

RESEARCH ARTICLE

Chimpanzees Prey on Army Ants with Specialized Tool Set

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Several populations of chimpanzees have been reported to prey upon *Dorylus* army ants. The most common tool-using technique to gather these ants is with “dipping” probes, which vary in length with regard to aggressiveness and lifestyle of the prey species. We report the use of a tool set in army ant predation by chimpanzees in the Goulougo Triangle, Republic of Congo. We recovered 1,060 tools used in this context and collected 25 video recordings of chimpanzee tool-using behavior at ant nests. Two different types of tools were distinguished based on their form and function. The chimpanzees use a woody sapling to perforate the ant nest, and then a herb stem as a dipping tool to harvest the ants. All of the species of ants preyed upon in Goulougo are present and consumed by chimpanzees at other sites, but there are no other reports of such a regular or widespread use of more than one type of tool to prey upon *Dorylus* ants. Furthermore, this tool set differs from other types of tool combinations used by chimpanzees at this site for preying upon termites or gathering honey. Therefore, we conclude that these chimpanzees have developed a specialized method for preying upon army ants, which involves the use of an additional tool for opening nests. Further research is needed to determine which specific ecological and social factors may have shaped the emergence and maintenance of this technology. *Am. J. Primatol.* 71:1–8, 2009. © 2009 Wiley-Liss, Inc.

Key words: *Pan troglodytes troglodytes*; ant-dip; perforation; army ants

INTRODUCTION

Chimpanzee tool use in predation on *Dorylus* army ants has been documented across Africa [McGrew, 1992; Schöning et al., 2008], and there have been detailed studies of the behavior of certain *Dorylus* species preyed upon by chimpanzees in West Africa [Humle & Matsuzawa, 2002; Möbius et al., 2008]. Schöning et al. [2008] concluded that much of the variation in tool use to prey upon army ants could be explained by the characteristics of the targeted species. However, it was inexplicable why some chimpanzee populations ignored certain ant taxa that are consumed at other sites, and why chimpanzees at Bossou and Taï used different techniques to gather the same prey species. In this study, we set out to document the tool use in army ant predation by a population of wild chimpanzees residing in the Congo Basin. Chimpanzee tools have been recovered at *Dorylus* ant nests in this region [Hicks et al., 2005], and army ant consumption has been confirmed without tools being present [Deblauwe & Janssens, 2007], but there have been no reports of the tool behaviors associated with ant predation. Based on tool assemblages recovered at ant nests, we have suggested that chimpanzees

may use two different types of tools to harvest ants [Sanz & Morgan, 2007].

Although the use of tools is observed across many diverse animal groups, the use of tool sets is relatively rare and has most often been observed in great apes [Fox et al., 1999; Sanz & Morgan, 2009a,b; Sanz et al., 2004; Sugiyama, 1997]. Tool sets are characterized by the use of more than one type of tool to achieve a goal [Brewer & McGrew, 1990]. The tools are typically used in serial order, such as the puncturing and fishing techniques used to harvest subterranean termites in central Africa [Sanz et al., 2004]. However, these chimpanzees exhibit more

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flexibility in the order of tool types used in honey gathering [Sanz & Morgan, 2009a]. Further research is needed on the hierarchical structuring of tool tasks, which could provide evidence of advanced causal understanding of object relations [Matsuzawa, 1996].

The most commonly observed behavior in army ant predation is dipping (Table I), which involves introducing a probe to a nest or column to gather ants that stream up the tool [McGrew, 1974]. This is in contrast to fishing of arboreal ant species which involves inserting a slender probe into a nest and gathering the ants that attack and cling to the probe [Nishida, 1973]. At Bossou and Seringbara in Guinea, there have also been descriptions of tools possibly used to dig open army ant nests [Humble, 2003; Humle & Matsuzawa, 2001]. These tools have been characterized as being sturdier than dipping tools, and having the function of opening the nest for dipping. Sugiyama [1995] reported that an adult female at Bossou was once observed to use a thick stick to dig into an army ant nest, after which she used a slender wand to dip for the ants. Although the use of digging tools by chimpanzees to open ant nests has been rarely observed (one instance at Bossou, Guinea) or based on indirect evidence (Seringbara, Guinea), there are several reports of

wild chimpanzees manually opening nests for dipping or gathering brood [Boesch & Boesch, 1990; McGrew, 1974].

In this study, we present our observations of chimpanzees using a tool set to prey upon *Dorylus* army ants in the Goualougo Triangle, Republic of Congo. We examine video recordings of chimpanzee predation on ants, analyze characteristics of tool assemblages at ant nests, and identify targeted prey species to assess whether our observations are similar to behaviors reported from other long-term chimpanzee studies. If tool sets are regularly used by chimpanzees in the Goualougo Triangle to prey upon ant taxa that are consumed by chimpanzees at other sites with a single tool technique, then this would warrant further investigations into the factors shaping these behavioral variants. We provide detailed descriptions of the types of tools to facilitate their recognition at sites where direct observations have not been made and/or to identify any stylistic differences in tool form between chimpanzee populations. Regardless of potential ecological explanations, if the behavior is widespread, then it is likely that there are some social mechanisms implicated in the transmission and maintenance of this behavior between individuals and groups.

TABLE I. Comparison of Chimpanzee Tool Use in Ant Predation Across Sites

Taxon study site	Dip tool		Dig/Perforate tool	
	<i>n</i>	Length \pm SD (cm)	<i>n</i>	Length \pm SD (cm)
<i>P.t. verus</i>				
Tenkere, Sierra Leone ^a	7	79.8 \pm 9.7		
Taï, Ivory Coast ^b	28	23.9 \pm 12.6		
Bossou, Guinea ^c	189	53.7 \pm 21.01	1	106
Seringbara, Guinea ^d	32	57.6 \pm 24.0	9	65.1 \pm 17.9
Assirik, Senegal ^e	48	72 \pm 20		
Fongoli, Senegal ^f	24	79 \pm 28.2		
<i>P.t. vellerosus</i>				
Gashaka, Nigeria ^g	72	83.8 \pm 27.4		
<i>P.t. troglodytes</i>				
Goualougo, Rep. Congo	716	64.4 \pm 17.5	228	92.3 \pm 36.0
Ngotto Forest, C.A.R. ^h	46	84.6 \pm 32.6		
<i>P.t. schweinfurthii</i>				
Gombe, Tanzania ⁱ	13, 30	66, 63		
Kalinzu, Uganda ^j	14	79 \pm 8		
North Bili-Uele, D.R.C. ^k	110	84.7 \pm 47.6		
South Bili-Uele, D.R.C. ^k	22	53.7 \pm 17.4		

^aAlp [1993].

^bBoesch and Boesch [1990].

^cSugiyama [1995]; Humle and Matsuzawa [2002].

^dHumble [2003]; Humle and Matsuzawa [2001].

^eMcGrew et al. [2003].

^fMcGrew et al. [2005].

^gFowler and Sommer [2007].

^hHicks et al. [2005].

ⁱMcGrew [1974].

^jHashimoto et al. [2000].

^kT. C. Hicks, unpublished data.

METHODS

Study site. The Goulougo Triangle is located within the southern sector of the Nouabalé-Ndoki National Park in northern Republic of Congo. The study area covers 380 km² of evergreen and semi-deciduous lowland forest with altitudes ranging between 330 and 600 m. The climate can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones. Rainfall and temperature were recorded daily at the Goulougo Triangle base camp. Rainfall was 1,650 mm in 2007 and 1,676 mm in 2008. Average monthly rainfall from September 2006 to February 2009 is shown in Figure 1. The average minimum and maximum temperatures were 21.5 and 24.2°C in 2007, and 21.5 and 24.1°C in 2008.

Data collection. Between February 1999 and September 2008, we spent a total of 111 months in the Goulougo Triangle habituating and studying wild chimpanzees. Chimpanzee tool assemblages were collected at army ant nests by several field teams conducting daily reconnaissance walks throughout the year. We recorded the location, materials used to make the tool, length, width, and any modifications to each tool. Chimpanzee tool-using behaviors were documented by direct observation and remote video monitoring at ant nests [for description of these methods, see Sanz et al., 2004]. For all the observations of tool-using behavior, we recorded the identification of the chimpanzee, type of object used, target of object, actions, context and/or goal of the tool-using behavior, and the outcome.

Video analysis. We archived data from digital video cassettes on external hard drive devices and converted them to MPEG files for review. We conducted video analysis using INTERACT software [Mangold, 2006]. Within each video recording, we scored the tool-using bouts of each chimpanzee.

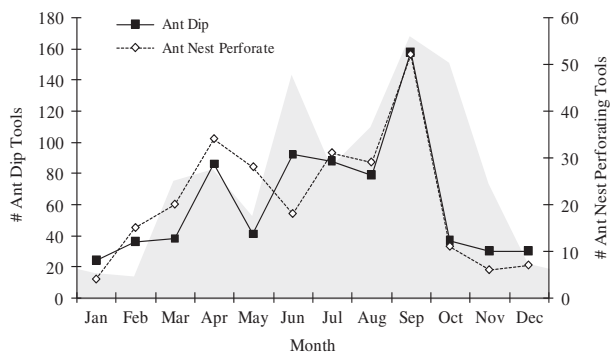


Fig. 1. Chimpanzees preyed upon army ants using both types of tools throughout the year in the Goulougo Triangle. Gray shading indicates average monthly rainfall (averaged for each month between September 2006 and February 2009) on a scale of 0–300 mm, with the lowest average rainfall of 34 mm in February and the average highest rainfall of 286 mm in September. The overall peak in frequency of both ant nest perforation and ant-dipping occurred at the beginning of the main rainy season.

Bouts were defined as beginning when a chimpanzee uses a tool toward achieving a goal, and ending when he/she starts using another tool, discards the tool, or pauses use of the tool for >5 sec [Sanz & Morgan, 2009a]. Video recordings were scored independently by two observers, and any divergences in scoring were reviewed by both observers, until a consensus was reached [adopted from Humle & Matsuzawa, 2002].

Statistical analyses. All statistics were conducted using SPSS 13 (SPSS, Chicago). The equality of variances among variables was evaluated with Levene's test. Measurements of the characteristics of individual tools were compared with independent sample *t*-tests across tool types.

Army ant identification and behavior. To document the availability and consumption of *Dorylus* prey species, we collected ant specimens from chimpanzee tool use sites and on reconnaissance surveys. Specimens were preserved in 90% ethanol and transported to Europe for identification. Voucher specimens of all *Dorylus* species found in this study have been deposited in the Entomology collection of the Zoological Museum Copenhagen. Lifestyles of different army ant species can be characterized as “epigaeic” or “intermediate” [Schöning et al., 2005]. Epigaeic species forage on the ground and up in the vegetation in large and conspicuous swarms, while intermediate species forage only in the leaf litter. Their responses to attacks also differ. When trails of epigaeic species are disturbed, the workers attack. In contrast, workers of intermediate species withdraw into underground tunnels or into the leaf litter when the exposed sections of their trails are disturbed. Workers of epigaeic species have longer legs and mandibles so that they can run faster and inflict more painful bites [Möbius et al., 2008; Schöning et al., 2008].

All the field protocols, data collection procedures, and data analyses were conducted in accordance with wildlife research protocols and ethical standards of the Wildlife Conservation Society of the USA, the Ministry of Science and Technology of the Republic of Congo, and the Ministry of Forest Economy of the Republic of Congo.

RESULTS

Diversity of Army Ants at the Site

We confirmed the presence of several epigaeic and intermediate army ants in the Goulougo Triangle. Epigaeic species included *Dorylus mayri*, *D. rubellus*, *D. sjoestedti*, and *D. wilverthi*. Intermediate species were represented by *D. emeryi*, *D. kohli*, and *D. opacus*. With a total of seven species, the assemblage of epigaeic and intermediate *Dorylus* army ants is the most diverse ever recorded. Each of these species is present and consumed at another chimpanzee study site [Schöning et al., 2008].

Chimpanzee predation involving tools was confirmed with all species, except *D. emeryi* and *D. opacus* of which very few samples were collected. Tool sets were associated with all four epigaeic species (*D. mayri*, *D. rubellus*, *D. sjoestedti*, *D. wilverthi*).

Tool Assemblages

We collected 284 tool assemblages totaling 1,060 tools at ant nests in the Goualougo Triangle. Chimpanzee predation upon ants occurred throughout the year, with a peak at the beginning of the long rainy season (Fig. 1). The average number of tools recovered at each site was 3.73 tools ($n = 284$, $SD = 3.27$, range = 1–18). Thirty-six percent of these assemblages contained two types of tools, nest-perforating tools and ant-dipping probes (Fig. 2).

Tools used to perforate ant nests had an average length of 92.3 cm ($n = 228$, $SD = 36.0$, range = 22–264) and an average diameter of 7.3 mm ($n = 226$, $SD = 1.8$, range = 1–14). Perforating tools were typically made from saplings within 3 m of the ant nest. The five most common species used for perforating tool material (*Diospyros* spp., *Tabernaemontana* spp., *Drypetes* spp., *Pleiocarpa pycnantha*, *Millettia sanagana*) composed 56% of the tools ($n = 66$) for which tree species were identified. The proximal end of these tools was usually associated with a small amount of fraying which occurred as a result of detaching the trunk or during ant nest perforation. There was no indication that the fraying of the end of the tools was intentional. Leafy branches were intact on the distal end of 78% of perforating tools ($n = 270$).

Ant-dipping tools had an average length of 64.4 cm ($n = 716$, $SD = 17.5$, range = 18–118) and an average diameter of 5.4 mm ($n = 721$, $SD = 1.1$, range = 1–10). In contrast to the woody puncturing sticks, dipping probes were made from flexible herbaceous materials. More than 96% of probes were manufactured from *Sarcophrynium* spp., *Ataenidia conferta*, *Megaphrynium* sp., or *Marantochloa* spp. Dipping tool materials were often gathered by uproot-



Fig. 2. Tool set used by chimpanzees to prey upon army ants in the Goualougo Triangle, Republic of Congo. The top two tools are herbaceous dipping probes. The bottom tool is a perforating tool with the leafy branches intact at one end. Above the perforating tool is a measuring tape totaling 20 cm in length.

ing the entire stem so it was common to recover tools with roots intact at the unused end. This was a distinction from termite fishing tools which were typically clipped near the base within the herb stand [Sanz et al., 2004]. The broad leaf of this stem was almost always removed before ant-dipping. These tools often have frayed ends, but it remains unclear if this is a premodification by the chimpanzees or a byproduct of removing ants from the end of the tool.

Ant-perforating and dipping tools were distinguishable not only by the materials, but also in their length and diameter. Nest-perforating tools were significantly longer (two-tailed unequal-variance t -test, $t = 11.61$, $DF = 272.83$, $P < 0.001$) and thicker in diameter than ant-dipping tools (two-tailed unequal-variance t -test, $t = -16.05$, $DF = 289.27$, $P < 0.001$).

Chimpanzee Tool Use in Army Ant Predation

Between 2004 and 2008, we collected 25 video recordings containing 59 bouts of chimpanzee tool-using behavior, which occurred at 10 ant nests within the Moto community range. We recognized 12 identified chimpanzees in these videos (adult males, 3; adult females, 4; subadult males, 2; subadult female, 1; juveniles, 2). Five individuals were observed on multiple occasions, with an average of 1.67 observations per individual in this sample. Four known individuals used ant nest-perforating tools and ant-dipping probes (for example, see Supplementary Video 1), and all other individuals used only ant-dipping probes.

Chimpanzees were observed to perforate an ant nest with a woody sapling on 11 occasions, often by grasping the leafy branches that were left intact at the unused end of the tool. The entire length of the tool was then inserted, with only the leafy branches left resting on top of the nest. The chimpanzee might partially withdraw and insert the sapling into the nest several times. The perforating tool was then withdrawn from the nest, and a herbaceous dipping tool either inserted into the nest or laid on the surface of the nest to gather ants that streamed onto the tool. We recorded a total of 48 bouts of ant-dipping with a flexible, herbaceous tool. Several chimpanzees were observed to bounce, twist, or tap the tool while ant-dipping, which may have been to stimulate movement of the ants onto or up the tool. We also observed reuse of perforating tools by three individuals (AM, AM, AF). On two occasions tools manufactured by another individual were used by a subsequent visitor to the ant nest (as shown in Supplementary Video 2), and on the third occasion an adult male reused a perforating tool that he had manufactured during a previous visit.

These chimpanzees were observed both pulling the herb stem through their hand to sweep the ants into their mouth (ant-dip-wipe, pull-through) and eating ants directly from the end of the tool

(ant-dip-single, direct-mouthing) [Humble & Matsuzawa, 2002; Whiten et al., 1999, 2001; Yamakoshi & Myowa-Yamakoshi, 2004]. Seventy-six percent of all observed feeding actions ($n = 286$) were the pull-through method, and the remainder were the direct mouthing technique. To avoid any potential biases associated with limited behavioral observations of some individuals, we also calculated the feeding techniques for the five most observed individuals (≥ 25 feeding actions observed). The results were nearly identical, with 78% of feeding actions being the pull-through technique. However, four of these individuals showed both techniques and the prevalence of direct mouthing ranged from 6 to 68% of their total feeding actions. Although the pull-through action was the dominant feeding technique, there were individuals that showed both the pull-through and direct mouthing method with the same tool and during the same visit to the ant nest.

The chimpanzees often positioned themselves above the ground to avoid the attacks of army ants. Moving up onto tree buttresses, lianas, or saplings near the ant nest was observed in 60% of the video recordings of individual chimpanzees, which is similar to the reports of 64% from Bossou and 74% from Gombe of ant-dipping episodes during which chimpanzees moved up off the ground [Humble & Matsuzawa, 2002; McGrew, 1974]. Although chimpanzees in Goulougo were likely to climb up at some point during their tool-using episode, it was more common for them to use tools while sitting or standing on the ground. Only 36% of the actual amount of time spent tool using was from a position perched above the nest.

DISCUSSION

We report the widespread and regular use of a tool set in ant predation by chimpanzees in the Goulougo Triangle, Republic of Congo. The two types of tools have distinctly different forms and functions. Chimpanzees use wooden tools made from small saplings to perforate the nest and then gather ants with wands made from herb stems. Although all of the species of army ants present at Goulougo are consumed at other chimpanzee study sites, this is the first study to confirm the regular use of tool sets by chimpanzees to prey upon army ants.

The forms of tools used for perforating and dipping in Goulougo are very easy to distinguish. Perforating tools are made from woody saplings that are thicker and longer than dipping tools, and the leafy branches of the tool are left intact. Not removing these branches may provide added length to the tool, provide a protective barrier from the ants on the surface of the nest, and also serve as a good grip for inserting the tool into the nest. Alternatively, the leafy branches do not seem to compromise the functionality of the perforating tool and so

simply may not require removal. The sturdy material and thicker diameter of the perforating tool enable the chimpanzee to insert this tool deep into the nest and clear any minor obstructions for the dipping probe. The perforating tool could also serve the function of “reactivating” a nest as described by McGrew [1974]. Although some ants can typically be found at the surface of the nest, the majority of the colony is located in the subterranean chambers and vigorous insertion of the wooden tool may cause them to emerge and attack. Dipping tools are manufactured from herb stalks, and are characterized as being slender and flexible with all leafy vegetation removed. Eighty percent of these probes were longer than 50 cm, which could be in response to the aggressiveness of the ant species most often preyed upon [Schöning et al., 2008].

Based on the observations of ant nest digging and ant-dipping tools in Guinea, it is possible that this tool set once had a wider distribution or has been independently innovated in different chimpanzee populations across western equatorial Africa. Sugiyama’s [1995] single observation of an adult female chimpanzee using a stout stick to dig into an ant nest before using a second slender tool to dip suggests that the behavior is not habitual or customary in Bossou. However, colleagues working in the area have suggested that chimpanzees use digging tools at the Seringbara site which is less than 10 km from Bossou [Humble, 2003]. The digging tools in Bossou and Seringbara were distinguished from dipping tools by having a thicker diameter and slightly longer length [Humble, 2003; Sugiyama, 1995]. This is similar to the perforating tools used by chimpanzees in Goulougo, but we also found that perforating tools were manufactured from different materials and have different forms than dipping tools. Perforating tools are made of stout saplings with the leaves intact, and dipping tools from flexible herb stems with the leaves detached.

As chimpanzees prey upon the same or similar ant species at other sites, one must ask why they do not regularly use perforating tools as we have documented at Goulougo. In Tai and Bossou, chimpanzees manually open epigeic nests and take brood directly with their hands [Boesch & Boesch, 1990; Humle, 2009]. This may also be the case at Dja in Cameroon where army ants are consumed, but no tools have been recovered at ant nests [Deblauwe & Janssens, 2007]. Chimpanzees in the Bossou and Nimba region in southwestern Guinea may sometimes use such tool sets but the frequency is much lower [Humble, 2003; Humle & Matsuzawa, 2001; Sugiyama, 1995]. The use of perforating tools instead of hands for opening nests might confer two advantages to chimpanzees in Goulougo (a) it elicits a less aggressive attack from the ants which may in turn allow overall longer dipping times and higher yields and/or (b) it causes less disturbance and

reduces the likelihood of an early migration of the army ant colony so that chimpanzees can continue to exploit the same nest repeatedly over the course of days or weeks. When chimpanzees rake a nest open with their hands, there will be a large opening which allows the chimpanzee to “dip” a tool into a large mass of prey ants, but the disturbance elicits a massive counter-attack response from the army ants. As chimpanzees are sensitive to the ants’ bites, the speed with which the defending ants cover the area and attack the predator might be the factor ultimately limiting dipping time and yield. Perforation tools may therefore serve the purpose of enticing the ants to come out and to allow the insertion of the dipping tool (or the harvesting of ants on the surface with the dipping tool) while at the same time reducing the ants’ aggressive response. If the chimpanzees are able to dip for a longer duration, then they are likely to increase their nutritional gain. Further research on the aggressive responses of particular ant species and chimpanzee dipping yields from different sites will be required to address this hypothesis. The other potential advantage of using perforating tools is that the structural integrity of the army ant nest is not dramatically compromised which means that the ants may stay longer in their nest and not quickly migrate to another location in response to the attack. Manually taking brood from a nest may allow a large yield, but it is likely that the associated degree of disturbance will cause the ant colony to migrate to another site. If the ants do not migrate as a result of the chimpanzees’ exploitation techniques, then the apes would be able to repeatedly visit the same nest to gather ants which reduces their search time and could also be a form of “sustainably harvesting” this food resource. This hypothesis could be tested experimentally by comparing the time until army ant colonies migrate after attacks simulating different predation techniques (opening nests with hands vs. perforating tools).

Parker and Gibson [1977] proposed that intelligent tool use in primates arose in extractive foraging contexts where these skills facilitated access to food resources that were encased in structures and otherwise not accessible. We have observed several different types of tool sets used by the chimpanzees of the Ndoki forest to open a substrate and then gather the embedded food resource. Puncturing and fishing tools are used to gather subterranean termites [Sanz et al., 2004]. Perforating and fishing tools are used to gather epigeic termites [Sanz et al., 2004]. Several different combinations of tool types have been observed in honey gathering [Sanz & Morgan, 2009a]. The tool set in army ant predation was similar in function to some of these other tool sets, but specialized for the ant gathering context. Tools used to open termite nests, bee hives, and army ant nests are typically made of wooden materials. For the puncturing context, the tool is made of a

particular tree species (*Thomandersia hensii*) that is well suited to the task. Bee hive pounding requires thick tools that are most often gathered from dead branches in the tree canopy where the hive is located. Ant nest-perforating tools are typically made after arrival at the army ant nest and from tree species in its vicinity. In contrast to puncturing and pounding tools, the perforating tools used at army ant nests often have many leafy branches intact on the end of the tool that is not inserted into the nest. The chimpanzees seem to recognize this tool form, as they have been observed to reuse tools discarded at the site by other individuals during previous visits. Herb stems are used in gathering both termites and ants, but ant-dipping probes are longer than termite fishing probes. We have found that ant-dipping probes may have frayed ends, but this does not seem to be a consistent premodification by the tool users as we have documented is the case with the brush-tip fishing probe used by this chimpanzee population [Sanz and Morgan, 2009a,b]. The broad repertoire of tool-using behaviors and relative abundance of tool sets may have developed as a means to cope with intra- and interspecific competition for food resources. Reducing their disturbance to army ant nests may enable these chimpanzees to reliably and sustainably harvest army ants within their community ranges and avoid conflict with neighboring groups. The Ndoki forest has a rich primate community consisting of ten diurnal species, several of which show dietary overlap with chimpanzees.

Variation in the predator-prey relationship of wild chimpanzees and army ants has perplexed scientists for decades. Despite the recent advances in this field, our findings prompt further study of the interactions between chimpanzee predation tactics and the distribution and characteristics of army ant prey species. Our observations of known individuals confirm that ant-dipping and ant nest perforating is at least habitual, if not customary in the Moto community. Based on the frequency and distribution of tool assemblages with both perforating and dipping tools, this behavior is widespread across several chimpanzee communities in this population. Further research is needed to determine the ecological and social factors shaping the diverse and complex tool technology of these apes. There is an immediate need to conduct this research, as the conservation status of great apes in the Congo Basin is jeopardized by mechanized logging, bushmeat hunting, and disease epidemics [Tutin et al., 2005]. Habitat modification has also been shown to have long-term impacts on communities of ground-living ants in general and *Dorylus* army ants in particular [Peters et al., 2009; Vasconcelos et al., 2000]. More than 50% of the range of great apes in western Equatorial Africa is currently allocated to logging concessions [Morgan & Sanz, 2007], and so scientists must act quickly if they wish to study the

predator–prey relationships of wild chimpanzees and army ants in pristine habitats.

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References

- Alp R. 1993. Meat eating and ant dipping by wild chimpanzees in Sierra Leone. *Primates* 34:463–468.
- Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatol* 54:86–99.
- Brewer SM, McGrew WC. 1990. Chimpanzee use of tool set to get honey. *Folia Primatol* 54:100–104.
- Deblauwe I, Janssens GPJ. 2007. New insights in insect prey choice by chimpanzees and gorillas in southeast Cameroon: the role of nutritional value. *Am J Phys Anthropol* 135:42–55.
- Fowler A, Sommer V. 2007. Subsistence technology of Nigerian chimpanzees. *Int J Primatol* 28:997–1023.
- Fox EA, Sitompul AF, van Schaik CP. 1999. Intelligent tool use in wild Sumatran orangutans. In: Parker ST, Mitchell RW, Miles HL, editors. *The mentalities of gorillas and orangutans: comparative perspectives*. Cambridge, UK: Cambridge University. p 99–116.
- Hashimoto C, Furuichi T, Tashiro Y. 2000. Ant dipping and meat eating by wild chimpanzees in the Kalinzu Forest, Uganda. *Primates* 41:103–108.
- Hicks TC, Fouts RS, Fouts DH. 2005. Chimpanzee (*Pan troglodytes troglodytes*) tool use in the Ngotto Forest, Central African Republic. *Am J Primatol* 65:221–237.
- Humle T. 2003. Culture and variation in wild chimpanzee behaviour: a study of three communities in West Africa. PhD thesis, University of Stirling.
- Humle T. 2009. How are army ants shedding new light on culture in chimpanzees? In: Lonsdorf EV, Ross SR, Matsuzawa T, editors. *The mind of the chimpanzee: ecological and empirical perspectives*. Chicago, IL: University of Chicago Press.
- Humle T, Matsuzawa T. 2001. Behavioural diversity among the wild chimpanzee populations of Bossou and neighbouring areas, Guinea and Cote d'Ivoire, West Africa. *Folia Primatol* 72:57–68.
- Humle T, Matsuzawa T. 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am J Primatol* 58:133–148.
- Mangold. 2006. INTERACT Software, version 8.04. Arnstorf, Germany.
- Matsuzawa T. 1996. Chimpanzee intelligence in nature and captivity: isomorphism of symbol use and tool use. In: McGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge, United Kingdom: Cambridge University Press.
- 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: Cambridge University Press.
- McGrew WC, Baldwin PJ, Marchant LF, Pruetz JD, Scott SE, Tutin CEG. 2003. Ethoarchaeology and elementary technology of unhabituated wild chimpanzees at Assirik, Senegal, West Africa. *PaleoAnthropology* 1:1–20.
- McGrew WC, Pruetz JD, Fulton SJ. 2005. Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatol* 76:222–226.
- Möbius Y, Boesch C, Koops K, Matsuzawa T, Humle T. 2008. Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Anim Behav* 76:37–45.
- Morgan D, Sanz C. 2007. Best practice guidelines for reducing the impact of commercial logging on wild apes in Western Equatorial Africa. Gland, Switzerland: IUCN/SSC Primate Specialist Group (PSG). 32p.
- Nishida T. 1973. The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. *J Hum Evol* 2:357–370.
- Parker ST, Gibson KR. 1977. Object manipulation, tool use, and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. *J Hum Evol* 6:623–641.
- Peters MK, Fischer G, Schaab G, Kraemer M. 2009. Species compensation maintains abundance and raid rates of African swarm-raiding army ants in rainforest fragments. *Biol Conser* 142:668–675.
- Sanz C, Morgan D. 2007. Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *J Hum Evol* 52:420–433.
- Sanz C, Morgan D. 2009a. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *Int J Primatol* 30:411–427.
- Sanz C, Morgan D. 2009b. Complexity of chimpanzee tool using behaviors. In: Lonsdorf EV, Ross SR, Matsuzawa T, editors. *The mind of the chimpanzee: ecological and empirical perspectives*. Chicago, IL: University of Chicago Press.
- Sanz C, Morgan D, Gulick S. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *Am Nat* 164:567–581.
- Schöning C, Kinuthia W, Franks NR. 2005. Evolution of allometries in the worker caste of *Dorylus* army ants. *Oikos* 110:231–240.
- Schöning C, Humle T, Möbius Y, McGrew WC. 2008. The nature of culture: technological variation in chimpanzee predation on army ants revisited. *J Hum Evol* 55:48–59.
- Sugiyama Y. 1995. Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates* 36:193–205.
- Sugiyama Y. 1997. Social tradition and the use of tool-composites by wild chimpanzees. *Evol Anthropol* 6:23–27.
- Tutin CEG, Stokes E, Boesch C, Morgan D, Sanz C, Reed P, Blom A, Walsh P, Blake S, Kormos R. 2005. Regional action plan for the conservation of chimpanzees and gorillas in Western Equatorial Africa. Washington, DC: Conservation International.

- Vasconcelos HL, Vilhena JMS, Caliri GJA. 2000. Responses of ants to selective logging of a central Amazonian forest. *J Appl Ecol* 37:508–514.
- 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.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham R, Boesch C. 2001. Charting cultural variation in chimpanzees. *Behaviour* 138:1481–1516.
- Yamakoshi G, Myowa-Yamakoshi M. 2004. New observations of ant-dipping techniques in wild chimpanzees at Bossou, Guinea. *Primates* 45:25–32.