

Gen Yamakoshi · Masako Myowa-Yamakoshi

New observations of ant-dipping techniques in wild chimpanzees at Bossou, Guinea

Received: 29 May 2002 / Accepted: 2 August 2003 / Published online: 18 October 2003
© Japan Monkey Centre and Springer-Verlag 2003

Abstract Ant-dipping behavior is often cited as a clear example of chimpanzee culture, since different populations have apparently different dipping techniques (the one-handed method used by chimpanzees in Bossou, Guinea and Taï, Côte d'Ivoire, and the two-handed method used in Gombe, Tanzania). Here we report a new observation of ant-dipping behavior from Bossou using the two-handed method, in addition to the first detailed description of the one-handed method. Although the main dipping pattern was the one-handed method in Bossou, one adult male was observed dipping for ants using the two-handed method, while other chimpanzees employed the conventional one-handed method in the same episode. The two-handed method was also sporadically observed in a juvenile and in adolescents, who were still immature in dipping techniques and hence prone to suffer from ant attacks. Cross-population comparisons of dipping techniques suggest that there are two sub-types of the one-handed method, and the Bossou one-handed technique may be substantially different from that of Taï. In terms of overall behavioral repertoire in ant dipping, the Bossou pattern appears more similar to that of Gombe than Taï. This may be explained by the difference in target ant species.

Keywords Culture · *Dorylus* · Idiosyncrasy · *Pan troglodytes* · Tool use

Electronic Supplementary Material Supplementary material is available in the online version of this article at <http://dx.doi.org/10.1007/s10329-003-0056-6>

G. Yamakoshi (✉)
Graduate School of Asian and African Area Studies,
Kyoto University, 46 Yoshida-Shimoadachicho,
Sakyo-Ku, Kyoto 606-8501, Japan
E-mail: yamakoshi@jambo.africa.kyoto-u.ac.jp

M. Myowa-Yamakoshi
Primate Research Institute, Kyoto University,
Kanrin, Inuyama, Aichi 484-8506, Japan

Introduction

A number of field studies have reported behavioral differences between populations of conspecific animals, which are termed “traditions” or “cultures” (Kawamura 1965; McGrew 1998). Chimpanzees provide one of the most abundant sources of locale-specific behaviors, such as feeding repertoires, tool-using techniques, communication gestures, and so on. (Nishida 1987; McGrew 1992; Sugiyama 1993). A recent extensive comparison of seven long-term wild-chimpanzee studies identified regional variations in 39 behavioral patterns that appeared unlikely to be due to differences in local environmental conditions (Whiten et al. 1999).

Ant-dipping behavior is often cited as one of the distinctive cultural differences among wild-chimpanzee populations (e.g., Whiten et al. 1999). Wild chimpanzees were first observed dipping for driver ants (*Dorylus* spp.) with a wooden stick (“wand”) detached from surrounding vegetation at Gombe National Park, Tanzania (Goodall 1963; McGrew 1974). This behavior was also observed directly in two West African populations: Bossou, Guinea (Sugiyama et al. 1988; Sugiyama 1995) and Taï, Côte d'Ivoire (Boesch and Boesch 1990). Indirect evidence suggested that this behavior was also practiced at Mt. Assirik, Senegal [Baldwin 1979 (cited in Alp 1993)], Tenkere, Sierra Leone (Alp 1993), Mt. Nimba, Guinea (Sugiyama 1995), and Kalinzu, Uganda (Hashimoto et al. 2000). In contrast, nearly 40 years of continuous intensive behavioral observations in the Mahale Mountains, Tanzania, have failed to yield a single observation of this behavior, although *Dorylus* ants are abundant in the area (Nishida and Hiraiwa 1982; Whiten et al. 1999).

Clear differences in dipping techniques have been reported among the three populations for which behavioral descriptions of ant dipping are available. In Gombe, a chimpanzee will typically hold the wand with

one hand, dip it into a hole in an ant nest, wait for some time until the agitated ants swarm up along the wand, then sweep the ants with the other hand while withdrawing the wand from the hole (“pull through”), and hastily put the mass of ants into its mouth (McGrew 1974). In Tai, chimpanzees have never been observed to perform the “pull through”, but always to dip for ants with one hand, and then sweep the wand directly with their lips (Boesch and Boesch 1990). Observations at Bossou were considered similar to those of Tai (Sugiyama 1995).

Here we present new data of ant dipping in Bossou, where relatively few episodes have been reported [seven direct observations by Sugiyama (1995) and two by Matsuzawa and Yamakoshi (1996)]. The new data include the first substantial observations of the two-handed method with the “pull through” from a community other than Gombe. This paper aims (1) to provide a detailed description of ant dipping by Bossou chimpanzees, based on video-recorded behavioral data; and (2) to compare important parameters, such as use of the hands, individual differences, developmental changes, wand lengths and so forth, with those of other populations.

Methods

Study animals and periods

We observed a community of wild chimpanzees in Bossou, Republic of Guinea, West Africa. Since 1976, this group has been habituated to researchers, and has been studied intensively; thus, all individuals have been identified. The chimpanzees were tolerant of researchers in close proximity (2–5 m away), although we tried to observe them from 5–10 m away. During the study period, the group contained about 20 individuals. For additional information on the Bossou community, see Sugiyama (1999) and Yamakoshi et al. (1999).

We followed the age-class definition of Sugiyama (1999), which classifies infants as 0–3 years old, juveniles as 4–7 years old, adolescents as 8–11 years old, and adults as more than 12 years old, for both sexes. It should be noted that this age-class definition is somewhat different from a more commonly used definition by Goodall (1986), reflecting relatively early maturation of Bossou chimpanzees (Sugiyama 1999).

Behavioral data were collected in three study periods in Bossou. The first author conducted a 4-month study from September 1993 to January 1994 [“period 1” (for details, see Yamakoshi and Sugiyama 1995)] and 13-month study from December 1994 to January 1996 [“period 2” (for details, see Yamakoshi 1998)]. Observations in these two periods did not include video recordings. A study period from August to October in 1999 (“period 3”) was carried out by the two authors with video recordings. We carried digital video recorders (Sony DCR-TRV9 and Sony DCR-PC10) and attempted to film as many behaviors as possible. In addition, when necessary, we used previously published ant-dipping data recorded from the same community by 14-month study in 1987–1991 (Sugiyama 1995), identified as “period 0” (Table 1).

In all the study periods, we attempted to collect and measure any dipping wands immediately after a party left an ant nest. However, the reliable comparison of wand length between methods was not possible because of difficulty in matching wands to the particular method (e.g., a wand is sometimes re-used by others).

Definition of terms

An ant-dipping bout was defined as a sequence of behavioral components that began with the insertion of a wand into the entrance of an ant nest and ended either with the ingestion of ants (successful bout), or with any type of cancellation of the sequence (unsuccessful bout). When an individual inserted a wand, released it to engage in other activities (e.g., scratching its body or removing biting ants), and then resumed dipping with the same inserted wand, we counted it as a single bout, provided that the interruption lasted less than 1 min.

An ant-dipping session was defined as a series of bouts targeted at the same ant nest on an individual basis, regardless of the time interval between bouts. We would have considered it to be a new session if an individual or a party had left a site, returned later to the same site, and dipped in the same nest, but no such cases were observed during this study.

An ant-dipping episode was thus defined as continuous dipping activity by members of the same party at the same ant nest. An episode was composed of multiple sessions when more than one individual of the same party engaged in ant dipping. Duration of an episode was defined as a total time from the first dipping bout of the first individual to the last bout of the last individual.

Results

General information

Twelve ant-dipping episodes comprising 34 sessions were filmed during period 3. In addition, two episodes with three sessions and 11 episodes with 26 sessions were observed without filming during periods 1 and 2, respectively (Table 1). All of these cases involved *Dorylus* ants, and observations in which the ant species was not confirmed were excluded from the analysis. Out of 29 individuals aged more than 2 years at the time of sampling during the study periods (including previously published data), 18 individuals performed ant dipping (Table 1). Thus, ant dipping was a group-wide behavior in Bossou.

The 12 episodes recorded in period 3 comprised a total of 268.6 min (Table 2). The mean duration of an episode was 22.4 min ($n = 12$, $SD = 21.3$, range 0.4–59.1). On average, 2.8 chimpanzees participated in each episode ($n = 12$, $SD = 2.3$, range 1–9). In these 12 episodes, 34 sessions were observed, involving 10 individuals, and a total of 559 bouts were recorded (Table 2), of which 508 were “successful” (i.e., the performer succeeded in ingesting ants). The average number of bouts in a session was 16.4 ($n = 34$, $SD = 15.9$, range 1–61), and the average duration of a session was 11.4 min ($n = 34$, $SD = 12.8$, range 0.0–51.5). These values are somewhat underestimated, because of bouts that were not completely recognized when visibility was poor. The average number of bouts per minute was 1.4.

Throughout the three study periods, we collected 48 wands, averaging 44.8 cm in length ($n = 48$, $SD = 11.9$, range 26.1–74.8). The mean diameter of the thicker end of the wands was 4.0 mm ($n = 45$, $SD = 2.0$, range 1.9–12.0), and that of the thinner end was 3.0 mm ($n = 37$, $SD = 1.4$, range 1.0–6.0). The number of wands (n) differs across the above analyses because we excluded values for broken ends, which were impractical to measure.

Table 1 Number of observed ant-dipping sessions across individuals present from October 1987 to October 1999 excluding infants 0–1 year old

Name	Sex	Birth year	Study periods				Total
			0	1	2	3	
			Durations				
			14 months	4 months	13 months	2 months	
Fn	+	n.a. ^a	2	0	0	0	2
Jr	+	n.a. ^a	1	1	0	3	5
Ka	+	n.a. ^a	2	1	5	2	10
Nn	+	n.a. ^a	0	0	0	0	0
Pm	+	n.a. ^a	0	0	0	0	0
TA	+	n.a. ^a	0	0	0	2	2
VI	+	n.a. ^a	0	0	0	2	2
Yo	+	n.a. ^a	1	1	3	3	8
Ki	+	n.a. ^a	2	b	b	b	2
JZ	+	1978	0	b	b	b	0
FF	+	1980	1	0	6	2	9
PR	+	1980	0	b	b	b	0
NP	+	1981	0	b	b	b	0
Vb	+	1982	0	b	b	b	0
Ja	+	1983	4	b	b	b	4
Yu	+	1984	2	b	b	b	2
NA	+	1985	1	0	1	b	2
Kk	+	1986	0	b	b	b	0
VI	+	1986	0	0	6	b	6
PI	+	1987	0	0	2	0	2
Jk	+	1989	1	b	b	b	1
Ft	+	1991	b	0	0	6	6
Vv	+	1991	b	0	2	4	6
YL	+	1991	b	0	1	3	4
PO	+	1993	b	b	0	0	0
Nt	+	1993	b	b	0	0	0
Ju	+	1993	b	b	0	7	7
PK	+	1996	b	b	b	0	0
Fl	+	1997	b	b	b	0	0
Total sessions			17	3	26	34	80
Total episodes			7	2	11	12	32

^aAge unknown; already present when the project began in 1976 (see Yamakoshi et al. 1999)

^bAbsent from the community

Table 2 Ant-dipping episodes observed in Period 3

Episode	Date	Duration (min)	No. of sessions	No. of bouts ^a	Performers
1	August 24 1999	30.7	4	31	Yo, Ft, YL, Ju
2	August 26 1999	4.6	1	6	FF
3	September 7 1999	52.7	2	45	Ft, Ju
4	September 13 1999	59.1	3	140	TA, VI, Vv
5	September 14 1999	48.2	4	70	Jr, Ka, Ft, Ju
6	September 20 1999	16.0	1	16	Ju
7	September 26 1999	28.5	9	207	Jr, Ka, TA, VI, Yo, FF, Vv, YL, Ju
8	September 27 1999	18.5	4	27	Ft, Vv, YL, Ju
9	September 28 1999	0.4	1	2	Ju
10	October 3 1999	6.6	2	8	Ft, Vv
11	October 9 1999	2.5	2	4	Jr, Ft
12	October 17 1999	0.8	1	3	Yo
Total		268.6	34	559	

^aAll sessions combined

Variation in dipping techniques among adults

Data described

Only filmed data collected in period 3 were used in this section. To portray the typical ant-dipping technique, we

describe three ant-dipping bouts from two episodes in detail from the replay of videotaped data. Episode numbers correspond to those in Table 2. The technique used in cases 1 and 3 was the “one-handed method”, a technique commonly used by Bossou chimpanzees. On the other hand, case 2 clearly illustrates the

“two-handed method” with the “pull through” motion, which thus far had only been observed at Gombe. Case 2 was the first definite (i.e., filmed) observation of the two-handed method in Bossou.

Summary of episode 4

A small party of three chimpanzees was observed from 1529 to 1655 hours at the north-western base of Gban Mountain. At 1549 hours VI began to dig hastily in the forest floor at the periphery of a well-developed secondary forest with a relatively closed canopy. The other two individuals approached the site, and an ant-dipping episode ensued. This episode lasted for 1 h and 6 min, during which each chimpanzee took substantial breaks, probably as a result of the rain that began during the episode.

Case 1: TA's 11th bout [adult male (see ESM 1)]

TA used his left hand to hold onto a stout overhanging branch, while his feet grasped vegetation just above the ground, where angry ants were doubtless scattering. In his right hand he held a wand, which he inserted into a hole in the ant nest. He thrust the wand back and forth eight times and then slowly withdrew it with an extremely large mass of ants (visually estimated as about 20 cm long and 3 cm wide) adhering to it. He shook the wand moderately but rapidly for about 2 s, seemingly attempting to shape the mass of ants or keep them away from his grip by centrifugal force. He then brought the proximal end of the wand to his mouth. As he put the end between his lips/teeth, he quickly pulled the wand so that it passed through his lips/teeth from proximal to distal end. Consequently, the ants were combed en masse into his mouth. TA then masticated them while frantically wiping escaped ants away from around his nose, which he did five times with his right hand. This lasted for 16 s.

Summary of episode 7

One morning, as a large party of chimpanzees crossed a human path, which was about 1.5 m wide, they began screaming, apparently very excited. A party of nine individuals (excluding infants) then started dipping for ants in a nest just beside the path, at 0924 hours. All nine individuals participated in the dipping episode, which ended at 0953 hours. The environment was open, since vegetation had been cleared for the path, which was adjacent to a high riverine forest.

Case 2: FF's 1st bout [adult male (see ESM 2)]

While screaming excitedly, FF uprooted a stem from some nearby vegetation with his left hand and made a wand by tearing all the leaves off with his teeth. Then,

standing quadrupedally, he inserted the wand into the ant nest with his left hand, and slowly moved it back and forth about 10 times over 13 s. He then withdrew the wand with his left hand and grabbed it with his right hand, just above the left hand, with his thumb directed towards the distal end of the wand. His right hand then swept the ants up along the wand to the distal end and smoothly brought the gathered ants into his mouth. He masticated the ants and picked at some remaining on his right hand with his lips. This sequence lasted for 21 s.

Case 3: Yo's 21st bout [adult female (see ESM 3)]

Standing quadrupedally, she held a wand with her right hand and inserted it into a hole. She gently thrust the wand in nine times, while picking ants from the back of her left hand several times and standing bipedally. She slowly withdrew the wand, and moved it to her mouth. She then put the proximal end of the wand between her lips/teeth, quickly pulled it through to the distal end, and chewed the ants. This took 20 s.

Dipping methods

Among adults, whose tool-using techniques are thought to be stereotyped (Yamakoshi 1996; Inoue-Nakamura and Matsuzawa 1997), the two-handed method was seen in only one individual, FF (Fig. 1). During his dipping session in episode 7, he dipped 11 times, and employed the two-handed method exclusively. It is notable that he used the conventional one-handed method in a session recorded 1 month previously (episode 2) and in all of his previously observed dipping bouts in earlier study periods, which were not videotaped.

During episode 7, when FF was observed employing the two-handed method, five other adult chimpanzees dipped in the same ant nest. These five adults used the conventional one-handed method exclusively (see

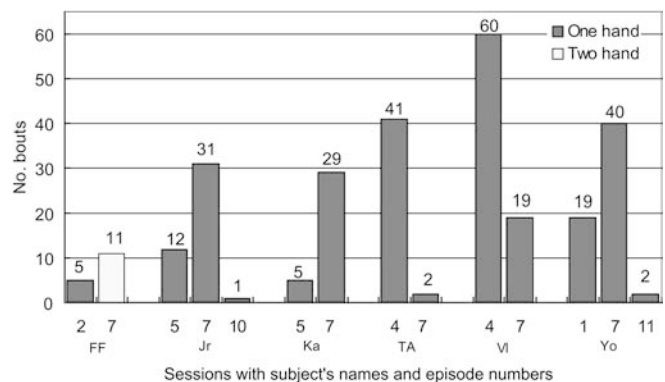


Fig. 1 Bout distribution of two dipping methods in period 3 among adult chimpanzees in Bossou: each bar represents one independent session. Only “successful” bouts were used. For episode number, see Table 2

description of Yo in case 3 above). This means that different individuals employed different dipping methods under apparently the same ecological conditions.

Age difference

Except for the FF's case of the two-handed method in episode 7, no other obvious session with the two-handed method was identified during period 3, as were the cases during previous periods. Subsequent careful observations using video-replay revealed, however, that some adolescents did show the two-handed method during period 3 (Fig. 2). In total, 11 bouts using the two-handed method were observed in three adolescents. In addition, two unsuccessful bouts using the two-handed method were observed in one juvenile (Ju), who wiped the ant wand with a "pull through" motion but did not bring the trophy to her mouth. The appearance of the two-handed method given by the juvenile/adolescents was quite different from that given by FF. In contrast to FF, who continually used the two-handed method 11 times in one session (Fig. 1), most of the juvenile/adolescent bouts using the two-handed method occurred as isolated bouts within a session (Fig. 2).

Components of ant dipping

Based on the videotape analysis, the minimum components of ant dipping in Bossou were described as follows:

[find an ant nest]—[prepare a dipping wand]—[dip for ants]—[eat ants]

The [dip for ants] section can be subdivided into the following behavioral components, which form a sub-routine (Byrne and Russon 1998) that is repeated one to more than 60 times in a session:

- A. Insert the wand into a nest hole;
- B. Thrust the wand back and forth;
- C. Withdraw the wand (with ants);
- D. Pull the wand through the mouth.

The conventional behavioral sequence in Bossou (the one-handed method) is represented here as: (A)—(B)—(C)—(D). A successful bout corresponds to the [dip for ants] subroutine. Although the subroutine abstracts the common ant-dipping behavior in Bossou fairly well, observed sequences often included optional components during or between obligatory components. In addition, each obligatory component was sometimes replaced by atypical components, which included the "pull through" or the two-handed method (Table 3).

The dipping skills of a juvenile and adolescents were less stereotyped than those of adults. Among 12 optional and atypical behavioral components listed in Table 3, only "interruption" had a high frequency (220 of 508 successful bouts) and was seen relatively evenly across individuals. Of the other 11 optional or atypical components, 6 were observed only in the juvenile and the adolescents.

Discussion

Ant dipping in Bossou

The first detailed description of the one-handed method based on video-recording and the first substantial observation of the two-handed method in the Bossou community clearly demonstrated that the two different dipping techniques coexist within the same community. With current small sample-sizes, it is too early to evaluate quantitatively whether the two-handed method in ant-dipping is "anecdotal", "idiosyncratic", "habitual", or "customary" (for definition, see McGrew and Marchant 1997), although it seems quite unlikely that the method has been "customary". Judging from its low frequency, the two-handed method must be one of the minor optional/atypical behavioral components, only occasionally seen among the conventional, one-handed behavioral sequences for the most of adults at Bossou.

Because the two-handed components were sporadically but commonly observed in juveniles/adolescents, we presume that it was less skillful performers who likely employ the two-handed method at Bossou. Why, then, did they use two-handed method and for what function? In one occasion, a juvenile (Ju) showed a wiping action similar to the two-handed method, although she did not lift the ants to her mouth. One adult female (VI) also performed wand wiping, but without bringing her hand to her mouth, after completing the normal one-handed method (Table 3). These suggest that the wand-wiping action has the obvious function of protecting the hand from aggressive ants. We hypothesize that less skillful chimpanzees may face the problem of protecting themselves from swarming ants when they dip using their

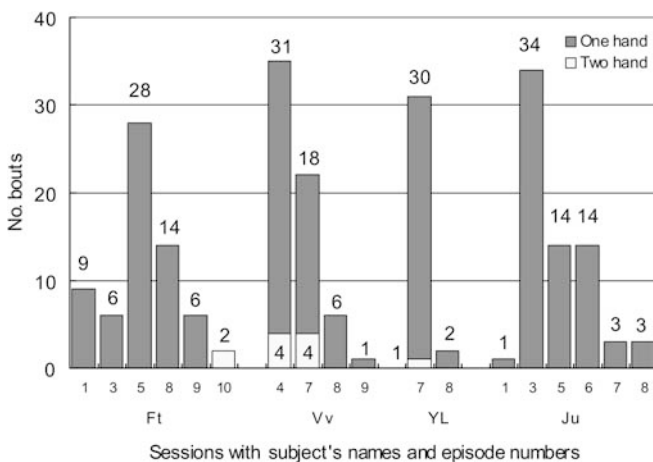


Fig. 2 Bout distribution of two dipping methods in period 3 among juvenile and adolescent chimpanzees in Bossou: each bar represents one independent session. Only "successful" bouts were used. For episode number, see Table 2

Table 3 Optional and atypical components in ant-dipping (number of bouts in which each component occurred at least once; thus the numbers do not represent actual number of times each component occurred, since each component could appear several times in one bout)

	Adults							Adolescents and juveniles					Total
	Jr	Ka	TA	VI	Yo	FF	Total for adults	Ft	Vv	YL	Ju	Total for adolescents and juveniles	
No. of successful bouts	44	34	43	79	61	16	277	65	64	33	69	231	508
Optional components													
Interruption ^a	20	26	7	42	21	3	119	2	39	21	39	101	220
Withdrawing wand ^b	0	0	0	1	0	0	1	0	3	1	4	8	9
Changing position ^c	2	0	0	1	2	0	5	1	2	2	3	8	13
Dropping wand	0	0	0	0	0	0	0	3	2	0	0	5	5
Modifying wand	0	0	0	0	0	0	0	0	0	0	2	2	2
Digging in the ground ^d	1	0	0	1	1	0	3	0	1	0	0	1	4
Tapping wand ^e	0	0	0	0	0	0	0	0	1	0	0	1	1
Wiping wand ^f	0	0	0	2	0	0	2	0	0	0	0	0	2
Atypical components													
Foot use ^g	0	0	0	0	0	0	0	1	3	0	1	5	5
Two limb use ^h	0	0	0	0	0	0	0	2	2	0	0	4	4
Reverse direction ⁱ	0	0	0	0	0	0	0	0	5	0	0	5	5
“Pull through”	0	0	0	0	0	11	11	2	8	1	0	11	22

^aInterruption of thrusting by releasing an inserted wand (to engage in other activities, predominantly picking off ants or scratching)

^bInterruption of thrusting by withdrawing an inserted wand

^cE.g., from quadrupedal standing to sitting

^dTo excavate the ant nest

^eTapping the upper part of an inserted wand probably to shake ants off the end of the wand

^fWiping a wand just like a “pull through” to clean off remaining ants after an ordinary dipping bout using the one-handed-method

^gUse of a foot to pull out a wand and bring it to the mouth

^hUse of two hands or one hand and one foot together to bring a wand to the mouth

ⁱBringing a wand to the mouth with the palm of hand turned up, and the back of the hand turned down (in the majority of cases, the palm is turned down); thus, if a chimpanzee manipulates a wand with his right hand, he slides a wand to the right in the conventional cases but to the left in this case

clumsy one-handed technique. They find their way out for a while by wiping away the ants with the other hand and this pattern becomes unimportant once their technique improves, and only a few individuals (probably the least skilled) may continue to use the pattern occasionally until adulthood.

In our hypothesis, we assumed that the two-handed method in Bossou may be effective for safety, but may not be very efficient for food gathering compared to the one-handed method, since it becomes useless following development of the one-handed method. This contradicts the common notion that the two-handed method in Gombe is much more productive than the one-handed method in Taï, based on mimic attempts by researchers (Boesch 1996). However, this may not be the case in Bossou. In an extremely productive case (episode 4), ants were collected in a mass approximately 20×3×3 cm (visual estimate) by the one-handed method, which is more than a palm could hold (see ESM 1). We attempted to mimic dipping behavior to estimate quantity, but we never succeeded in obtaining such a large mass of ants on the wand. It is therefore possible that the one-handed method is an ecologically optimal tactic for the Bossou chimpanzees.

Comparison with Gombe and Taï

Our study reconfirmed that the one-handed method is the main dipping pattern in Bossou, and a small number of individuals occasionally use the two-handed method.

Similarly, in Gombe, where the two-handed method dominates, at least two individuals were reported to specialize in the one-handed method (Goodall 1986, p 252). No explanation, however, has been given as to why these two individuals (McGregor and Pom) did not use the conventional two-handed method. Overall, the technical difference between Bossou and Gombe appears to be more of a quantitative difference than a qualitative one, since both have the two dipping methods in common in their behavioral repertoires.

Chimpanzees in Bossou and Taï were thought to use the same dipping method [i.e., the one-handed method (Boesch and Boesch 1990; Sugiyama 1995)]. Our first detailed observation with video-recording of one-handed ant dipping at Bossou revealed, however, that there are considerable differences in the details of the dipping methods between the two sites. Ant dipping in Taï was described as follows: “When the ants have swarmed about 10 cm up the tool, the chimpanzee withdraws it, *twists the hand* holding it and directly sweeps off the ants with the lips” (Boesch and Boesch 1990, our emphasis); and “...she rapidly *turns the end of the stick upwards* into her mouth...” (Boesch 1996, our emphasis). An apparent difference seems to exist in the motion wherein the chimpanzee lifts the wand to the mouth after withdrawing it from an ant nest. In a typical case in Bossou, there is no “twisting” or “turning” of the hand holding the wand; instead, the chimpanzee lifts the wand straight up, with its ends in a horizontal position. This is significant because it follows that the wand approaches the mouth vertically in the Taï case, but horizontally in the

Bossou case. Tai chimpanzees sweep the distal end of the wand, whereas Bossou chimpanzees sweep the wand from the proximal end (see cases 1 and 3).

According to the only available description of the one-handed method by a Gombe chimpanzee, “he thrust the stick down into the nest, ... he then pulled it through his mouth with a rapid sideways movement” (Goodall 1963, our emphasis). The one-handed method in Gombe thus sounds more similar to that used in Bossou than to that observed in Tai. It may be that there are two different types of “one-handed method”, which could be described as the “vertical one-handed method” in Tai, and the “horizontal one-handed method” in Gombe and Bossou.

A comparative analysis of wand lengths between study sites may support this new classification. Based on comparison of reported wand lengths among five study sites (Asirik, Bossou, Gombe, Tai, and Tenkere), Alp (1993) pointed out that Tai chimpanzees use much shorter wands (23.6 cm) than chimpanzees in the other sites (66.0–79.8 cm), which implies substantial technical differences. Subsequent reports on wand lengths also fall within this range [72.5 cm for Mt. Nimba (Sugiyama 1995) and 79 cm for Kalinzu (Hashimoto et al. 2000)]. The wand length in Bossou has been confirmed to be shorter with larger sample sizes [46.7 cm (Sugiyama 1995) and 44.8 cm in this study], but is still almost twice that of Tai examples. These comparisons suggest that chimpanzees in Bossou and Gombe share the basic techniques of the two-handed method and the horizontal one-handed method, although the frequency of each method varies greatly. Only chimpanzees in Tai use a systematically different technique (the vertical one-handed-method).

We suspect that the characteristics of target ant species could be a key factor to explain these local differences in ant-dipping techniques, since the chimpanzees in each community may dip for different varieties of driver ants (*Dorylus* spp.). Bossou chimpanzees dip for *D. molestus* (Sugiyama et al. 1988), while Gombe chimpanzees were formerly described to dip for *D. nigricans* (McGrew 1974), which is recently re-identified as *D. molestus* (Gotwald 1995; W.C. McGrew, personal communication). In Tai, chimpanzees were observed to dip for two species of driver ants, *D. nigricans* and *D. gerstaeckeri*, but dipping for the former species was only observed as an exception [by one young adolescent female (Boesch and Boesch 1990)].

D. nigricans and *D. molestus* are taxonomically closer to each other than *D. gerstaeckeri* (Raignier and van Boven 1955). Although behavioral details of the soldiers of each species are not documented, Boesch and Boesch (1990) wrote that “...the bites of the smaller species (i.e., *D. gerstaeckeri*) are more painful, but they move less rapidly up the stick” (our parentheses). If the Tai chimpanzees dip for less mobile but more painful ants, their employment of the vertical one-handed method using shorter wands seems reasonable, because they are less likely to be bitten without manual wiping.

It is surely too early, however, to paint the whole picture of local differences in ant dipping. Finer descriptions of ant-dipping behaviors from both Gombe and Tai, hopefully with video recordings comparable to those from Bossou, are definitely needed to confirm the above hypothesis. Rigorous identification of ant species and of the behavioral differences of each species is also vital. In this respect, we should remember that a detailed ecological investigation revealed that the presence and absence of termite-fishing behavior in neighboring Mahale K and B communities were explained by subtle differences in the termite species found at each site (Nishida and Uehara 1980; Uehara 1982; Collins and McGrew 1987). Although a comprehensive comparison between chimpanzee study sites has been completed (Whiten et al. 1999), its substantiation of ecological parameters was superficial and based largely on assumption. Further ecological investigation at each site will surely be fruitful, and much work remains to be done before we can better understand the “chimpanzee culture” phenomenon.

Acknowledgements This study was financed by the following research grants: (1) International Scientific Research Program to Y. Sugiyama (Nos. 0441066, 07041135, and 10041168) from the Ministry of Education, Science, Sports, and Culture, Japan; (2) the 1996 research grant from the Nakayama Foundation for Human Science; and (3) the grant under Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists to the first author (No. 2670). We are grateful to Direction Nationale de la Recherche Scientifique et Technique, and Institut de Recherche Environnementale de Bossou of the Republic of Guinea for permission to conduct this study. Thanks are due to G. Goumy, T. Camara, P. Goumy, P. Cherif, D. Samy, H. Tsubaki, H. Takemoto, T. Matsuzawa, and Y. Sugiyama for their assistance in the field, and to R. W. Byrne, T. Humle, H. Ihobe, W. C. McGrew, T. Nishida, A. E. Pusey, S. Uehara, J. Wallis, R. Wittig, and two anonymous referees for their helpful comments on the earlier draft of this paper.

References

- Alp R (1993) Meat eating and ant dipping by wild chimpanzees in Sierra Leone. *Primates* 34:463–468
- Boesch C (1996) Three approaches for assessing chimpanzee culture. In: Russon A, Bard K, Parker S (eds) *Reaching into thought: the minds of the great apes*. Cambridge University Press, Cambridge, pp 404–429
- Boesch C, Boesch H (1990) Tool use and tool making in wild chimpanzees. *Folia Primatol* 54:86–99
- Byrne RW, Russon AE (1998) Learning by imitation: a hierarchical approach. *Behav Brain Sci* 21:667–721
- Collins DA, McGrew WC (1987) Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates* 28:457–471
- Goodall J (1963) Feeding behaviour of wild chimpanzees: a preliminary report. *Symp Zool Soc Lond* 10:39–48
- Goodall J (1986) *The chimpanzees of Gombe: patterns of behavior*. Harvard University Press, Cambridge, Mass.
- Gotwald WH Jr (1995) *Army ants: the biology of social predation*. Comstock, Ithaca
- Hashimoto C, Furuichi T, Tashiro Y (2000) Ant dipping and meat eating by wild chimpanzees in the Kalinzu Forest, Uganda. *Primates* 41:103–108

- Inoue-Nakamura N, Matsuzawa T (1997) Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J Comp Psychol* 111:159–173
- Kawamura S (1965) Nihonzaru ni okeru rui-culture (Proto-culture in Japanese macaques) (in Japanese). In: Kawamura S, Itani J (eds) *Saru: shakaigakuteki kenkyu*. Chuo-Koronsha, Tokyo, pp 237–289
- McGrew WC (1974) Tool use by wild chimpanzees in feeding upon driver ants. *J Hum Evol* 3:501–508
- McGrew WC (1992) Chimpanzee material culture: implications for human evolution. Cambridge University Press, Cambridge
- McGrew WC (1998) Culture in nonhuman primates? *Annu Rev Anthropol* 27:301–328
- McGrew WC, Marchant LF (1997) Using the tools at hand: manual laterality and elementary technology in *Cebus* spp. and *Pan* spp. *Int J Primatol* 18:787–810
- Matsuzawa T, Yamakoshi G (1996) Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: Russon A, Bard K, Parker S (eds) *Reaching into thought: the minds of the great apes*. Cambridge University Press, Cambridge, pp 211–232
- Nishida T (1987) Local traditions and cultural transmission. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 462–474
- Nishida T, Hiraiwa M (1982) Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *J Hum Evol* 11:73–99
- Nishida T, Uehara S (1980) Chimpanzees, tools, and termites: another example from Tanzania. *Curr Anthropol* 21:671–672
- Raignier A, van Boven J (1955) Etude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera: Formicidae). *Ann Mus R Congo Belge* 2:1–362
- Sugiyama Y (1993) Local variation of tools and tool use among wild chimpanzee populations. In: Berthelet A, Chavaillon J (eds) *The use of tools by human and non-human primates*. Oxford University Press, Oxford, pp 175–187
- Sugiyama Y (1995) Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates* 36:193–205
- Sugiyama Y (1999) Socioecological factors of male chimpanzee migration at Bossou, Guinea. *Primates* 40:61–68
- Sugiyama Y, Koman J, Sow MB (1988) Ant-catching wands of wild chimpanzees at Bossou, Guinea. *Folia Primatol* 51:56–60
- Uehara S (1982) Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). *Folia Primatol* 37:44–76
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399:682–685
- Yamakoshi G (1996) Individual differences in the tool manipulation of wild chimpanzees at Bossou, Guinea. *Primate Res* 12:283
- Yamakoshi G (1998) Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. *Am J Phys Anthropol* 106:283–295
- Yamakoshi G, Sugiyama Y (1995) Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: a newly observed tool-using behavior. *Primates* 36:489–500
- Yamakoshi G, Takemoto H, Matsuzawa T, Sugiyama Y (1999) Research history and conservation status of chimpanzees at Bossou, Guinea (in Japanese). *Primate Res* 15:101–114