RESEARCH ARTICLE

Ant-Dipping Among the Chimpanzees of Bossou, Guinea, and Some Comparisons With Other Sites

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We present a detailed study of ant-dipping among the wild chimpanzees (*Pan troglodytes verus*) of Bossou, in southeastern Guinea, West Africa. Observations suggest a strong influence of prey (*Dorylus* spp.) characteristics, including aggressiveness and/or gregariousness, on tool length and technique employed by the chimpanzees. Bossou chimpanzees exhibit two ant-dipping techniques: 1) direct mouthing, and 2) pull-through. In addition, they were observed dipping for several species of *Dorylus* ants, classed into two categories: Red and Black. Tool length was longer when dipping in higher-risk contexts, i.e., at the ants' nest site or on Black ants. The pull-through technique was almost exclusively associated with dipping at the nest site. This latter technique was associated with tools over 50 cm long, whereas direct mouthing was the only technique observed with tools <50 cm long. Our experimental findings, together with our observations on the behavior of the chimpanzees, suggest that at the nest, the pull-through technique was a more efficient technique than direct mouthing. We review our results in the context of ant-dipping observed at two other long-term chimpanzee study sites, i.e., Gombe (Tanzania) and Taï (Côte d'Ivoire), where differences in tool length, technique used, and focal *Dorylus* ant species have been reported. Finally, we urge similar detailed studies of this tool-use behavior in both Gombe and Taï to shed further light upon our results and their implications. Am. J. Primatol. 58:133–148, 2002. © 2002 Wiley-Liss, Inc.

INTRODUCTION

Probe-using behavior is one of the most prominent and diversified forms of tool use by chimpanzees in their natural habitat. Based on data from long-term field sites and (with the exception of Budongo, Uganda) stick- or stalk-using for catching social insects on the ground and in trees is common to chimpanzees throughout their range [Whiten et al., 1999]. However, the prevalence of each type of behavior differs by locality, implying cultural differences across chimpanzee communities [McGrew, 1992; Whiten et al., 1999; Yamakoshi, 2001]. The ubiquity of stick- or stalk-using behaviors has been linked to the ready availability of diverse materials for tool-making and the presence of potential target prey in all habitats in which chimpanzees live [McGrew & Collins, 1985; Collins & McGrew, 1987]. In most cases of tool use to obtain social insects, a tool is used to gain access to the prey within a protected structure, i.e., the nest in termite fishing and ant fishing. However, ant-dipping, a tool-use behavior aimed at driver ants (*Dorylus* spp.), differs slightly in that it is focused on columns of migrating ants, or on the nest the ants use as a temporary bivouac, which is usually structurally unprotected.

Chimpanzees eat many ant species across different regions of Africa, and all subspecies of chimpanzees feed on ants [c.f. McGrew, 1992]. However, not all ant species consumed at some sites are eaten by chimpanzees at others, even when available. For example, *Dorylus nigricans*, a widespread species of driver ants, has never been recorded as being eaten by chimpanzees at Lopé (Gabon), Mahale and Kasakati (Tanzania), and Budongo (Uganda) (Lopé [Tutin et al., 1995], Mahale [Nishida, 1973], Kasakati [Suzuki, 1966], and Budongo [Reynolds & Reynolds, 1965]). Also, for a given prey species, tool use is not consistent across all sites. For example, the weaver ant (*Oecophylla longinoda*) is reportedly consumed at five field sites, but only at Bossou have chimpanzees been observed to use tools to obtain these ants [Sugiyama, 1995]. Moreover, *Camponotus vividus*, a species of wood-boring ant, is eaten at Mahale with the aid of a tool, while it is consumed directly by hand without a tool at Lopé [Nishida, 1973; Tutin et al., 1995].

Dipping for driver ants, *Dorylus* spp., is often cited as one of the best examples of culture in chimpanzees [Boesch & Boesch, 1990; McGrew, 1992]. Driver or safari ants, which occur at all sites where chimpanzees have been studied, often migrate on the ground or amongst low terrestrial herbaceous vegetation in great numbers (up to several million individuals) hunting for prey [Gotwald, 1972]. These ants construct tunnel-nests underground, which can reach up to 1 m in diameter and 1/2 m in depth. The entrance of the nest is often covered by a layer of fallen leaves, loose soil, and vegetation, and is therefore well camouflaged. Safari ants are usually very aggressive, and soldier ants can cause painful bites to chimpanzees. The use of a tool for ant-dipping allows more efficient and less painful harvesting of these biting ants, than taking them directly by hand or mouth [McGrew, 1974]. So far, three species of *Dorylus* ants preyed on by chimpanzees have been distinguished: *D. gerstaeckeri* (Emery) (Taï [Boesch and Boesch, 1990]), *D. molestus* (Gerstaecker) (Bossou [Sugiyama, 1995]), and *D. nigricans* (Illiger) (Taï [Boesch and Boesch, 1990] and Gombe [McGrew, 1974; Goodall, 1986]).

Ant-dipping has so far only been observed directly at three long-term study sites: Gombe (Tanzania), Taï (Côte d'Ivoire), and Bossou (Guinea). At other field sites, where indirect evidence of this behavior (e.g., abandoned tools) has been found, sample size is generally too small to infer any general trends in tool length

at the community level. Interesting differences in wand length are nevertheless emerging. Wands at Gombe are significantly longer than at Taï [McGrew, 1974; Boesch & Boesch, 1990]. Moreover, based on data of Sugiyama [1995] and Yamakoshi and Myowa-Yamakoshi (unpublished results), mean tool length at Bossou is intermediate between those at Gombe and Taï.

Differences in ant-dipping between Gombe and Taï are not restricted to tool length but also involve the technique employed. Gombe chimpanzees generally employ the ''pull-through'' technique, i.e., swift and meticulous drawing of the length of the tool from the proximal to the distal end, and ingesting the gathered bundle of ants from the collecting hand [McGrew, 1974]. However, chimpanzees at Gombe occasionally take ants directly from the tool by ''direct mouthing,'' either by nibbling or by pulling the tool sideways through the lips [McGrew, 1974]. At Taï, direct mouthing of the safari ants by nibbling them off the tool is the only technique recorded so far [Boesch & Boesch, 1990].

Boesch [1996] explored ecological factors at both sites that might favor the use of either technique, but he could not find any. It has been suggested that the differences in ant-dipping technique and wand length between Gombe and Taï are based on social learning and reflect cultural variation among chimpanzees [Boesch & Boesch, 1990; McGrew, 1992]. The pull-through technique has also been observed at Bossou (Yamakoshi and Myowa-Yamakoshi, unpublished results), and Sugiyama [1995] described Bossou chimpanzees employing a direct mouthing technique, occasionally nibbling the ants off the wand, but more often swiping the tool sideways through the lips. Thus, chimpanzees at Bossou employ two ant-dipping techniques, presenting a good opportunity to explore variables that may influence tool length and technique used.

Several hypotheses have been put forward regarding differences in tool length and technique between Gombe and Taï. Hashimoto et al. [2000] suggested that differences in the length of wands might reflect the difference in techniques used for catching ants. Sugiyama [1995, p. 203] earlier proposed that 1) the length of the wand, 2) the technique employed, 3) the working position, and 4) the selection of material ''must be determined by the characteristic features of the prey, and may to some extent reflect a tradition of the chimpanzee community.'' In the present work the first three of the above-mentioned variables are explored, focusing on their interrelationships and their variability in relation to prey characteristics (aggressiveness and/or gregariousness), and the tool users' behavioral efficiency.

METHODS

Study Site and Subject

The village of Bossou ($7°\ 39'$ N and $8°\ 30'$ W) is situated in the southeastern region of Guinea, about 6 km from the foot of the Nimba Mountains on the border with Côte d'Ivoire and Liberia. Bossou was established as a chimpanzee field site in 1976 [Sugiyama Sugiyama, 1981]. Since then, this community of wild chimpanzees has been habituated to observers, without provisioning. Presently, a population of 18 chimpanzees (*Pan troglodytes verus*) inhabits the forest surrounding the village of Bossou, and group size has remained stable (range: 16–23) since 1976 [Sugiyama, 1981, 1984, 1999]. For further details about this field site refer to Sugiyama [1999], Humle and Matsuzawa [2001], and Matsuzawa et al. [2001].

Data Collection and Analysis

The first author relied mainly on video records, filmed using a Sony DCR-TRV20 digital camera in June–September 2000 and June–September 2001, and a Sony Hi8 video camera during October 1997. Video data collected in August–October 1999 were gathered by G. Yamakoshi using a Sony DCR-TRV9 digital camera, and one session was recorded in August 2001 by G. Ohashi. Over 10 hr of video data were thus accumulated, encompassing 24 ant-dipping sessions. Five additional ant-dipping sessions, for which ant species and ant condition were identified, were observed by TH but not video recorded. A session is defined as a period during which at least one chimpanzee is engaged in tool behavior; the session is terminated when the last remaining chimpanzee of the subgroup ends tool-use. After each filming session, the ant species dipped for was collected for subsequent identification, and the condition of the ants (nest or migrating) was noted. All of the video data were analyzed twice by TH, and 14 sessions were analyzed once by a second observer blind to the hypotheses being tested. Any divergences in scoring were reviewed by both observers until a consensus was reached.

During the video analysis, tool length was recorded for each individual as either less than, greater than, or equal to 50 cm. This 50 cm demarcation was based on the average between mean tool length reported by Sugiyama [1995] (46.7 cm) and that found in the present tool sample set (53.7 cm). Ascription to these two categories was based on either precise tool length data when available from direct observations of the behavior (48.5% of tools) or simply comparing the length of the wand with objects of known length in the environment. Tools were assigned to one of five categories depending on which technique was observed during the use of that tool: 1) mouth only; 2) pull-through only; 3) mouth dominant (i.e., more than 50% mouthing observed during the use of that tool); 4) pull-through dominant; and 5) both equal (i.e., technique ratio for that tool was 50:50). The position of the tool user was noted as above ground (i.e., sitting on a liana or a bent-over sapling, or hanging from a liana or a branch) or on the ground (i.e., sitting or standing at ground level).

Tools were collected over four study periods: July–October 1997; July–September 1999, June–September 2000, and June–September 2001. Ant species dipped for could not be assigned for tools recovered from deserted driver ants' nests during daily tracking of the chimpanzees. During the 1997 study period, ant condition was not recorded for retrieved tools, and ants were not collected but only classed by ant type: Red or Black. However, systematic length measurements were obtained for all tools collected, along with information about tool-user identity, whenever possible.

The following ant-dipping experiment was conducted in September 2001 using measures based on 89 wands collected by T.H. at Bossou during the first three study periods. A human dipped for ants using wands of three different lengths: 1) mean lower quartile length (28.1 cm), 2) mean length (55.3 cm), and 3) mean upper quartile length (101.7 cm). Each tool was made from *Maranthacloa* sp., the commonest plant species used for wand-making at Bossou. Since several species of driver ants were consumed by chimpanzees at Bossou (see Results section), dipping sessions were done on *Dorylus lamottei* (Bernard) and *Dorylus militaris* (Santschi), classed as the Red type and *Dorylus nigricans* (Illiger), classed as the Black type, in both nesting and migrating conditions, thus creating four conditions. *D. kohli* (Wasmann), the third species classed as Red, was not included in the experiment, since at the time we were still unaware of the presence of a third species of the Red type. For each tool used and on a random

basis over a total of eight sessions, we dipped for ants using different bout durations (range = 2–120 sec), averaging 37 dips per tool for each session. The ants harvested from each dip were placed in a sealable polythene bag and counted. A bout duration corresponded to the time from when the wand made contact with the ants to when the wand was just being inserted into the sealable bag. One person timed the experiment while another (the same throughout the experiment) dipped for the ants in a fashion similar to that observed among Bossou chimpanzees, making slight regular back and forth movements of the tool to stimulate swarming of the ants. A new tool was made for each session. The time taken for the ants to swarm up the length of the tool was also recorded over several trials interspersed within the original experiment.

The purpose of the experiment was to assess differences in prey density and belligerence across ant condition and the two types of *Dorylus* ants. In addition, we were able to acquire an estimate of ant speed and a measure of the number of ants harvested across tools of different length under these four conditions.

Nonparametric two-tailed tests were used for the data analysis. For 2×2 contingency tables with expected values of <5, the Fisher's exact test was employed instead. A one-tailed Z-test was employed to compare two proportions. When a significant result was obtained using a Kruskal-Wallis test, Dunn's post hoc test was utilized. Careful attention was given to the independence of data points, so that, for example, only one data point was given for position until the individual changed position from being above ground to being at ground level or vice versa. For technique used, i.e., direct mouthing or pull-through, a single data point was given each time there was a switch in technique employed or in tool used.

RESULTS

Driver Ant Species Available at Bossou

Samples of driver ants were assigned to species by an ant specialist, Dr. B. Taylor. This taxonomic evaluation revealed that Bossou chimpanzees consume several species of *Dorylus* ants. These have been classed into two categories: 1) Red, including *D. kohli* (Wasmann), *D. lamottei* (Bernard) and *D. militaris* (Santschi); and 2) Black, corresponding to *D. nigricans* (Illiger). During the ant-dipping experiment, there was no difference in the quantity of ants harvested between the two Red species used, either overall or in either of the two conditions, which justified pooling them (see Table I).

Moreover, the Red species have morphological similarities, such as size and color of the soldier ants, that distinguish them from *Dorylus nigricans*, which is predominantly black and whose soldier ants are generally larger. *D. molestus*, which had previously been noted as present at Bossou by Sugiyama et al. [1988], was not identified in the samples collected. Since this original identification was not performed by an ant expert, it is likely that a misidentification of the species occurred (Sugiyama, personal communication).

Length of Ant-Dipping Tools

Based on 189 recovered tools, the mean wand length was 53.7 cm (range: 23–154 cm; SD = 21.01; median = 48.2 cm), intermediate between those found at Gombe [McGrew, 1974]: n = 13; mean = 66 cm; range: 15–113 cm) and Taï [Boesch and Boesch, 1990]: n = 35; mean = 23.9 cm; range: 11–50 cm). This mean does not differ significantly from previous results on ant-dipping tools from Bossou [Sugiyama, 1995]: n = 60; mean = 46.7 cm; SD = 15.9). The sample of wands from

TABLE I. Number of *Dorylus* Ants Harvested During the Ant Dipping Experiment Compared within Two Species of the Red Type, Across Ant Type, and Ant Condition

Condition	Groups compared	N dips	Mean/dip	SD	Median/dip	Range	Mann-Whitney: z value and P-value
Overall	*D. lamottei*	124	36.6	29.7	31	5–266	$z = -0.132$; n.s.
	D. militaris	115	44.8	66.5	30	4–599	
Nest	*D. lamottei*	64	42.6	36.9	40.5	5–266	$z = -0.933$; n.s.
	D. militaris	49	42.6	20.7	43	4–93	
Migrating	*D. lamottei*	60	30.2	17.6	25.5	6–76	$z = -0.995$; n.s.
	D. militaris	66	46.4	86.2	21	4–599	
Overall	Red	239	38.9	51.2	29	2–599	$z = -4.783$; $P < 0.001$
	Black	205	63.5	72.5	39	3–544	
Nest	Red	113	42.6	30.8	42	4–266	$z = -5.85$; $P < 0.001$
	Black	99	93.9	88.0	66	19–544	
Migrating	Red	126	35.6	64.2	21	2–599	$z = -2.312$; $P < 0.05$
	Black	106	35.0	36.2	27	3–243	
Overall	Nest	212	66.6	69.0	47	4–544	$z = -9.137$; $P < 0.001$
	Migrating	232	35.3	53.1	24	2–599	
Red	Nest	113	42.6	30.8	42	4–266	$z = -5.17$; $P < 0.001$
	Migrating	126	35.6	64.2	21	2–599	
Black	Nest	99	93.9	88.0	66	19–544	$z = -7.976$; $P < 0.001$
	Migrating	106	35.0	36.2	27	3–243	

this study is, however, much larger, and thus may better reflect mean tool length at the community level.

Aggressiveness and/or Gregariousness of Red and Black *Dorylus*

During the ant-dipping experiment, under each condition and overall, significantly more Black than Red ants were harvested (see Table I), suggesting more aggressiveness and/or gregariousness for Black ants compared to Red. Furthermore, observations of the chimpanzees' behavior at Bossou and across other sites support their sensitivity to these biting ants, regardless of the species involved [McGrew, 1974; Boesch and Boesch, 1990]. The chimpanzees will vigorously brush off the ants from their fur and bare skin (i.e., feet and face) when exposed to driver ants. Our own experiences with these ants, though, indicate that Black *Dorylus* soldier ants inflict more painful bites than Red soldier ants, which are slightly smaller in size.

Therefore, whether based on their higher level of aggressiveness/gregariousness or their more painful bites, Black *Dorylus* clearly appear to pose a greater risk to the ant-dipping chimpanzee than the Red type. Confirming the view that Black ants posed a greater risk than Red, egg or grub feeding directly by hand was observed in 66.7% of the ant-dipping sessions taking place at the nest site (n = 9), with seven of 10 individuals observed dipping at a nest eating eggs or grubs. However, this behavior involved only Red *Dorylus* ants' nests.

Tool Length in Relation to the Type of *Dorylus* Species Dipped for

Given the more aggressive and/or gregariousness nature of the Black ants, we predicted that longer tools would be used on Black ants, to allow the tool user to better keep its distance from the ants while dipping. Overall, and at the nest site, Bossou chimpanzees used significantly longer tools while dipping for Black *Dorylus* ants than they did for the Red ones (see Table II).

TABLE II. Length of Ant Dipping Tools Employed by Chimpanzees, Compared Across *Dorylus* Types and/or Ant Condition

Condition	Groups compared	N	Mean (cm)	SD	Median (cm)	Range (cm)	Mann-Whitney: z value and P-value
Overall	Red	117	50.8	18.6	46.4	23–126	$z = -2.802$; $P < 0.01$
	Black	52	62.4	26.0	59.65	24–154	
Nest	Red	54	58.4	20.6	55.1	26–126	$z = -2.563$; $P < 0.01$
	Black	30	72.5	26.0	70.65	33–154	
Migrating	Red	55	44.3	13.2	43.6	23–89	$z = -0.389$; n.s.
	Black	7	46.7	13.7	42	31–69	
Overall	Nest	86	63.1	23.3	58	26–154	$z = -5.383$; $P < 0.001$
	Migrating	62	44.6	13.2	43.55	23–89	
Red	Nest	54	58.4	20.6	55.1	26–126	$z = -3.918$; $P < 0.001$
	Migrating	55	44.3	13.2	43.6	23–89	
Black	Nest	30	72.5	26.0	70.65	33–154	$z = -2.715$; $P < 0.01$
	Migrating	7	46.7	13.7	42	31–69	

Although the trend was in the same direction, this difference was not significant for ants dipped while migrating on the ground (see Table II), but the sample size for Black ants was relatively small. In a second analysis based on the categorical data from the video analysis, yielding a larger and more equal sample size, a one-tailed Z-test comparing two proportions indicated that the chimpanzees were significantly more likely to use tools ≥ 50 cm long for the Black driver ants (≥ 50 cm: 11/23) than the Red (≥ 50 cm: 4/33) when ants were moving on the ground ($z = 3.01$; $\rho < 0.01$). These results support the prey aggressiveness/gregariousness hypothesis.

Dorylus Density/Aggressiveness at the Nest vs. Migrating

During the ant-dipping experiment, more ants were harvested at the nest site than in migrating columns whether the data were pooled for both *Dorylus* types or analyzed separately (see Table I). This result clearly indicates that driver ants occur at greater density and/or are more belligerent at the nest than while they are moving on the ground.

Tool Length in Relation to the Condition of the Ants

Having established that the density of safari ants and/or their aggressiveness is greater at the nest than during migration, we predicted that longer tools would be used for dipping at the nest site than when the ants were migrating. The data showed that wand length was significantly greater for ant-dipping at the nest, both overall and for each driver ant type analyzed separately (see Table II). This result supports the hypothesis that the chimpanzees use longer tools at the nest site to reduce the risk of being bitten. However, it is also conceivable that extra tool length may be required at the nest because the wand may be inserted into the nest rather than just placed against the ground, as when dipping for migrating ants. However, close observations of dipping at the nest site indicate that the chimpanzees most often dip near the nest entrance where swarming soldier ants gather, rather than insert their tools into the nest cavity.

Dipping Technique and Ant Condition

The direct mouthing technique was more frequently observed at Bossou than the pull-through technique (see Fig. 1). When analyzing independent occurrences
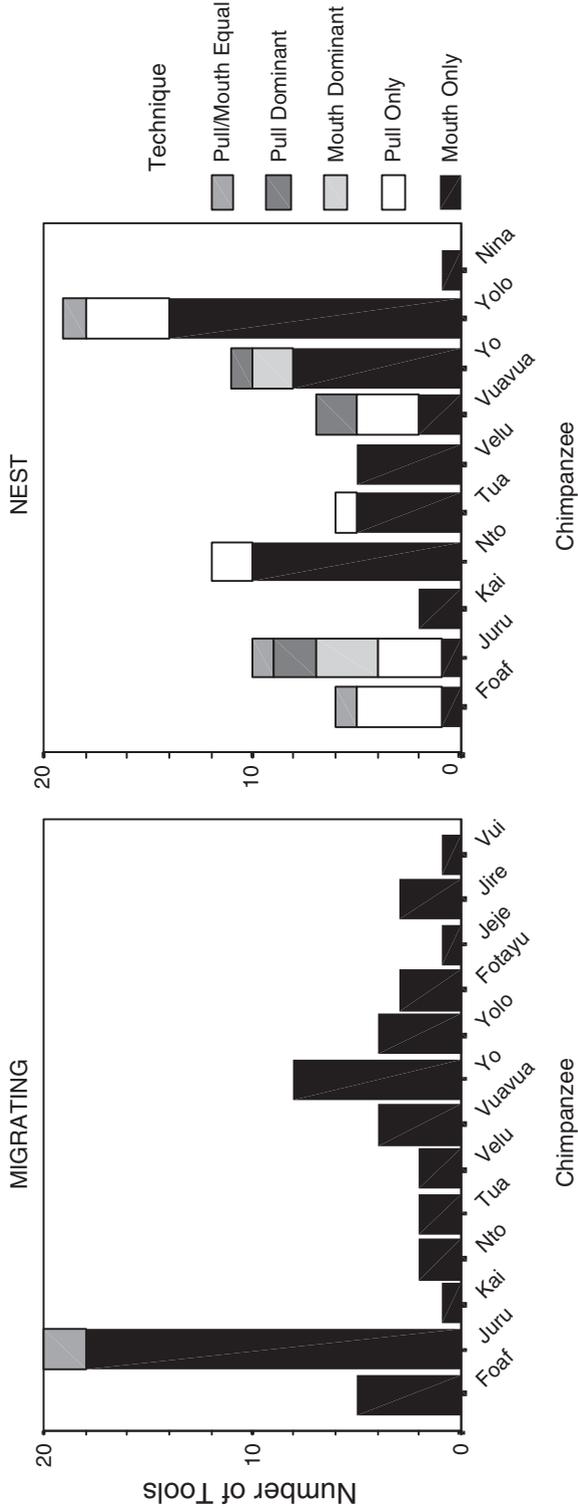
Fig. 1. Ant-dipping at the nest site and for migrating ants, and associated technique for each individual chimpanzee (pull: pull-through; mouth: mouth directly).

of either technique, a one-tailed Z-test comparing two proportions indicated that the chimpanzees were significantly more likely to employ the pull-through technique at the nest site (pull-through: 40/111) than on migrating ants (pull-through: 3/59) ($z = 5.75$; $\rho < 0.001$). One young female, Juru, was responsible for all instances of pull-through observed on migrating ants (see Fig. 1). Juru was observed pulling-through once on migrating ants as a juvenile (4–7 years old) and twice as an adolescent (8–11 years old).

Although the pull-through technique was more likely to be observed with dipping at the nest site than on migrating ants, individual variation among chimpanzees was observed (see Fig. 1). For example, three adult females (Kai, Nina, and Velu) were never seen using the pull-through technique while dipping for ants at the nest. However, the latter technique was observed in other adults, as well as adolescents and juveniles of both sexes. There was no clear association between mother and offspring in technique employed. Two mother–offspring pairs (Nina/Nto and Velu/Vuavua) did not match in the repertoire of techniques they displayed, but one pair did (Yo/Yolo) (see Fig. 1). Both Nto and Vuavua were observed occasionally pulling-through while dipping for ants at the nest site, but neither mother did so.

Frequency of Dipping for the Different *Dorylus* spps and Conditions

Based on a single data point for each ant-dipping session, the frequency of dipping for the different types of *Dorylus* appeared to be independent of condition (Fisher's exact test: $n_{nest/Black} = 3$; $n_{nest/Red} = 6$; $n_{migrating/Black} = 7$; $n_{migrating/Red} = 13$; n.s.). Overall, we were more likely to observe chimpanzees dipping for migrating ants than for ants at the nest; however, this trend fell short of significance (binomial test: $n_{nest} = 9$; $n_{migrating} = 20$; $\rho = 0.063$).

Technique and Tool Length

The video data revealed that the pull-through technique was significantly more likely to occur when the chimpanzees employed tools ≥ 50 cm long than when they used wands < 50 cm in length (see Fig. 2). This tendency was significant overall (with tools ≥ 50 cm: 25/80; with tools < 50 cm: 0/55; one-tailed Z-test comparing two proportions: $z = 6.03$; $\rho < 0.001$) and at the nest site (with tools ≥ 50 cm: 23/65; with tools < 50 cm: 0/14; one-tailed Z-test comparing two proportions: $z = 5.97$; $\rho < 0.001$). Even when the analysis was restricted to "pull-through only" vs. "mouthing only" tools, the association was still highly significant (overall: with tools ≥ 50 cm: 17/65; with tools < 50 cm: 0/55; one-tailed Z-test comparing two proportions: $z = 4.80$; $\rho < 0.001$; nest: with tools ≥ 50 cm: 17/35; with tools < 50 cm: 0/14; one-tailed Z-test comparing two proportions: $z = 5.75$; $\rho < 0.001$). Indeed, all cases of use of tools < 50 cm long were associated with direct mouthing, while the pull-through technique was only observed with tools ≥ 50 cm long (see Fig. 2).

However, the associations between pulling-through and tools ≥ 50 cm long, and pulling-through and ant-dipping at the nest call for a reexamination of the previously detected positive relationship between longer tools and dipping at the nest (see Fig. 1 and Table II). This analysis was carried out on "mouthing only" tools. Wands ≥ 50 cm long were significantly more likely to be used when dipping on ants at the nest (35/49) than on migrating ants (13/54) (one-tailed Z-test comparing two proportions: $z = 5.45$; $\rho < 0.001$).
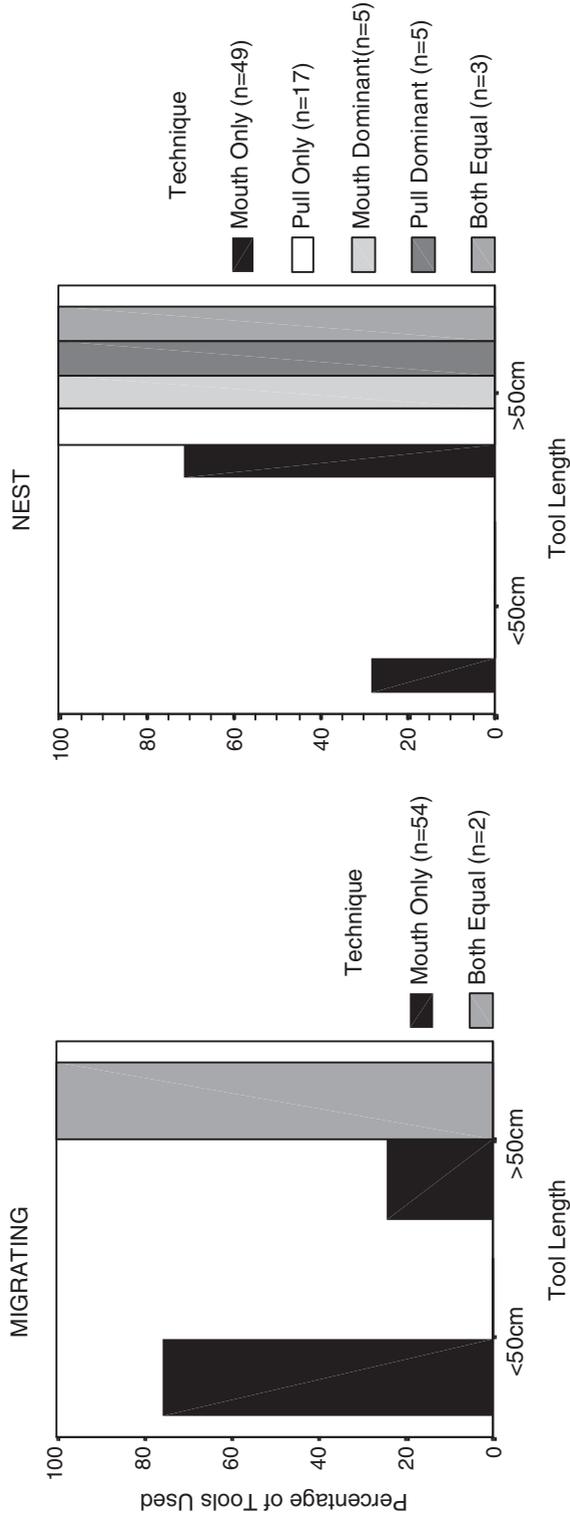
Fig. 2. Tool size and technique observed at the nest site and when dipping for migrating ants (pull: pull-through; mouth: mouth directly).

Ant-Dipping Position

Regardless of ant condition, the above-ground and ground-level positions were independent of tool length (overall: $\chi^2(1, n=238)=0.107$; n.s; nest: $\chi^2(1, n=135)=0.083$; n.s; migrating: $\chi^2(1, n=103)=2.979$; n.s), technique used (overall: $\chi^2(1, n=238)=1.433$; n.s; nest: $\chi^2(1, n=130)=0.413$; n.s; migrating: Fisher's exact test: $n=101$; n.s) and type of *Dorylus* ant dipped for (overall: $\chi^2(1, n=238)=0.210$; n.s; nest: Fisher's exact test: $n=135$; n.s; migrating: $\chi^2(1, n=103)=0.114$; n.s.) (see Table III).

Chimpanzees dipping at the nest site (above ground: 86/135) were significantly more likely to be above ground than chimpanzees dipping on migrating ants (above ground: 47/103) (one-tailed Z-test comparing two proportions: $z=2.82$; $\rho<0.01$). This result again suggests that the chimpanzees respond to the greater risk of being bitten by ants at the nest. Dipping from a position above ground probably provides more protection from biting ants.

Technique, Dipping Time, and Efficiency

Dipping time in seconds was assessed from the video records. Dipping time refers to the time elapsed between the chimpanzee placing its wand into the mass of ants and starting to ingest the ants. The question was, what is the relationship between dipping time and technique used? A Wilcoxon signed ranks test indicated that dipping times were significantly longer for pulling-through than mouthing ($n=8$, $z=-2.100$, $\rho<0.05$) (see Table IV).

Overall, dipping time was also significantly longer when dipping for Black *Dorylus* than for the Red type (Wilcoxon signed ranks test: $n=8$, $z=-2.521$; $\rho<0.05$) (see Table IV). However, the Red species ($n_{Red}=63$; mean $=3.9$ cm/sec; SD $=1.4$; median $=4.02$ cm/sec; range: 0.73–8.25 cm/sec) were faster at climbing

TABLE III. Frequency of Position Scores Overall and When Dipping on Nesting and Migrating Ants Depending on Tool Length, Ant Type, and Technique used

Ant condition	Position	Tool length		Ant type		Technique used	
		<50 cm	≥50 cm	Black	Red	Mouth	Pull-through
Overall	Above ground	56	77	23	117	111	28
	Ground level	42	64	15	90	85	14
Nest	Above ground	23	63	4	82	59	23
	Ground level	12	37	0	49	37	11
Migrating	Above ground	33	14	14	33	47	3
	Ground level	30	26	15	41	48	3

TABLE IV. Summary Statistics of Dipping Time (sec) Depending on Technique Used, Ant Type Dipped for, and Ant Condition

	Variable	Mean (sec)	Median (sec)	SD	Range (sec)
Technique	Pull-through	31.5	28.0	10.9	19.5–50.0
	Direct mouthing	24.6	25.5	6.9	14.5–35.0
Ant type	Black	28.8	28.0	5.4	23.0–39.0
	Red	20.7	22.0	5.4	13.0–28.0
Ant condition	Nest	23.3	21.0	9.4	13.0–38.0
	Migrating	23.5	24.0	7.7	7.0–33.0

TABLE V. Summary Statistics of the Number of Ants Gathered During the Ant Dipping Experiment According to Ant Condition and Depending on Tool Length Employed

Ant condition	Tool length	No.	Mean	Median	SD	Range
Nest	Short (28.1 cm)	70	67.3	45.0	81.5	4–404
	Medium (55.3 cm)	68	54.2	43.0	42.1	5–220
	Long (101.7 cm)	74	77.2	59.5	74.7	13–544
Migrating	Short (28.1 cm)	82	35.9	21.0	69.6	2–599
	Medium (55.3 cm)	78	35.8	26.0	41.5	4–243
	Long (101.7 cm)	72	34.1	24.0	42.2	3–263

up the wand than *Dorylus nigricans* ($n_{Black} = 53$; mean $= 3.4$ cm/sec; SD $= 1.5$; median $= 2.98$ cm/sec; range: 1.12–9.16 cm/sec) (Mann-Whitney U-test: $z = -2.696$; $\rho = 0.007$).

Another question posed was, does dipping time vary according to whether the ants are at the nest site or are moving on the ground. However, no significant difference in dipping time emerged between the two ant conditions (Wilcoxon signed ranks test: n $= 9$, $z = -0.415$; n.s.) (see Table IV).

In the ant-dipping experiment, there was no correlation between dipping time and quantity of ants harvested either overall ($R_s = 0.041$; n $= 444$; n.s.) or on migrating ants ($R_s = -0.102$; n $= 232$; n.s.). In contrast, there was a significant positive correlation between dipping time and the number of ants collected when ants were dipped for at the nest ($R_s = 0.316$; n $= 212$; $\rho < 0.001$). Thus, longer dipping times at the nest were related to enhanced ant harvesting.

During the ant-dipping experiment, a significant difference in the amount of ants gathered at the nest site was found across the three different tool lengths employed (Kruskal-Wallis test: $\chi^2 = 8.521$ df $= 2$; $\rho < 0.05$) (see Table V). Dunn's post hoc test indicated that the long tool yielded more ants than either the short tool or the medium-length tool; however, there was no difference between the latter two (see Table V). No difference across the three tools occurred for migrating ants (Kruskal-Wallis test: $\chi^2 = 1.747$; df $= 2$; n.s.) (see Table V). Therefore, the use of longer tools at the nest site is probably not simply a response to the greater biting risk, but also an adaptation for greater ant harvesting.

Chimpanzees at Bossou performed the dipping movement on average 2.37 times/min (SD $= 2.7$) (based upon 1,104 successful dips). Adult chimpanzees (12+ years old) performed dipping acts 2.6 times/min (SD $= 2.3$), based upon 610 successful dips. Based on 444 dips across both types of *Dorylus* and under both ant conditions, the overall mean number of ants harvested during the ant-dipping experiment was 50.24 per dip (SD $= 63.1$). Based on these figures, chimpanzees at Bossou gathered on average 119 ants/min (SD $= 105.1$) during an average dipping session, and adults gathered an average of 131 ants/min (SD $= 77.6$).

DISCUSSION

A clear influence of prey condition and behavior on the length of ant-dipping wands used by Bossou chimpanzees emerged. An influence of insect behavior on tool attributes and employment has previously been reported for honey feeding [cf. Tutin et al., 1995; Stanford et al., 2000; Boesch and Boesch, 1990], as well as ant-dipping at Taï [Boesch & Boesch, 1990]. This study revealed that Bossou chimpanzees employed significantly longer tools when dipping for

ants at their nest than on migrating ants; ants at their nest were at higher densities and/or were more belligerent compared to migrating ants. This trend was independent of the technique employed or type of ants examined, and suggests that the chimpanzees were responding to the risk of being bitten by the ants.

Bossou chimpanzees dip for several species of driver ants. The Black type, *D. nigricans,* was found to be more gregarious and/or more belligerent than the Red *Dorylus*. Analysis of tools and video records indicated that when dipping for the Black type compared to the Red, the chimpanzees tended to use significantly longer tools at the nest site and were more likely to employ tools ≥ 50 cm long on migrating columns. The ant-dipping experiment failed, though, to distinguish between gregariousness and aggressiveness in the two *Dorylus* types. These two variables were inevitably confounded, as the number of ants biting or attacking the intruding object, i.e., the wand, is dependent upon both the density and the belligerence of the ants.

Regardless, some form of risk assessment appeared to influence tool-making, and therefore tool length, among the chimpanzees of Bossou. The finding that tool length was influenced by the condition of the prey supports Sugiyama's [1995] hypothesis that characteristic features of the prey must determine the length of the wand. However, other variables, such as technique employed, were also influenced by prey condition and were closely associated with tool length.

The slight discrepancy between mean tool length observed during this study and that reported in other studies from Bossou [Sugiyama, 1995] (Yamakoshi and Myowa-Yamakoshi, unpublished results) could be an artifact from different frequencies of chimpanzee dipping under both conditions, or from different ant types between the study periods over which tools were gathered. Unfortunately, frequency data were not reported in any of the previous studies.

Two ant-dipping techniques were observed at Bossou: 1) direct mouthing of the tool, removing the ants with the teeth or lips; and 2) swiping the length of the tool to gather the ants in the hand before rapid transfer to the mouth, also known as the pull-through technique. There were individual differences in the relative employment of the techniques, which were age-independent and not necessarily consistent between mother and offspring.

At Bossou, the technique employed was related to the condition of the ants and tool length. The pull-through technique was only observed with the use of tools ≥ 50 cm long and almost solely associated with dipping at the nest. In addition, although direct mouthing took place under both ant conditions, it was more likely to occur on migrating ants than on ants at the nest, and tools < 50 cm in length were exclusively associated with this technique.

Differences in prey aggressiveness and behavior may lead to differences in tool length within and between communities of chimpanzees. However, as suggested by Hashimoto et al. [2000], differences in tool length may also reflect the different techniques used for catching ants. These two hypotheses are supported by the findings of this study, but to what extent can these results be applied to what was observed at Taï and Gombe? Extrapolating from the present study, Gombe chimpanzees would be expected to exhibit the pull-through technique since they more often employ tools > 50 cm long (n $= 13$; mean $= 66$ cm; range: 15–113 cm [McGrew, 1974]) than do the Taï chimpanzees (n $= 35$; mean $= 23.9$ cm; range: 11–50 cm [Boesch and Boesch, 1990]). Finally, Taï chimpanzees should only perform direct mouthing, since they use wands shorter than 50 cm. Observations of ant-dipping techniques at those sites support these predictions [McGrew, 1974; Boesch and Boesch, 1990].

Considering that longer tools at Bossou were associated with greater prey aggressiveness/gregariousness, one may predict that the *Dorylus* species dipped for at Gombe (*D. nigricans*) is more aggressive or better at deterring intruders than the species dipped for at either Taï (*D. nigricans* and *D. gerstaeckeri*) or Bossou. As yet, no data contrasting prey aggressiveness or density across these three sites are available to test this prediction.

However, there may be indirect measures by which to compare differences in prey aggressiveness. McGrew [1974] pointed out that Gombe chimpanzees stayed off the ground in 74% of ant-dipping episodes, while Bossou chimpanzees, in this study, ant-dipped from above ground only 55.9% of the time (number of independent ''above-ground'' data points/total number of independent position data points). Although we found position to be independent of tool length, technique used, and type of *Dorylus* species dipped for, Bossou chimpanzees were significantly more likely to be positioned above ground when dipping for nesting ants than for migrating ones. This result suggests an influence of prey density or aggressiveness on chimpanzee position during ant-dipping, thus supporting the argument that the species of *Dorylus* ant found at Gombe may pose a greater risk to the chimpanzees than at Bossou. To date no such data have been published for chimpanzees at Taï.

The extent of feeding on ant eggs and grubs, which are more nutritious than adult ants [Wu Leung, 1968, cited in Boesch and Boesch, 1990], could also be a good indicator of prey aggressiveness. Boesch and Boesch [1990] noted a difference in prey emphasis among the chimpanzees of Taï, where two species of *Dorylus* ants are dipped for. The grubs of the larger species (*D. nigricans*) are more frequently eaten than those of the more aggressive species (*D. gerstaeckeri*), for which tools are most frequently used to capture adults [Boesch & Boesch, 1990].

This behavior has rarely been observed at Gombe [Goodall, 1986; McGrew, 1974], but is quite common at Taï [Boesch & Boesch, 1990]. At Bossou, chimpanzees also fed on eggs and grubs, but solely targeted the Red species of *Dorylus*. If the frequency of this behavior is indeed influenced by prey belligerence or density, this would suggest that *D. nigricans* at Gombe is fiercer or more gregarious than those species of *Dorylus* found at either Bossou or Taï. Gombe chimpanzees would thus be more likely to use longer tools to avoid being bitten.

It is also possible that the pull-through technique may be the most effective method of gathering ants off a long tool, which would then explain the predominance of this technique at Gombe. During pull-through, the gathered mass of ants is crumpled and jumbled so that few can bite the chimpanzee before they are consumed, whereas they pose a greater biting risk to the chimpanzee if the long tool is mouthed.

It has been suggested that the pull-through technique is generally a more efficient technique than direct mouthing [Boesch & Boesch, 1990]. At Bossou, the pull-through technique was associated with longer dipping times and at the nest site only, with better ant harvesting. Also, the longer tools used during the ant-dipping experiment yielded more ants, but again at the nest site only. Significantly longer dipping times were also observed while dipping for the Black type; however, the Red type was found to climb the length of the wand more rapidly than the Black type.

Nevertheless, Bossou chimpanzees were found to gather on average only 119 ants/min (131 ants/min for adults) during an average dipping session, which is lower than at Taï (180 ants/min [Boesch & Boesch, 1990]) or Gombe [760 ants/min [McGrew, 1974]). Boesch [1996] suggested that Taï chimpanzees could gain

more ants if they employed the Gombe pull-through technique, and that their current technique is not optimal. But why, then, do chimpanzees at Bossou, who exhibit the pull-through technique, appear to have such a low level of efficiency compared to those at Gombe and Taï? We believe that a replication of these efficiency measures based on more dipping simulations (number of ants/dip) and a larger set of chimpanzee dips (dips/min) are required from both Gombe and Taï. Moreover, a taxonomic reexamination of *Dorylus* species found at the sites where chimpanzees have been shown to dip may be required, since field workers lacking an entomological background may have misidentified some species and hence the number of species available in each habitat.

Finally, this study clearly shows the potential usefulness of detailed investigations of ant-dipping across various field sites, especially at Taï and Gombe, so that the influence of prey behavior and characteristics, such as aggressiveness and gregariousness, at the nest and during migration can further be assessed.

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