. Some researchers have also argued that individual communities of chimpanzees have their own "tradition" in tool use (Matsuzawa and Yamakoshi 1996; McGrew 1992). For example, chimpanzees at Bossou in West Africa crack oil-palm nuts with stone hammers using one hand (Sugiyama and Koman 1979; Matsuzawa 1994), whereas chimpanzees at Taï Forest in Côte d'Ivore, 230 km away from Bossou, crack five species of nuts mainly with wooden hammers using both hands (Boesch and Boesch 1983). Chimpanzees in the Mahale Mountains in East Africa have never been observed using tools to crack nuts (see Whiten et al. 1999). There is, however, still a controversy about "cultural transmission" (e.g., Fragaszy and Visalberghi 1996; Heyes and Galef 1996; Tomasello 1996; Tomasello et al. 1993; Visalberghi 1990), and little is known about what learning processes may contribute to these regional population level variations.

In order to discuss the "tradition" of tool-using behavior, we need to accumulate precise and quantitative descriptions of community-specific tool-using behaviors

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R. Tonooka (✉)
Department of Behavioral and Brain Sciences,
Primate Research Institute, Kyoto University,
Kanrin, Inuyama, Aichi 484-8506, Japan
e-mail: tono-p@ma2.justnet.ne.jp,
Tel.: +81-568-616873, Fax: +81-568-616873

and clarify the differences among communities. In this study, I focused on water drinking with leaves. Wild chimpanzees often drink rainwater from the hollows of trees using leaves as tools, as reported for several chimpanzee populations: Gombe, Tanzania (Goodall 1964, 1968, 1986; McGrew 1977), Mahale, Tanzania (Nishida 1990), Budongo, Uganda (Quiatt and Kiwede 1994), Tongo, Zaire (see Wrangham 1992), Kibale, Uganda (Ghiglieri 1984; Wrangham 1992), Taï, Ivory Coast (Boesch and Boesch 1990) and Bossou, Guinea (Sugiyama 1993, 1995a; Tonooka et al. 1994).

There have been, however, only a few reports describing the details of this type of leaf use (Goodall 1968; McGrew 1977; Sugiyama 1989a). This may be due to the rare occurrence of the behavior and the difficulties of direct, close observations in the natural habitat. Among these reports, Goodall (1968) set up a water bowl at the feeding area of Gombe, where chimpanzees could drink water from a natural stream, in order to observe leaf-using behavior in more detail. She observed that eight chimpanzees drank water with leaf sponges from this bowl, although they could reach the water with their hands.

There have also been only a few detailed descriptions of the techniques and the materials used. Leaf-using behavior is classified into two major types with regard to the technique used. One is called "leaf sponge" (Goodall 1968; McGrew 1977, 1992), where chimpanzees crumple leaves in their mouth, soak them in a tree hollow with their hands, and suck the water from them. The other type is "leaf spoon" (Goodall 1968; McGrew 1977; Sugiyama 1995a), where they use leaves like a spoon, without crumpling them up, to scoop out the water. With regard to materials, Goodall (1968) reported that Gombe chimpanzees used five species of leaves for drinking, three of which were also food items for them. McGrew (1977) observed 23 episodes of leaf sponging by 16 chimpanzees at Gombe, and reported that they showed no preference for tool material. He also reported that chimpanzees did not move more than 2 m from the water source to obtain leaves.

Recently, leaf-using behavior for drinking was described in detail at Bossou (Sugiyama 1995a; Tonooka et al. 1994). Sugiyama (1995a) analyzed 25 episodes of leaf use for drinking collected from over 17 years of field observations. He noted that chimpanzees showed a tendency to use a few kinds of soft, hairless leaves. Tonooka et al. (1994) set up a container in the ground and filled it with water at the outdoor laboratory for detailed observations of nut-cracking behavior at Bossou (Fushimi et al. 1991; Matsuzawa 1994; Sakura and Matsuzawa 1991). Tonooka et al. (1994) preliminarily reported that three chimpanzees (one adult and two adolescent males) drank water from this container using leaves. They found a new technique of leaf use for drinking which is called "leaf folding". The chimpanzees folded leaves at about 3-cm intervals while stuffing them into the mouth. The resulting folds resembled those of the side ribs of a bellows or of Japanese *origami* (paper folding). The leaves were soaked in the container, and the water was sucked from the leaf or leaves when they were removed. Although there were various plants with leaves present around the container, chimpanzees moved about 5 m away from the site to obtain leaves from specific plants. Four out of five leaves were from the same species, *Hybophrynium braunianum*. In addition, 23 sets of leaves used for drinking water were found around the base of a tree with a big hole found in their home range. A total of 28 sets of leaves were identified and 75% of them were from *H. braunianum*. These preliminary observations suggest that Bossou chimpanzees prefer the leaves of a particular species for use as a water-drinking tool.

The preliminary report of Tonooka et al. (1994) suggests that the leaf-using behavior of Bossou chimpanzees is community-specific in various aspects such as leaf selectivity and technique. To investigate details of this leaf-using behavior further, I conducted a "field experiment". That is, I selected a tree with a big hollow that had been used by chimpanzees to get rainwater in order to observe multiple episodes of this behavior, and supplied measured amounts of water. The aims of this study were to find out (1) what kind of tools the chimpanzees of Bossou use to get water from the tree hollow, (2) what kind of materials (leaves) do they use, and (3) how do chimpanzees drink water with the tool. In addition, I also describe and discuss differences in drinking behavior between age classes, especially infants and older individuals.

Methods

Subjects

The subjects were a group of wild chimpanzees (*Pan troglodytes verus* Schwarz, 1934) at Bossou, in the southeastern corner of the Republic of Guinea, West Africa. The ecology and behavior of this group have been studied by Y. Sugiyama and his colleagues since 1976 (Sugiyama 1981, 1989a, 1989b, 1994a, 1994b; Sugiyama and Koman 1979). The group's core area is estimated to be about 5–6 km^2 and covered with primary and open secondary forests. At the time of this study, the group consisted of 18 individuals (Table 1). Their ages ranged from 2 years old to full adults. They were divided into four age classes (Goodall 1986; Sugiyama 1994b): young infants (under 3 years old), old infants (3–4 years old), adolescents (8–11 years old), and adults (12 and more years old). There were no juveniles (5–7 years old) in this period. At the same period as this study, 2 kg of oil-palm nuts (*Elaeis guineensis*) per day were supplied to the chimpanzees at a different area for observation of nut-cracking behavior (Inoue-Nakamura and Matsuzawa 1997).

Procedure

The present study was conducted for 33 days from December 1994 to January 1995. In this period, the dry season has just begun in Bossou, so that water is becoming scarce in the habitat of chimpanzees. A tree (*Aningeria robusta*) with a big hollow, located in the core area of the group, was selected for this study. This tree was located halfway up the mountain and near the pathway which chimpanzees often used. Chimpanzees have frequently been observed to utilize this tree for drinking water (Sugiyama 1995a). It was about 20 m high and about 2 m diameter at breast height. The hollow of the tree was 70 cm above the ground and 43 cm in depth. The opening was elliptical in shape and about 940 cm^2 (35 cm× 27 cm). Chimpanzees could drink water by using their hands but not directly by mouth.

Table 1 Members of the Bossou unit group during the present study and summary of results

Age class	Name	Age	Sex	Number of episodes	Duration per episode (min)	Drinking actions per episode	Drinking actions per min	Leaf selectivity Frequency (%)			Technique Frequency (%)		
								H.b.[b]	Other	UID[c)]	Folding	Sponge	UID[d])
Young infants	Julu	1	F	0	–	–	–	–	–	–	–	–	–
	Nto	1.5	M	0	–	–	–	–	–	–	–	–	–
	Poni	2	M	0	–	–	–	–	–	–	–	–	–
Old infants	Yolo	3	M	10	5.4	32.3	6	8 (53.3)	7 (46.7)	0 (0)	1 (6.7)	8 (53.3)	6 (40.0)
	Fotayu	3.5	F	4	2.2	9.5	4.3	4 (80.0)	1 (20.0)	0 (0)	3 (60.0)	0 (0)	2 (40.0)
	Vuavua	3.5	F	2	3.7	12.5	3.4	1 (33.3)	2 (66.7)	0 (0)	2 (66.7)	0 (0)	1 (33.3)
Adolescents	Vui	8	M	8	1.7	23.8	14.1	9 (75.0)	1 (8.3)	2 (16.7)	8 (66.7)	2 (16.7)	2 (16.7)
	Pili	8.5	F	3	1.9	4.3	2.2	3 (75.0)	1 (25.0)	0 (0)	1 (25.0)	0 (0)	3 (75.0)
	Na	9	M	7	3.3	38.6	11.8	11 (78.6)	3 (21.4)	0 (0)	11 (78.6)	0 (0)	3 (21.4)
Adults	Foaf	14	M	2	2.1	27.5	13.1	2 (100)	0 (0)	0 (0)	2 (100.)	0 (0)	0 (0)
	Pama	Ad[a]	F	0	–	–	–	–	–	–	–	–	–
	Yo	Ad	F	9	6.8	92.9	13.8	9 (90.0)	0 (0)	1 (10.0)	9 (90.0)	0 (0)	1 (10.0)
	Velu	Ad	F	2	3.7	41.5	11.4	2 (50.0)	1 (25.0)	1 (25.0)	3 (75.0)	0 (0)	1 (25.0)
	Jire	Ad	F	5	1.5	9.2	6	1 (20.0)	4 (80.0)	0 (0)	1 (20.0)	0 (0)	4 (80.0)
	Fana	Ad	F	4	1.2	13.8	11.5	6 (85.7)	1 (14.3)	0 (0)	6 (85.7)	0 (0)	1 (14.3)
	Tua	Ad	M	9	2.4	31.6	13.2	13 (92.9)	1 (7.1)	0 (0)	12 (85.7)	0 (0)	2 (14.3)
	Nina	Ad	F	1	1.5	14	9.3	1 (100)	0 (0)	0 (0)	0 (0)	0 (0)	1 (100)
	Kai	Ad	F	4	1.8	20.5	11.4	2 (50.0)	1 (25.0)	1 (25.0)	2 (50.0)	1 (25.0)	1 (25.0)

[a]*Ad* exact age is unknown but estimated as full adult
[b]*Hybophrynium braunianum*
[c]Unidentifiable species of leaves
[d]Unidentifiable technique

Table 2 Species of plants found around the hollow within 3 m

Scientific name	Distance (m) from the hollow[a]	Amount of leaves[b]	Number of leaf sets used as tool
Blighia sapida	0.6	1	6
Aningueria robusta	0.8	2	6
Hybophrynium braunianum	1.0	3	71
Mareya spicata	1.0	2	1
Myrianthus serratus	1.0	1	0
Olyra latifolia	1.0	2	0
Piper guineenses	1.1	3	0
Carapa procera	1.2	2	1
Fougerea deter	1.4	1	0
Alchornea cordifolia	1.5	2	0
Blighia unijugata	1.6	2	0
Napoleona vogelii	1.7	3	0
Thaumatococcus daniellii	2	3	5
Peptadinia africana	2.2	2	2
Millettia zechiana	2.3	2	0
Ficus varifolia	2.6	3	0

[a]The distance was measured from the hollow to a nearest tree or stem of each species
[b]The amount of leaves was estimated using 3 levels by visual inspection: *1* scarce, *2* medium, *3* abundant

Table 2 shows the species of plants found around the tree: 16 species were identified within 3 m of the hollow opening. Since there were several plants of the same species, the distance of each species was defined as the distance from the hollow to the nearest one of that species. The amount of leaves was estimated by visual inspection by the three observers (the author, a local guide, and a botanist) and classified into three levels.

When the chimpanzees appeared (within 6 m), all behaviors were directly observed and video-recorded. A video camera (SONY CCD-TR1000) was set up 8 m from the tree and covered with a grass blind (1.5 m high, 2.5 m long). The observer stayed behind the blind from 0630 to 1730 hours. The hollow was filled up with fresh water every morning (at 0630 hours). The volume of water used to fill up the hollow was measured. I also estimated the amount of evaporation of water, by measuring the amount of water needed to refill the hollow in the morning after days on which chimpanzees did not visit. Based on these values, the mean amount of the water consumed by the chimpanzees was estimated. During the first 10 days of the study period, small amounts of banana (20 pieces per day) were additionally provided around the tree to attract chimpanzees. After this period no food was provided.

Focal animal sampling was applied to the video-recorded data. A *party* is defined as the group of chimpanzee(s) who appear around the tree regardless of the occurrence of drinking behavior. An *episode* is defined as a sequence of drinking behavior by an individual in the party. An episode started when chimpanzee(s) appeared near the tree and then drank water with leaves, and ended when the individual(s) left. Episodes were counted for each individual. For example, when four chimpanzees appeared around the tree together and none of them drank water, it was counted as one party, but no episode. When four chimpanzees appeared around the tree, and three of them drank water from the hollow, it was counted as one party and three episodes. The behavior of young and old infants with their mothers, showing no drinking but observing their mother's or the other's drinking, was also analyzed.

Results

Chimpanzees' visits to the study site

On 25 out of 33 days of the study period, 65 parties of chimpanzees appeared around the tree. On 19 out of the 25 days, in 33 parties out of 65 (50.8%), chimpanzees drank water using leaves. In total, 70 episodes involving 14 chimpanzees were observed. Nearly all of the members of this group except one adult female (Pama) and three young infants (Julu, Nto, Poni), used leaves for drinking water. Among 70 episodes, 26 occurred in the morning (0630–1159 hours), and the other 44 episodes occurred in the afternoon (1200–1730 hours). There were two peak times of occurrence of drinking: 0800–0900 hours (14 episodes) and 1500–1600 hours (19 episodes). Only 3 episodes out of 70 were not video-recorded. The total duration of this tool-using behavior observed was 227 min. The shortest episode lasted for less than 1 min, and the longest for 12 min.

Sequence of drinking behavior

Figure 1 (see also electronic supplementary material, ESM, S1) shows a typical sequence of drinking behavior by an adult chimpanzee named Tua. This episode occurred on the 13th day from the beginning of this study. Tua came around the tree alone and stopped and looked at the video camera for a second. Then he went to the tree, saw the water in the hollow and changed his posture to a bipedal one (Fig. 1a). He looked around, walked to a stem of *H. braunianum*, located 1 m away from the hollow, and tore two leaves from the plant with his right hand. Then he turned back to the tree with the leaves. He stuffed the leaves into his mouth without chewing them (Fig. 1b), and took them out again with the right hand. Using these leaves he started drinking water by soaking them in the hollow (Fig. 1c), picking them up, and sucking water from them (Fig. 1d) without moving his jaws. Again, he took the leaves out of his mouth, repeating these drinking actions three times. Suddenly he reached out again to *H. braunianum*, tore off a leaf, and added the leaf, without dropping it, to the first ones. He repeated drinking actions 19 more times, and then removed the leaves from his mouth and

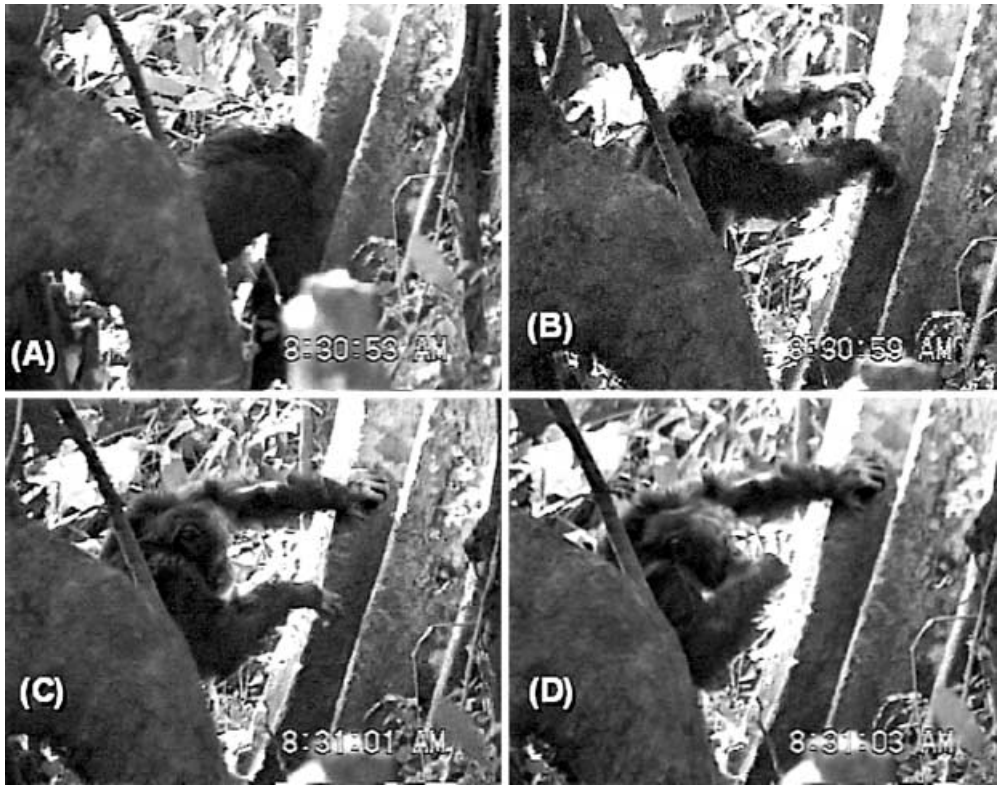

Fig. 1a–d Video-captured images of a typical sequence of leaf-folding behavior by an adult male (Tua). **a** Seeing water in the hollow. **b** Stuffing the leaf into his mouth. **c** Soaking the leaf in the hollow. **d** Sucking water from the leaf (for a color version of this figure, see electronic supplementary material, ESM, S1)

left the tree. The total duration of this episode was approximately 2 min.

As illustrated in this example, each episode consisted of the following behavioral components: (1) appearing near the tree (IN), (2) seeing water in the hollow (SEE), (3) seeing another individual drinking (OTHER), or (4) seeing their mother drinking (MOTHER), (5) tearing a leaf or leaves from a branch by hand or mouth (TEAR), (6) stuffing a leaf or leaves into the mouth (STUFF), (7) chewing a leaf or leaves repeatedly in the mouth (CHEW), (8) taking a leaf or leaves out of the mouth and holding it between index and middle fingers (TAKE OUT), (9) soaking a leaf or leaves in water in the hollow (SOAK), (10) picking up a leaf or leaves from the hollow (PICK UP), (11) sucking water from a leaf or leaves (SUCK), (12) dropping a leaf or leaves on the ground or in the tree hollow (DROP), and (13) going away from the tree (OUT). These components can be classified into three sub-categories: *observation* (2, 3, and 4), *tool making* (5, 6, and 7) and *drinking actions* (8, 9, 10, 11, and 12, see also Fig. 4).

In each episode, chimpanzees drank 26.6 times on average (range 1–123). In each drinking action, they sucked-up approximately 10 ml of water (based on the measurement of how much water was consumed by a party). A chimpanzee was estimated to drink on average about 266 ml in each episode.

Chimpanzees often tore off several leaves at a time (1.5 on average, range 1–4) and stuffed them into their mouths all at once. Furthermore, in 26% of the total episodes, partway through they added more leaves (1.2 on average) and continued drinking. In 17% of the total episodes, chimpanzees changed to new leaves in the course of an episode.

Leaf selectivity

After chimpanzees had left, the leaves they used were collected and pictures were taken. From visual inspection of the leaves, the pictures, and video-recordings, species of leaves and the techniques used were identified and classified. When techniques were difficult to identify, they were counted as *unidentifiable*. I collected 85 sets of leaves used by chimpanzees directly after they left and identified them by species, and identified an additional 15 sets from video-recordings. The chimpanzees showed high selectivity in leaves. Among the total of 100 sets of leaves, 71 sets were from *H. braunianum* (76.3% excluding unidentifiable leaves), 6 were *Blighia sapida* (6.5%), and 6 were *A. robusta* (6.5%). Figure 2 also shows leaf selectivity averaged for each individual: *H. braunianum* (70.3%) was used more frequently than the other species (24.3%), showing a significant difference (two-tailed paired-comparison *t*-test; t_{13}=3.543, P<0.01). A leaf of *H. braunianum* is flexible and hairless, larger than the other leaves, and is elliptical in shape. The mean size of *H. braunianum* leaves used was 10 cm (±2 cm SD) by 20 cm (±6 cm) (n=47, Fig. 3). The mean size of *B. sapida* was 6.0 cm (±2 cm) by 13.5 cm (±6 cm) (n=19) and of *A. robusta* was 6.0 cm (±1.5 cm) by 16.3 cm (±4 cm) (n=15).

In five episodes, during the later part of the study, adult females appeared around the tree with leaves already in

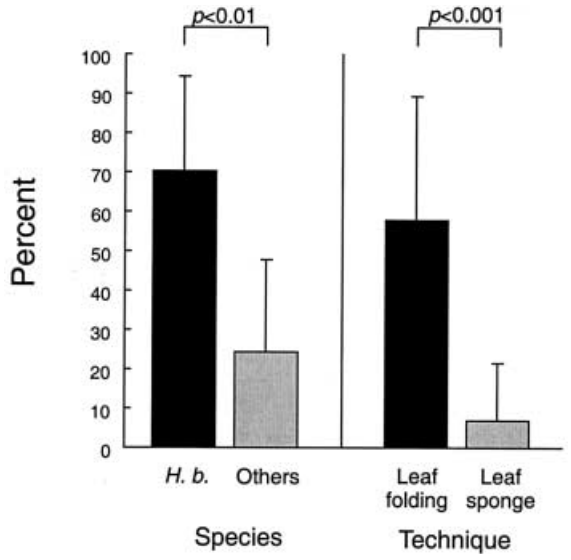

Fig. 2 Percentages (+SD) of leaf selectivity (*left*) and techniques (*right*), averaged for each individual (*H.b. Hybophrynium brauniunum*)

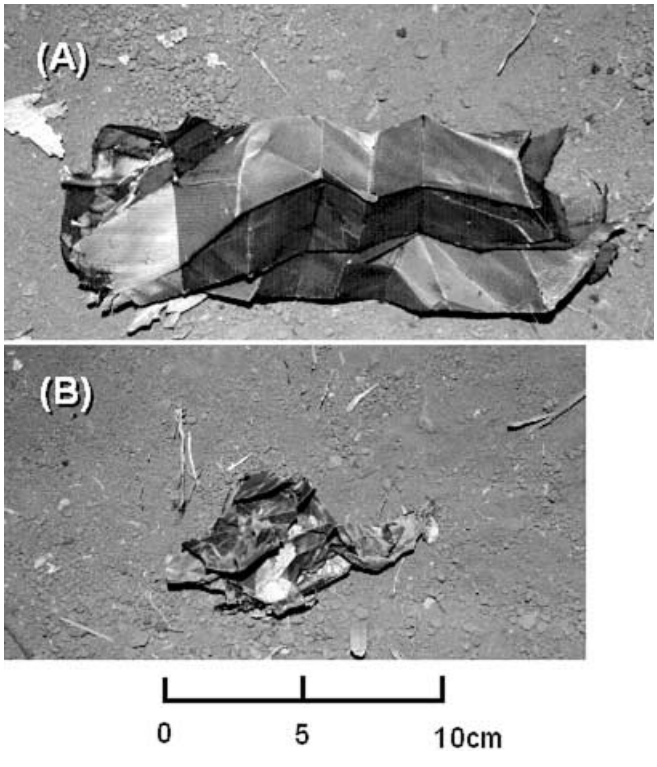

Fig. 3a, b Two examples of leaf-using techniques. **a** Leaf folding. **b** Leaf sponge. Both leaves are from *H. brauniunum* (for a color version of this figure, see ESM, S2)

their mouths (Kai, once, Jire, once and Yo, three times). In this period, the *H. braunianum* leaves nearest the hollow became scarce because of their intensive utilization by chimpanzees. Consequently, this behavior seemed "anticipatory". This was never observed in the other individuals. The leaves used in two of these five episodes were identified as *H. braunianum*, while the others were unidentifiable.

Leaf folding

Based on the collected leaves and detailed analyses of the chimpanzees' behavior (see Fig. 4), techniques used for drinking were classified into three types. When an adolescent or adult chimpanzee stuffed a leaf into its mouth, it moved its jaws two to four times. It was, however, very rare for them to chew the leaf after stuffing it into the mouth. As a result, these leaves were not crumpled like sponges but were neatly folded at about 3-cm intervals. Such a technique has never been reported previously for other groups of wild chimpanzees. This technique was named *leaf folding* (Tonooka et al. 1994). Interestingly, however, in its outcome this technique somewhat resembles the technique used by chimpanzees in leaf-swallowing for the purpose of self-medication, observed in numerous populations across Africa (Huffman 1997). In contrast, a *leaf sponge* was defined as leaves fully crumpled up. Figure 3 shows examples of leaf folding (Fig. 3a) and leaf sponges (Fig. 3b; see also ESM, S2). As shown in Fig. 2, leaf folding was more frequently observed (57.9% averaged for each individual) than leaf sponge (6.8%; t_{13}=4.598, P<0.001). A *leaf spoon*, defined as leaves used as a scoop without folding or crumpling, was only used by Vuavua (3.5 years old). She used this leaf spoon only during one drinking action, and then put it in her mouth to make a sponge.

Age differences

Table 3 summarizes the comparisons of various aspects of leaf-using behavior between old infants (n=3) who showed leaf-using behavior, and adolescents and adults combined (n=11). These tables also show the results of two-tailed t-tests. Young infants (1–2 years old) never showed leaf-using behavior (see Table 1). Since adolescents and adults showed the same patterns for these variables, these two age classes were combined for the subsequent analyses.

For drinking behavior, old infants showed fewer drinking actions per episode than adolescents/adults, but this difference was not statistically significant because of the large variance for the adolescents/adults. On the other hand, infants showed significantly slower actions than adolescents/adults. Old infants also showed less leaf selectivity and less leaf-folding behavior than adolescents/adults. However, again, these differences were not statistically significant.

Old infants and adolescents/adults showed some critical differences in behavioral sequences of drinking behavior. Figure 4 shows the flow of behavioral components in old infants (A) and adolescents/adults (B). Arrows indicate the relative frequencies of transitions of components per episode averaged for each individual. Old infants always started drinking after or while their mothers did. They first carefully observed the leaf-using behavior of their mothers or other adults. Mean occurrence of observation of others' behavior (excluding mothers) per single episode for each individual was 0.95 for old infants and

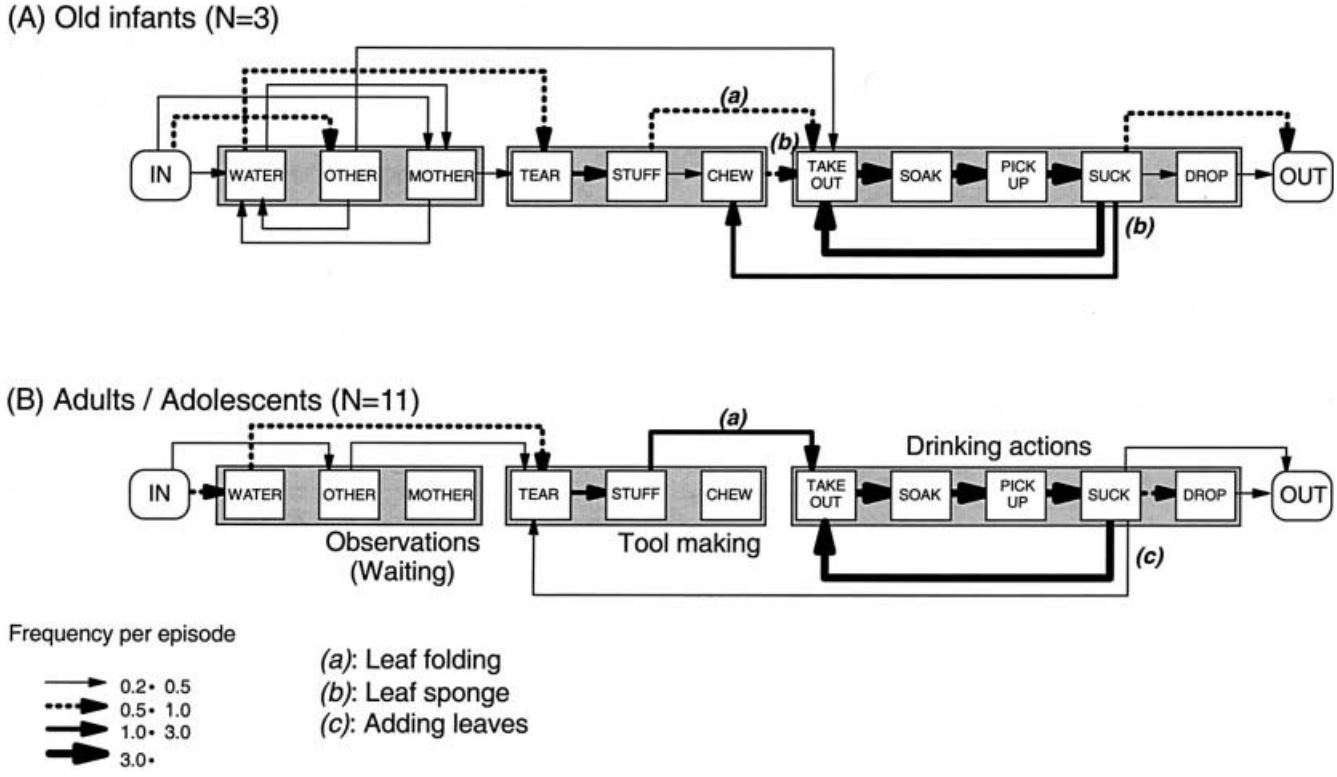

Fig. 4 Flow of behavioral components in **a** old infants, and **b** adults/adolescents. *Arrows* indicate relative frequencies of transition of each component (*a* leaf folding, *b* leaf sponge, *c* adding leaves)

0.36 for adolescents/adults, showing a significant difference (Table 3). Observing mother's behavior occurred 0.73 times per episode for old infants and 0.04 times per episode for adolescents/adults (note that data from individuals who had no mothers in the group were excluded). Note that young infants who came with their mothers observed closely the behavior of their mother as well as old infants, although they did not show leaf-using behavior.

In some cases, old infants did not make tools by themselves but utilized the tools made by others, especially by their mothers. In three episodes, two of the 3-year-old infants (Fotayu and Vuavua) took the leaves from their mother's hand while she was drinking. The infants used these leaves to dip into the water. Their mothers tore off new leaves. In another episode, Fotayu used the leaves which someone else had used and dropped in the water of the hollow.

As shown in Fig. 4 and Table 3, old infants chewed leaves several times after stuffing them into the mouth and frequently showed interruptions of drinking actions while chewing the leaves in their mouth (*b* in Fig. 4). This chewing behavior might result in a leaf sponge, although there was no significant difference in the frequency of leaf sponging between infants and adolescents/adults (17.8% for infants vs. 3.8% for adolescents/adults). This chewing behavior was observed significantly more in old infants than adolescents/adults (see Table 3).

There was no difference in the number of leaves used for drinking between age classes. However, adolescents and adults often added leaves during drinking actions (0.33 times per single episode, *c* in Fig. 4), while old infants showed this behavior less frequently (0.03). This difference was significant (see Table 3).

Discussion

This field study revealed that most of the group members, 3 years or older at Bossou used leaves for drinking water while young infants under 3 years old did not. After the present observations, one adult chimpanzee, Pama, who had not performed drinking in this observation period, was observed to drink water with leaves (T. Matsuzawa, personal communication). T. Matsuzawa also found that three chimpanzees (Julu, Nto and Poni) started to use leaves for drinking after they reached 2.5 years of age. It can be concluded that all members of the Bossou group over 2.5 years old can drink water with leaves, and that leaf-using behavior is habitual among Bossou chimpanzees. It is also suggested that there might be a lower age limit for the acquisition of this tool use at around 2.5 years old. This corresponds to the observations of Gombe chimpanzees (Goodall 1968). It is almost 1 year earlier than the appearance of nut-cracking behavior that requires the use of a set of stones as tools (Inoue-Nakamura and Matsuzawa 1997; Inoue-Nakamura et al. 1996). Compared to nut-cracking behavior, leaf-folding behavior is easier to acquire because of its relative simplicity, that is, a small number of objects are involved

Table 3 Comparisons of various aspects of leaf-using behavior between age classes

Age classes	Mean duration of episode	Number of drinking actions		Leaf selectivity (%)		Technique (%)		No. of leaves per episode	Adding leaves per episode	Chewing per episode	Observations (per episode)	
		Per episode	Per min.	*H.b.*	Other species	Folding	Sponge				Mother[b]	Others
Infants (n=3)	3.8 (1.31)[a]	18.1 (10.1)	4.6 (1.1)	55.6 (19.1)	44.4 (19.1)	44.4 (26.9)	17.8 (25.1)	1.38 (0.25)	0.03 (0.05)	1.03 (1.13)	0.73 (0.33)	0.95 (0.61)
Adolescents/ adults (n=11)	2.5 (1.53)	28.9 (23.2)	10.7 (3.5)	74.3 (23.7)	18.7 (21.7)	61.5 (31.5)	3.8 (8.2)	1.56 (0.38)	0.33 (0.33)	0.01 (0.04)	0.04 (0.06)	0.36 (0.21)
Two-tailed t-test: t_{12}	1.175	0.728	2.803	1.167	1.723	0.793	1.448	0.724	2.658	2.779		2.472
P	0.263	0.481	*0.016*	0.266	0.110	0.443	0.173	0.483	*0.021*	*0.017*	–	*0.029*

[a]Values in parentheses show SDs across subjects
[b]Data from individuals who had no mothers in the group were excluded

(Matsuzawa 1994, 1996). This hierarchical simplicity might result in the difference in emergence between these two tool-using behaviors. Inoue-Nakamura and Matsuzawa (1997) suggested that "emulation" (Tomasello et al. 1987) might be involved in the acquisition of tool-using behavior. Emulation requires the ability to understand cause-effect relationships. The hierarchical simplicity of leaf-using behavior may lead to an easier understanding of the cause-effect relationship and result in the faster acquisition of leaf-using behavior compared to nut-cracking behavior. Bossou chimpanzees use various kinds of tools (Hirata et al. 1998; Inoue-Nakamura and Matsuzawa 1997; Matsuzawa 1994, 1996; Matsuzawa et al. 2001; Sugiyama 1994a, 1995a, 1995b; Sugiyama and Koman 1979; Yamakoshi and Sugiyama 1995). Comparisons of development across these tool-using behaviors will give us further suggestions about the relationship between understanding of cause-effect relationships and the hierarchical structure of tool-using behavior.

In addition, old infants sometimes took their mothers' leaves and used them. This indicates that they not only observed adults but also practised the behavior by themselves using their mothers' leaves. McGrew (1977) also noted that an infant chimpanzee drank water from the leaves dropped by the mother. This kind of behavior was also observed in infants' nut-cracking behavior (Inoue-Nakamura and Matsuzawa 1997). Furthermore, Tonooka et al. (1997) found that adult captive chimpanzees in the tool-using experiment used leaves that others had used and dropped around the apparatus. They note that both observation and self practice are prerequisites for acquiring novel tool use even in adult captive chimpanzees (see also Hirata and Morimura 2000). It is plausible that these two factors also affect developmental changes in tool-using behavior in the wild chimpanzees (Inoue-Nakamura and Matsuzawa 1997).

Chimpanzees at Bossou selected a particular kind of leaves for drinking, namely *H. braunianum*. In this study, 70.3% of the leaves used were *H. braunianum*. Sugiyama (1995a) noted that chimpanzees search for leaves farther than 2 m away from the water site, supporting their preference for a certain species of leaves as tool material. Boesch (1991) also reported that chimpanzees of the Taï forest used wadges of a particular kind of fruit for drinking water at a water puddle. At Gombe, on the contrary, chimpanzees seem to show no selectivity of leaves as materials for the drinking tool (McGrew 1977). These results from the three different habitats imply local traditions for selecting tool materials (McGrew 1992; Sugiyama 1993).

Why do Bossou chimpanzees preferentially select *H. brauniunum*? Sugiyama (1995a) noted that the majority of leaves used for drinking water belonged to two species *H. brauniunum* and *Carapa procera*. Both leaves have the same characteristics: they are flexible, large, and hairless. In Y. Sugiyama's observation, the leaves of *C. procera* were used when the chimpanzees drank water in the *Carapa* trees. In the present study, however, chimpanzees used only one set of leaves of *C. procera*, although the distance between the nearest *C. procera* tree and the hol-

low was only 1.2 m and was equal to that of *H. brauniianum*. One of the differences between the two species is leaf size. As shown in the Results, leaves of *H. brauniiunum* (10 cm wide, 20 cm long) are a little wider than those of *C. procera* (7 cm wide, 19 cm long). Both leaves are flexible but *H. brauniiunum* is much tougher than *C. procera*.

In our simulation study of tool-using behavior in captive chimpanzees (Tonooka et al. 1997), members of a group of nine captive chimpanzees also showed a high selectivity of leaves for drinking juice in an outdoor compound. In that study, chimpanzees used a particular kind of leaves (*Thuja occidentalis*) from among over 28 species available at the time of the test sessions. Although they could drink juice with their hands, they preferred to use these particular leaves as drinking tools. Interestingly, the shape of *T. occidentalis* and *H. brauniiunum* is extremely different. *T. occidentalis* is a conifer, and does not grow in tropical and sub-tropical areas. *T. occidentalis* is, however, more efficient than other leaves of broad-leaved trees. As in captive chimpanzees, one of the reasons why Bossou chimpanzees select *H. brauniiunum* may be its higher efficiency over other species. Unfortunately, there were no data concerning efficiency for drinking water for each species that the Bossou chimpanzees used. It is necessary to measure efficiency for a further discussion about the leaf selection.

The Bossou chimpanzees used a previously unobserved technique for making leaves into drinking tools, that is, leaf folding. As shown in Fig. 3, the sets of leaves classified as used for leaf folding were clearly different in shape from those used for leaf sponges. As mentioned in the Results, adult chimpanzees did not chew leaves after stuffing them into their mouths. On the other hand, old infants tended to chew leaves several times when stuffing them into their mouths and in the middle of drinking. It is supposed that this chewing behavior makes the leaves into a sponge shape. In other words, leaf sponges might be transient forms of leaf folding in Bossou.

Why has leaf-folding behavior never been reported in other habitats? There is a possibility that previous reports on leaf sponges might have included leaf folding. To address this question, field research to increase the number of observations of drinking behavior may also be useful at other sites.

Folded leaves resembled bellows and were regularly folded at about 3-cm intervals. It is considered that water was absorbed between the pleats of the folded leaves and consequently the total amount of absorbed water was more than that of a typical leaf sponge. However, comparison of the amount of absorbed water between leaf folding and sponging was not possible in the present conditions. Since old infants always came to the hollow with their mothers to drink, separate measurements of the amount of water taken were impossible to make in the present setting. Needless to say, efficiency should be assessed with respect to both physical properties of leaves and techniques used. In the future, a comparison of the efficiency between leaf folding, leaf sponge, and leaf spoon when using various types of leaves should be examined under more controlled conditions.

Another interesting finding was that adult chimpanzees sometimes appeared around the tree with leaves already in their mouths when the availability of leaves of *H. brauniiunum* near the hollow decreased because of intensive use by chimpanzees. These episodes can be discussed with regards to their *ecological* knowledge (Menzel 1997) and anticipation and planning for the future behavior.

In conclusion, this study enabled description of wild chimpanzees' leaf-using behavior for drinking water by manipulating the water content in a natural setting. This enabled us to observe this tool-using behavior more intensively than before, and gave us more detailed information about this behavior. I found that the chimpanzees showed high selectivity of the specific kind of leaves and they showed a newly discovered technique, leaf folding. I also found age-related differences in some aspects of this tool-using behavior, especially the frequency of the observations of other's (mother's) behavior, and more frequent occurrences of chewing of leaves, suggesting differences in technique between infants and adults. In the future, more data should be collected from the same individuals in longitudinal studies for more detailed analyses of the ontogenetic development of leaf-using behavior with respect to leaf selectivity and the techniques employed.

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