

## RESEARCH ARTICLE

## Chimpanzees Prey on Army Ants at Seringbara, Nimba Mountains, Guinea: Predation Patterns and Tool Use Characteristics

KATHELIJNE KOOPS<sup>1\*</sup>, CASPAR SCHÖNING<sup>2</sup>, WILLIAM C. MCGREW<sup>1</sup>, AND TETSURO MATSUZAWA<sup>3</sup><sup>1</sup>Department of Archaeology and Anthropology, Division of Biological Anthropology, University of Cambridge, Cambridge, United Kingdom<sup>2</sup>Institut für Biologie, Arbeitsgruppe Funktionelle Biodiversität, Freie Universität Berlin, Berlin, Germany<sup>3</sup>Primate Research Institute, Kyoto University, Aichi, Japan

Chimpanzees are renowned for their use of foraging tools in harvesting social insects and some populations use tools to prey on aggressive army ants (*Dorylus* spp.). Tool use in army ant predation varies across chimpanzee study sites with differences in tool length, harvesting technique, and army ant species targeted. However, surprisingly little is known about the detailed ecology of army ant predation. We studied army ant predation by chimpanzees (*Pan troglodytes verus*) at the Seringbara study site in the Nimba Mountains, Guinea (West Africa), over 10 years (2003–2013). We investigated chimpanzee selectivity with regards to army ant prey species. We assessed the temporal variation in army ant-feeding and examined whether army ant predation was related to rainfall or ripe fruit availability. Moreover, we examined whether chimpanzees showed selectivity regarding plant species used for tool manufacture, as well as the relationship between tool species preference and tool collection distance. Lastly, we measured tool properties and investigated the use of tool sets and composite tools in army ant predation. Seringbara chimpanzees preyed on one army ant species (*D. nigricans*) more often than expected based on encounter rates, which may be explained by the overlap in altitudinal distribution between chimpanzees and *D. nigricans*. Army ant predation was not related to rainfall or fruit availability. Chimpanzees were selective in their choice of tool materials and collected their preferred tool species (*Alchornea hirtella*) from greater distances than they did other species. Lastly, Seringbara chimpanzees used both tool sets and composite tools (tree perch) in army ant predation. Tool types (dig vs. dip) differed in width and strength, but not length. Tool composites were found at 40% of ant-feeding sites. Our study sheds new light on the ecology of army ant predation and provides novel insights into chimpanzee selection of army ant prey and tool species. *Am. J. Primatol.* 77:319–329, 2015.

© 2014 Wiley Periodicals, Inc.

**Key words:** insectivory; tool use; army ants; chimpanzee; ant dip

## INTRODUCTION

Insects are eaten by a wide variety of primate species, ranging from prosimians to great apes [McGrew, 2001, 2014]. Among the African apes, chimpanzees are renowned for using different types of tools to feed on social insects, including termites (Isoptera) and ants (Formicidae). Social insects provide a concentrated and sizeable food source, but they also have defense strategies, such as painful bites and formidable mounds. By using extractive foraging tools, chimpanzees are able to access these prized food sources less painfully and to increase their feeding efficiency and caloric intake [McGrew, 1992]. A well-studied type of extractive insect foraging is ant-dipping to prey upon army (or driver) ants in the subgenus *Dorylus* (*Anomma*) [McGrew, 1974]. In ant-dipping, chimpanzees use a stiff “wand” of woody or herbaceous vegetation to

Contract grant sponsor: Gates Cambridge Trust; contract grant sponsor: Lucie Burgers Foundation for Comparative Behaviour Research (The Netherlands); contract grant sponsor: Schure-Beijerinck-Popping Foundation (The Netherlands); contract grant sponsor: International Primatological Society; contract grant sponsor: St. John's College (Cambridge); contract grant sponsor: Homerton College (Cambridge) and Newnham College (Cambridge); contract grant sponsor: MEXT; contract grant numbers: #12002009, #16002001, #20002001, #24000001, JSPS-U04-PWS; contract grant sponsor: Leverhulme Emeritus Fellowship

\*Correspondence to: Dr. Kathelijne Koops, Department of Archaeology and Anthropology, Division of Biological Anthropology, University of Cambridge, Henry Wellcome Building, Fitzwilliam St, Cambridge CB2 1QH, United Kingdom. E-mail: kk370@cam.ac.uk

Received 20 March 2014; revised 30 August 2014; revision accepted 7 September 2014

DOI: 10.1002/ajp.22347

Published online 14 October 2014 in Wiley Online Library (wileyonlinelibrary.com).

extract the highly aggressive army ants from their temporary underground nests [McGrew, 1974] or directly from surface trails [Humle & Matsuzawa, 2002; Sugiyama, 1995]. Army ants are ubiquitous across chimpanzee study sites, and tool use in army ant predation has been recorded in more than a dozen chimpanzee populations [see review in Schöning et al., 2008a].

Army ant predation by chimpanzees shows considerable variation across study sites [Schöning et al., 2008a]. Whereas some chimpanzee communities feed predominantly on brood and eggs dug by hand from the nest, others focus on ant-dipping [Möbius et al., 2008]. Tool use in army ant predation also varies across sites with differences in tool length, harvesting technique, context (nest vs. trail) and army ant species targeted. A detailed study on ant-dipping behavior at Bossou, Guinea, showed an effect of prey characteristics on tool length (i.e., longer tools for more aggressive ants) and dipping technique, thereby highlighting how the prey species shapes the predator's behavior [Humle & Matsuzawa, 2002].

However, little is known about the detailed ecology of chimpanzee predation on army ants. Specifically, chimpanzee selectivity with regard to prey species of army ants has remained unstudied. To assess whether or not chimpanzees selectively eat certain army ant species, we need to know army ant species availability and chimpanzee predation patterns. Additionally, chimpanzee tool selectivity with regards to plant species has yet to be systematically tested. Tool-material selectivity in ant-dipping has been reported for chimpanzees at Goualougo, Republic of Congo [Sanz & Morgan, 2007], but information on tool material availability was not assessed. Generally, chimpanzees seem to collect tools for ant-dipping within arm's reach of the nest [Boesch & Boesch, 1990; Hashimoto et al., 2002; McGrew, 1974; Pascual-Garrido et al., 2012; Sanz & Morgan, 2007; Sanz et al., 2010; Sugiyama, 1995], but no data are currently available on the potential preference for certain plant species as raw material.

Chimpanzees at Goualougo use "tool sets" in army ant predation, involving perforating and dipping tools [Sanz et al., 2010]. Tool sets are defined as the obligate sequence of two or more types of tools used to achieve a single goal [Brewer & McGrew, 1990; McGrew, 2013]. Tool sets have been reported at several chimpanzee study sites for termite-fishing [e.g. Republic of Congo: Sanz et al., 2004; Cameroon: Deblauwe et al., 2006; Gabon: McGrew and Rogers, 1983] and honey-gathering [e.g. Republic of Congo: Sanz & Morgan, 2009; Gabon: Boesch et al., 2009; Central African Republic: Hicks et al., 2005], but ant-dipping tool sets are observed rarely [Bossou, Guinea: Sugiyama, 1995; Seringbara, Guinea: Humle & Matsuzawa, 2001; Goualougo, Republic of Congo: Sanz et al., 2010]. In addition to tool sets, chimpanzees use "tool composites" in army ant predation

[McGrew, 1974, 2013]. Tool composites are defined as two or more types of tools used simultaneously and complementarily to achieve a goal. In army ant predation, this entails the use of a tree sapling to make an elevated perch from which to dip more securely for biting army ants on the ground below [McGrew, 1974]. A tree perch can be considered a tool in that it comprises a "manipulable attached" object [Shumaker et al., 2011]. Little is known about this type of tool composite use within and across chimpanzee populations.

In this study, we examine tool use in army ant predation by chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea (West Africa). First, we investigate army ant species preference by comparing chimpanzee consumption of army ant species to their availability. Moreover, we examine the altitudinal distribution of army ant species in relation to chimpanzee range use. Chimpanzees at Seringbara inhabit mountainous terrain with the highest peak reaching 1,752 m [Koops, 2011]. The chimpanzees preferentially use areas above 900 m, whereas they use areas below 800 m less often than expected [Koops et al., 2013]. We test whether the relative abundance of prey ant species differed with regards to altitude and habitat type and whether such potential differences were linked to the relative predation frequencies. Second, we assess army ant-feeding tool species selectivity, as well as the effect of tool species preference on tool collection distance. If certain plant species are preferred as tool material, we expect the chimpanzees to invest more effort into collecting these preferred species. Lastly, we investigate the use of "tool sets" and "composite tools" at Seringbara. Preliminary findings suggested that Seringbara chimpanzees use "digging" tools to open ant nests [Humle & Matsuzawa, 2001]. We investigate this potential use of a tool set in army ant predation using long-term data and compare tool types ("dip" vs. "dig") with regards to tool dimensions and strength. In addition, we examine the use of tool composites in the form of "tree perches."

## METHODS

### Study Site

The Seringbara study site (N 07.37°; W 08.28°) is in the Nimba Mountains in southeastern Republic of Guinea, West Africa. The study site covers about 25 km<sup>2</sup> of steep hills and valleys 6 km from Bossou, where a community of 12–23 chimpanzees has been studied for over 30 years [Matsuzawa et al., 2011]. The Nimba region has been surveyed intermittently since 1992 [Humle & Matsuzawa, 2001; Matsuzawa & Yamakoshi, 1996; Shimada, 2000]. The climate is characterized by one long rainy season between February–November and a 3-month dry season (monthly rainfall <60 mm). Since 2003, researchers or field assistants have maintained a near-constant

presence at the Seringbara study site. The study population remains largely unhabituated to human observers. For more information on the study site, see Koops [2011].

### Data Collection

We collected data during 62 months in six study periods: 1. September 2003 to May 2004; 2. April to August and December 2006; 3. November 2007 to December 2008; 4. March 2011 to December 2011; 5. January to December 2012; 6. January to December 2013 (Table I). K.K. collected the data with the help of local field assistants and students.

We estimated army ant availability to chimpanzees by recording all army ant encounters during daily reconnaissance surveys (20 days per month) in Periods 2, 3, 5, and 6. In Period 6, army ants were collected until the end of March. For each army ant encounter, we recorded habitat type, altitude and GPS location. Habitat types recorded were: 1. Primary forest (excluding riverine forest): undisturbed forest; 2. Secondary forest: forest burned or cultivated in the past; 3. Riverine forest: forest <30 m wide, along permanent watercourse; 4. THV-dominated forest: forest with understory dominated by herbaceous plants of the Marantaceae and Zingiberaceae families; 5. Savannah: low- and high-altitude grasslands.

In addition, we noted for each ant column whether the column was: (1) Migrating: emigration columns link nests and all the brood is transported on them from the old to the new nest and many workers carry the colony's brood; (2) Foraging: workers running in both directions and food items being transported back to the nest. We sampled workers from each ant column, swarm raid and occupied nest for species identification. Army ant species included both "epigaic" and "intermediate" species [Schöning et al., 2005]. Species with an epigaic lifestyle form conspicuous swarm raids on the ground and in the vegetation, as well as conspicuous nests with piles of excavated soil. Intermediate species hunt only in the leaf litter, and their nests are less conspicuous.

Army ant swarms can be highly branched, especially towards the front of the swarm [Peters et al., 2009]. To avoid counting the same army ant colony twice, we only considered foraging columns and swarm raids of the same *Dorylus* species to be independent (i.e., belonging to different colonies) when the distance between them was >100 m [*sensu* Peters et al., 2009]. If trails or swarm raids of the same species were found within 100 m distance, we counted them only once. A three-person team walked single file to survey for ants, so as to ensure detection of all ant trails and swarms. By walking single file, even inconspicuous trails of intermediate species in the leaf-litter should have become visible to the second or third person, due to dispersal of the ants from the trail after disturbance by footsteps of the first or second person.

Availability of raw materials (i.e., living plants) for ant-feeding tools was recorded around a subset of army ant nests exploited by chimpanzees in Periods 3, 5, and 6. We measured all potential tool sources in the NW 90° quadrant of a 5-m radius around the ant nest [*sensu* McBeath & McGrew, 1982; McGrew et al., 2007]. We recorded plant species and classified potential tool sources as twig (tree or shrub), vine, THV, or other (monocot or fern).

We identified ant-feeding tool sources whenever possible by systematically searching the area surrounding exploited ant nests and by re-fitting tools to tool sources (Periods 3, 5, and 6). We measured the distance from tool sources to the ant-dipping site with a meter tape. For ant-feeding tools we recorded the following variables:

1. Plant species.
2. Plant type: tree, vine, or herb.
3. Length: measured with meter tape (in cm).
4. Width at midpoint: measured with a ruler (in mm).
5. Possible tool function: dip, dig, or unknown. Digging tools are heavily coated in mud particularly at end(s). Dipping wands are usually thinner, less sturdy and not coated in mud. If no clear function could be ascribed based on the above criteria, tools were classed as "unknown."

**TABLE I. Study Periods With Study Duration, Fecal Samples Collected, Fecal Samples With Army Ants (%), Ant Samples Collected, Dipping Sites Recorded, Tools Recorded and Tool Availability Plots Measured**

Study period	Duration (months)	Fecal samples	Fecal samples with ants (%)	Ant samples	Dipping sites	Tools	Tool plots
1. 2003–2004	9	95	21	0	0	0	0
2. 2006	6	48	6	23	6	32	0
3. 2007–2008	13	106	35	125	5	27	4
4. 2011	9	60	8	194	8	41	0
5. 2012	12	409	19	405	13	51	4
6. 2013	12	371	2	54 <sup>a</sup>	14	70	14
Total	62	1,089	14	801	46	221	22

<sup>a</sup>Ant sampling in 2013 until the end of March.

6. Breaking torque (Nm): calculated by multiplying the force (measured in kg) required to break a tool by the length of the lever arm (m) of the applied force. We measured the force necessary to break a tool by fixing the tool to an immobile surface at one end and bending it with a spring balance (force applied at 90° angle) until breaking. We measured the distance between breaking point and point of attachment of the spring balance (standard arm = 0.25 m). We converted kilogram meter into Newton meter (Nm) using the formula: 1 kgm = 9.81 Nm.

Breaking torque changes over time as tools dry out and become brittle. We therefore measured breaking torque only of ant-feeding tools that were <1 day old when found. For tools >1 day old, we approximated a torque value based on fresh material from the same plant species. We calculated a breaking torque for these tools based on measured breaking torques of fresh (non-tool) wands ( $N=5$ ) of the same plant species of varying widths. We interpolated the breaking torque for a tool of a certain width by using the regression equation of breaking torque and width for that plant species. Breaking torque was recorded for tools found only in Period 3.

In addition, at ant feeding sites in Periods 5 and 6, we recorded the presence or absence of composite tools in the form of so-called “tree perches.” Tree perches were defined as bend over tree saplings or small trees at ant-feeding sites with clear marks of chimpanzee use (i.e. marks from hands and/or feet). We recorded all tree perches used, as well as the tree species of each tree perch.

For evidence of the diet of the chimpanzees, we collected fresh (<2 days old) fecal samples below nests that were recently occupied and on trails where chimpanzees were tracked. We pre-soaked fecal samples in water and sieved them with a 1-mm mesh [*sensu* McGrew et al., 2009]. We scored army ant remains as present or absent, then stored army ant heads in 95% ethanol for later identification to species.

To monitor temporal variation in fruit availability, we created two 500-m transects (N–S, E–W) on each of 4–8 hills, yielding a total transect length of 4–8 km. We established transects according to a stratified random design across the study site. We tagged and measured the DBH of all trees and vines belonging to confirmed chimpanzee food species with a DBH  $\geq 10$  cm and with the trunk midpoint within 5 m to each side of the transect line. We noted the presence of ripe and unripe fruit during the first half of each month. Fruit was scored as: (0) Fruit absent; (1) 1–25% of canopy in fruit; (2) 26–50%; (3) 51–75%; (4) 76–100%. Phenology data were collected for July 2003 to April 2004, January to December 2008 and May 2011 to December 2013.

We calculated a monthly fruit availability index (FAI) for chimpanzee food species with the following formula [*sensu* Takemoto, 2004]:

$$\text{FAI} = \left[ \frac{\sum (P_i \times F_i)}{\sum (P_i \times 4)} \right] \times 100$$

In which FAI is the fruit availability index (%),  $P_i$  is the basal area of the tree ( $\text{cm}^2$ ) and  $F_i$  is the fruiting score of the tree.

## Data Analyses

We tested data for normality using a normal probability plot and a Kolmogorov–Smirnov test [Field, 2005]. All analyses were two-tailed and significance levels were set at 0.05. We performed statistical tests in IBM SPSS version 21.0. We used Spearman’s rank correlations to analyze the proportion of fecal samples containing army ant remains per month in relation to rainfall and FAI. We only included months with >10 fecal samples collected for dietary analyses. We used a Chi-square test to compare the proportion of fecal samples with army ants between the wet and the dry season months (<60 mm rainfall). We used Chi-square tests and binomial tests to compare *Dorylus* species abundance versus chimpanzee consumption. We compared *Dorylus* species distribution across altitude categories and habitat types with a Chi-square test. Subsequently, we determined the altitudinal categories in which the proportions of *Dorylus* species differed from expected proportions, based on marginal totals of the different species. We inspected the adjusted residuals (adj. res.), which are approximately standard normally distributed, and controlled for multiple testing by means of the improved Bonferroni procedure [Hochberg, 1988]. We used Mann–Whitney  $U$  tests to compare altitude use between *Dorylus* species and to compare tool properties between tool types (dip and dig).

We used a discriminant function analysis [Field, 2005] to construct a predictive model of ant-feeding tool types (dip, dig, unknown) with tool properties, that is, length, width and breaking torque, as predictors. First, we established whether or not tool properties predicted group membership (i.e., tool type). We entered all independent variables together and determined the number of underlying dimensions (i.e., functions) by assessing significance of Wilk’s  $\lambda$  for each variate. Second, we determined which tool properties differentiated tool types by examining canonical variate correlation coefficients. Third, we assessed whether tools with unknown function clustered with “dipping” or “digging” tools by examining group centroids (i.e., mean variate scores) for each tool type. Finally, we cross-validated the model and determined the percentage of tools correctly assigned to tool type.

## Ethics

The research adhered to guidelines as set down by the Division of Biological Anthropology, University of Cambridge, and the American Society of Primatologists' principles for the ethical treatment of nonhuman primates. The Direction Nationale de la Recherche Scientifique in Guinea permitted data collection on the Seringbara chimpanzees in the Nimba Mountains.

## RESULTS

### Army Ant Species Diversity

We collected 801 army ant samples (Table II). Most samples were *D. emeryi* (35%), followed by *D. nigricans* (34%), *D. mayri* (18%), *D. burmeisteri* (8%), and *D. gribodoi* (7%). The majority of army ants (85% of samples) encountered were foraging, whereas migration trails and nests were rare. Chimpanzees at Seringbara ate all five *Dorylus* species recorded, as do chimpanzees at several other sites (Table II).

### Army Ant Consumption

#### Temporal variation

We collected 1,089 chimpanzee fecal samples, 14% ( $N = 148$ ) of which contained army ant remains. The proportion of fecal samples with army ant remains varied across study periods, ranging from 2% to 35% of samples (Table I). The monthly consumption of army ants was not correlated with monthly rainfall (Spearman rank correlation:  $r_s = -0.20$ ,  $N = 45$ ,  $P = 0.18$ , Fig. 1). Furthermore, there was no difference in the proportion of fecal samples containing army ants between the wet (12%) and the

dry (16%) seasons ( $\chi^2 = 2.9$ ,  $df = 2$ ,  $P = 0.09$ ). In addition, army ant consumption was not correlated with the monthly availability of ripe fruit represented by FAI (Spearman rank correlation:  $r_s = 0.34$ ,  $N = 31$ ,  $P = 0.06$ ). In sum, chimpanzees consumed army ants across seasons, irrespective of rainfall and fruit availability.

#### Army ant species

We confirmed consumption of all five *Dorylus* species at Seringbara through dietary analyses. *Dorylus nigricans* was found in 59% ( $N = 61$ ) of fecal samples with identified army ant remains ( $N = 104$ ) and was the most frequent species in the chimpanzees' diet. *D. emeryi* was found in 19% (20/104), *D. burmeisteri* in 14% (15/104), *D. mayri* in 13% (14/104), and *D. gribodoi* in 7% (7/104) of fecal samples with identified army ant remains (Fig. 2). Furthermore, 12% (12/104) of fecal samples contained more than one army ant species and the maximum number of species per fecal sample was three species. Chimpanzee consumption of *Dorylus* species did not reflect abundance of army ant species based on all occurrences sampling ( $\chi^2 = 28.9$ ,  $df = 4$ ,  $P < 0.0001$ , Fig. 2). The chimpanzees consumed *D. emeryi* less (Binomial test:  $P < 0.0001$ ) and *D. nigricans* more (Binomial test:  $P < 0.0001$ ) than expected based on availability of these army ant species.

We assessed whether the observed differences in consumption by chimpanzees compared to availability may be linked to spatial distributions of *D. emeryi* and *D. nigricans*. The two species did not differ in abundance across habitat types ( $\chi^2 = 4.7$ ,  $df = 4$ ,  $P = 0.32$ ). However, *D. emeryi* and *D. nigricans* differed in abundance across altitude categories ( $\chi^2 = 57.8$ ,  $df = 3$ ,  $P < 0.0001$ ). *D. emeryi* was

**TABLE II. *Dorylus (Anomma)* Army Ant Species at the Seringbara Study Site, and Availability and Consumption at Other Chimpanzee Study Sites (+ = Consumption With Tools; - = Consumption Without Tools; ? = Unknown)**

Species	Samples <sup>a</sup>	Nests <sup>a</sup>	Foraging <sup>a</sup>	Migrating <sup>a</sup>	Present	Eaten (with or without tools)
Intermediate						
<i>D. emeryi</i>	277	1	271	5	Bossou <sup>b,c</sup> , Tai <sup>b,c</sup> , Dja <sup>d</sup> , Goualougo <sup>e</sup>	Bossou <sup>b,c</sup> (+), Tai <sup>b,c</sup> (+), Dja <sup>d</sup> (-), Goualougo <sup>e</sup> (?)
<i>D. gribodoi</i>	52	2	52	0	Bossou <sup>b,c</sup> , Tai <sup>b,c</sup> , Gashaka <sup>b,f</sup>	Bossou <sup>b,c</sup> (+), Tai <sup>b,c</sup> (+)
Epigaiec						
<i>D. burmeisteri</i>	61	0	57	4	Bossou <sup>b,c</sup> , Tai <sup>b,c</sup> , Fongoli <sup>b</sup>	Bossou <sup>b,c</sup> (+), Tai <sup>b,c</sup> (-), Fongoli <sup>b</sup> (+)
<i>D. mayri</i>	141	11	116	14	Bossou <sup>b,c</sup> , Tai <sup>b,c</sup> , Dja <sup>d</sup> , Goualougo <sup>e</sup>	Bossou <sup>b,c</sup> (+), Tai <sup>b,c</sup> (-), Dja <sup>d</sup> (-), Goualougo <sup>e</sup> (+)
<i>D. nigricans</i>	268	7	184	77	Bossou <sup>b,c</sup> , Tai <sup>b,c</sup>	Bossou <sup>b,c</sup> (+), Tai <sup>b,c</sup> (-)
Total	801	21	680	100		

Note *D. gribodoi* was formerly called *D. gerstaeckeri* [Möbius et al., 2008; Schöning et al., 2007, 2008b].

<sup>a</sup>This study.

<sup>b</sup>Schöning et al. [2008a] and references therein.

<sup>c</sup>Möbius et al. [2008].

<sup>d</sup>Deblauwe and Janssens [2008].

<sup>e</sup>Sanz et al. [2010].

<sup>f</sup>Schöning et al. [2007].

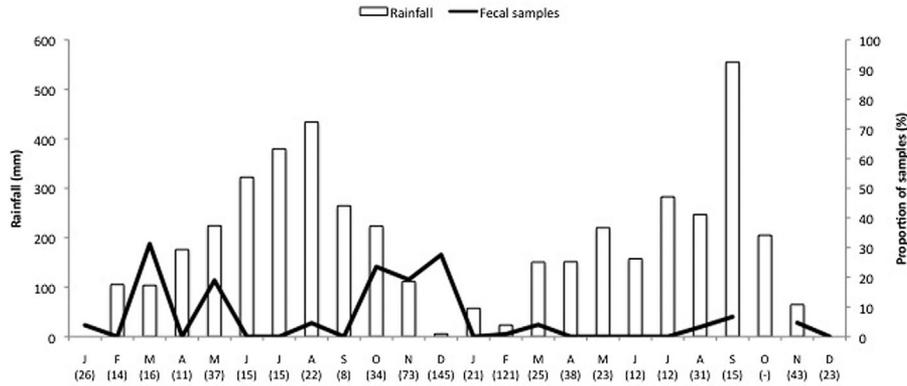


Fig. 1. Monthly proportions of fecal samples with army ant remains in relation to rainfall in 2012–2013. Values in brackets indicate monthly samples sizes.

encountered proportionately more often below 800 m (adj. res. = 4.7,  $P < 0.0001$ , Fig. 3) and *D. nigricans* more often above 1,000 m (adj. res. = 7.4,  $P < 0.0001$ , Fig. 3). Mean altitude was  $855 \pm \text{SD } 137$  m ( $N = 276$ ) for *D. emeryi* and  $947 \pm \text{SD } 155$  m ( $N = 268$ ) for *D. nigricans*, which was significantly different (Mann–Whitney  $U$  test:  $Z = -7.0$ ,  $P < 0.0001$ ). Chimpanzees at Seringbara preferentially use areas above 900 m and avoid areas below 800 m [Koops et al., 2013], and thus encounter *D. nigricans* more than *D. emeryi*.

**Ant-feeding sites**

We found 46 tool-assisted ant-feeding sites, all at ant nests. For 12 sites we were able to obtain ant samples, seven of which were identified as *D. mayri*, three as *D. nigricans* and two as *D. gribodoi*. It thus remains to be seen if chimpanzees at Seringbara use tools to harvest army ants at trails.

**Tool Use in Army Ant Predation**

**Plant species**

We collected 221 ant-feeding tools at 46 sites, ranging from 1 to 15 tools per site (mean =  $4.9 \pm \text{SD } 3.1$  tools/site). The Seringbara chimpanzees made tools from at least 51 plant species belonging to 28 families, including trees, shrubs, vines, and herbs (Table III). The most used species (43% tools) was

*Alchornea hirtella*, a small tree or shrub. For 11 tools, we could not identify the plant species.

**Raw material availability and tool selection**

On average, 31 potential tool sources were available per 90° NW quadrant at ant nests ( $N = 22$ , range: 14–104). The mean number of *A. hirtella* tool sources, the most frequently used species, was 5 per quadrant ( $N = 22$ , range: 0–19) and these comprised 15% (98/675) of available tool sources. The proportion of tools made from *A. hirtella* plants was significantly higher than expected based on the proportion of *A. hirtella* tool sources around ant nests ( $\chi^2 = 139.8$ ,  $df = 1$ ,  $P < 0.0001$ ; Table III). If *A. hirtella* was available at an ant-feeding site, it almost always was used as a tool source (15/16 cases). Conversely, in six out of seven cases when *A. hirtella* was not used as a tool, *A. hirtella* also was not available as a tool source in the vicinity of the ant-feeding site. In other words, chimpanzees preferred to use *A. hirtella* for their ant dipping tools (Table III).

The mean distance from the nest at which tools were collected was  $2.7 \pm \text{SD } 2.3$  m ( $N = 119$ , range: 0–12 m). The tool collection distance did not differ between *A. hirtella* and other tool species (Mann–Whitney  $U$  test:  $N_1 = 45$ ,  $N_2 = 74$ ,  $Z = 0.066$ ,  $P = 0.95$ ). However, *A. hirtella* differed from other plant species in the distribution across collection

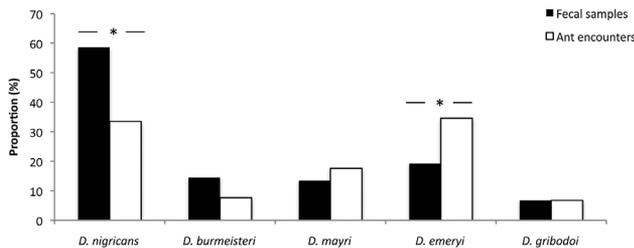


Fig. 2. Proportion of fecal samples with army ant remains ( $N = 104$ ) versus ant trails encountered ( $N = 801$ ) of different army ant species. \*Binomial test:  $P < 0.05$ .

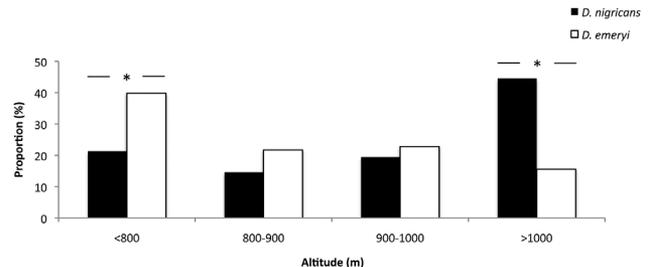


Fig. 3. Proportion of encounters for *D. emeryi* ( $N = 276$ ) and *D. nigricans* ( $N = 267$ ) across altitude categories. \* $P < 0.05$ .

TABLE III. Ant-Feeding Tools (Used Species) and Tool Sources by Plant Species (N = 50)

Species	Family	Plant type	Tools (#)	Tools (%)	Sources (#)	Sources (%)
<i>Alchornea hirtella</i>	Euphorbiaceae	Tree	94	42.5	98	14.5
<i>Whitfieldia lateritia</i>	Acanthaceae	Shrub	8	3.6	25	3.7
<i>Thaumatococcus daniellii</i>	Marantaceae	Herb	7	3.2	12	1.8
<i>Vernonia confexanse</i>	Asteraceae	Shrub	7	3.2	—	—
<i>Microdesmis puberula</i>	Pandaceae	Tree	6	2.7	2	0.3
<i>Tricalysia bracteata</i>	Rubiaceae	Shrub	6	2.7	7	1.0
<i>Tricalysia afzelii</i>	Rubiaceae	Tree	6	2.7	3	0.4
<i>Calycobolus africanus</i>	Convolvulaceae	Vine	5	2.3	11	1.6
<i>Vangueriella campylacantha</i>	Rubiaceae	Tree	5	2.3	1	0.1
<i>Rinorea oblongifolia</i>	Violaceae	Shrub	4	1.8	27	4.0
<i>Santiria trimera</i>	Burseraceae	Tree	4	1.8	6	0.9
<i>Chrysophyllum africanum</i>	Sapotaceae	Tree	3	1.4	11	1.6
<i>Drypetes afzelii</i>	Euphorbiaceae	Tree	3	1.4	11	1.6
<i>Claoxylon hexandrum</i>	Euphorbiaceae	Tree	3	1.4	3	0.4
<i>Manilkara obovata</i>	Sapotaceae	Tree	3	1.4	2	0.3
<i>Canthium horizontale</i>	Rubiaceae	Tree	2	0.9	—	—
<i>Diospyros heudelotii</i>	Ebenaceae	Tree	2	0.9	6	0.9
<i>Garcinia ovalifolia</i>	Guttiferae	Tree	2	0.9	22	3.3
<i>Hannoa klaineana</i>	Simaroubaceae	Tree	2	0.9	4	0.6
<i>Marantochloa macrophylla</i>	Marantaceae	Herb	2	0.9	—	—
<i>Napoleonaea leonensis</i>	Lecythidaceae	Tree	2	0.9	9	1.3
<i>Rothmannia whitfieldii</i>	Rubiaceae	Tree	2	0.9	4	0.6
<i>Tarenna vignei</i>	Rubiaceae	Tree	2	0.9	15	2.2
<i>Terminalia ivorensis</i>	Combretaceae	Tree	2	0.9	—	—
<i>Trichoscypha chevalieri</i>	Anacardiaceae	Tree	2	0.9	1	0.1
<i>Xylia evansii</i>	Leguminosae	Tree	2	0.9	1	0.1
<i>Aframomum longiscapum</i>	Zingiberaceae	Herb	1	0.5	3	0.4
<i>Aganope leucobotrya</i>	Leguminosae	Liane	1	0.5	12	1.8
<i>Albizia lebbek</i>	Leguminosae	Tree	1	0.5	—	—
<i>Amanoa bracteosa</i>	Euphorbiaceae	Tree	1	0.5	2	0.3
<i>Bersama abyssinica</i>	Meliantaceae	Tree	1	0.5	—	—
<i>Bussea occidentalis</i>	Leguminosae	Tree	1	0.5	4	0.6
<i>Carapa procera</i>	Meliaceae	Tree	1	0.5	—	—
<i>Drypetes chevalieri</i>	Euphorbiaceae	Tree	1	0.5	3	0.4
<i>Enantia polycarpa</i>	Annonaceae	Tree	1	0.5	4	0.6
<i>Entandrophragma utile</i>	Meliaceae	Tree	1	0.5	1	0.1
<i>Gilbertiodendron limba</i>	Leguminosae	Tree	1	0.5	—	—
<i>Holarrhena floribunda</i>	Apocynaceae	Tree	1	0.5	—	—
<i>Hugonia platysepala</i>	Linaceae	Liane	1	0.5	1	0.1
<i>Ilex mitis</i>	Aquifoliaceae	Tree	1	0.5	5	0.7
<i>Ituridendron bequaertii</i>	Sapotaceae	Tree	1	0.5	—	—
<i>Maesobotrya barteri</i>	Euphorbiaceae	Tree	1	0.5	2	0.3
<i>Manniophyton fulvum</i>	Euphorbiaceae	Vine	1	0.5	1	0.1
<i>Maratochloa leucantha</i>	Marantaceae	Herb	1	0.5	3	0.4
<i>Monodora tenuifolia</i>	Annonaceae	Tree	1	0.5	3	0.4
<i>Sarcophrynium prionogonium</i>	Marantaceae	Herb	1	0.5	21	4.6
<i>Strychnos</i> sp.	Loganiaceae	Vine	1	0.5	4	0.6
<i>Tabernaemontana longiflora</i>	Apocynaceae	Tree	1	0.5	3	0.4
<i>Trichilia</i> sp.	Meliaceae	Tree	1	0.5	3	0.4
<i>Xylopiya aethiopica</i>	Annonaceae	Tree	1	0.5	2	0.3
Total			210			

—, Tool source not recorded in tool availability plots.

distance categories ( $\chi^2 = 9.3$ ,  $df = 2$ ,  $P = 0.01$ , Fig. 4). Tools made of *A. hirtella* were collected significantly more often at >8 m distance compared to all other plant species combined (adj. res. = 2.4,  $P = 0.016$ ,

Fig. 4). In sum, *A. hirtella* tools were used preferentially and chimpanzees collected these tool materials more often at a greater distance from the ant nest than tool materials of other plant species.

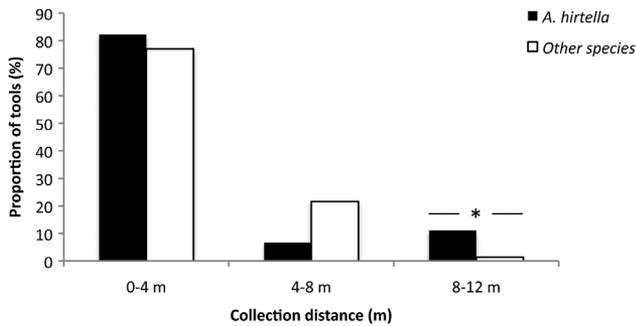


Fig. 4. Tool collection distance from army ant nests (0–12 m) for *A. hirtella* tools compared to all other tool species. \* $P < 0.05$ .

### Tool properties and tool types

The mean tool length was  $64.2 \pm \text{SD } 24.0$  cm ( $N = 191$ , range: 25.0–190 cm) and mean tool width was  $6.7 \pm \text{SD } 2.1$  mm ( $N = 191$ , range: 3.0–14.0). Tools collected in Periods 3–6 were assigned upon collection to possible tool function: Dip ( $N = 112$ ), Dig ( $N = 26$ ), or Unknown ( $N = 22$ ). “Digging” tools were found at 10 ant-dipping sites and at 9 of these they co-occurred with one or more dipping tools (Fig. 5). Tool length did not differ between “dipping” and “digging” tools (mean “dip” =  $60.2 \pm \text{SD } 24.3$  cm, mean “dig” =  $70.0 \pm \text{SD } 27.4$  cm; Mann–Whitney  $U$  test:  $Z = 1.67$ ,  $P = 0.094$ ). However, tool width differed significantly between tool types (mean “dip” =  $6.2 \text{ mm} \pm \text{SD } 1.7$  mm, mean “dig” =  $7.4 \pm 2.8 \text{ SD mm}$ ; Mann–Whitney  $U$  test:  $Z = 2.15$ ,  $P = 0.032$ ).

To assess whether category of tool could be predicted statistically based on tool characteristics, we performed a discriminant function analysis (DFA) with tool length, width and breaking torque as predictors (Period 3 only,  $N = 27$  tools). The mean breaking torque was  $3.5 \pm \text{SD } 3.4$  Nm ( $N = 27$ , range: 0.10–14.71 Nm). Of the two discriminant functions calculated, the first accounted for 83% of the variance in tool characteristics and the second for 17%. The  $\chi^2$  for the two functions combined equaled 20.8 ( $df = 6$ ,  $P = 0.002$ ). The second function alone was not



Fig. 5. Ant-feeding tool set found at Seringbara with a digging stick above and two dipping wands below.

significant ( $\chi^2 = 4.5$ ,  $df = 2$ ,  $P = 0.11$ ). For Function 1, the highest canonical correlation found was with tool width (0.874), followed by tool torque (0.590) and tool length (0.033). This indicates that tool width and torque were most important in differentiating between tool types. The distribution of discriminant scores along discriminant Function 1 shows that dipping tools are differentiated from “digging” tools and tools with unknown function and that “unknown” tools cluster together with “digging” tools (Fig. 6).

In a cross-validated analysis, Function 1 correctly assigned 78% of tools (21/27) to tool type, which is well above the level expected by chance. Dipping tools were assigned correctly more often (94%) than “digging” (40%) and unknown tools (60%). In sum, these preliminary results show that ant-feeding tools seemingly fall into two groups based on tool width and torque. Thus, differences in tool form suggest a possible difference in tool function.

### Composite tools

Seringbara chimpanzees used composite tools (i.e., ant predation tools together with a tree perch) at 40% (10/25) of army ant predation sites in 2012–2013 (while at two sites presence/absence of tree perch was not recorded). Chimpanzees used 1–3 tree perches per site. A single tree perch was used at six sites, two perches at two sites, and three perches at two sites. A total of 11 tree species were used as tree perch: *Rinoria oblongifolia* ( $N = 4$ ), *Chidlowia sanguinea* ( $N = 3$ ), *Neostenanthera gabonensis* ( $N = 2$ ), *Alchornea hirtella* ( $N = 1$ ), *Chrysophyllum giganteum* ( $N = 1$ ), *Drypetes afzelii* ( $N = 1$ ), *Manilkara obovata* ( $N = 1$ ), *Pouteria altissima* ( $N = 1$ ), *Terminalia ivorensis* ( $N = 1$ ), *Tetracera potatoria* ( $N = 1$ ), and *Xylopia parviflora* ( $N = 1$ ).

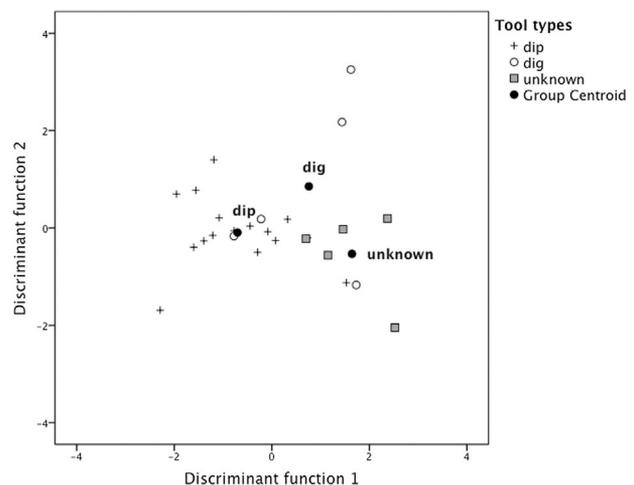


Fig. 6. Distribution of discriminant scores along two functions used to predict ant-feeding tool types (Eigen values: Function 1 = 1.034,  $P = 0.002$ ; Function 2 = 0.218, n.s.). Black circles represent group centroids.

## DISCUSSION

### Army Ant Consumption

Chimpanzees at Seringbara ate all army ant species present. Originally, the chimpanzees were reported to prey on only two out of five species, *Dorylus nigricans* and *D. emeryi* [Schöning et al., 2008a], but this was due to limited sampling. Army ant species availability, measured as ant species encounter rates, did not predict consumption by chimpanzees. The abundant species, *D. emeryi*, was eaten less often than expected, whereas the similarly abundant species *D. nigricans* was consumed more often. However, when the altitudinal distribution of army ant species was taken into account, army ant availability could explain chimpanzee consumption patterns. *D. emeryi* was most abundant below 800 m, whereas *D. nigricans* occurred mostly above 1,000 m. Given that Seringbara chimpanzees preferentially used areas above 900 m [Koops et al., 2013], the ants' spatial distribution and thus chimpanzee encounter probabilities with *Dorylus* species seemingly influenced the likelihood of ant predation. However, further studies are necessary to test whether or not altitudinal overlap fully explains the relatively high consumption rates of *D. nigricans*.

We estimated the relative availability of army ant prey species to chimpanzees as relative encounter rates during reconnaissance surveys. Whether encounter rates reliably reflect availability as perceived by chimpanzees is difficult to determine as the cues chimpanzees use to detect army ant prey are unclear [Pascual-Garrido et al., 2013] and as we currently do not know whether the Seringbara chimpanzees prey on army ants only at nests or also at ant trails. Moreover, reconnaissance surveys have shortcomings compared to standardized insect sampling methods, such as transects or pitfall traps. However, our conclusion concerning differences in relative densities of the various prey species in different altitudinal zones is well supported. This is because any possible systematic error in estimating relative densities would have the same effect for the data of each altitudinal zone so that our comparison yields valid results.

Our results suggest that no prey species is actively preferred or avoided so that chimpanzee predation on army ants is largely opportunistic. At sites with habituated chimpanzees researchers could examine whether chimpanzees indeed show no bias in decisions to attack or not attack after detecting army ants of different species. Information on the nutritional value of the different army ant species at Seringbara may also prove informative and these analyses are currently underway. Army ant consumption at Seringbara was not linked to rainfall or fruit availability. Similarly, at Gashaka (Nigeria), consumption of army ants was the same in the wet and the dry seasons [Pascual-Garrido et al., 2013]. At

Seringbara, we did observe interannual variation in army ant consumption (Table I), which may be due to ecological variables not addressed in this study. In sum, chimpanzees fed on army ants across seasons, suggesting a consistent role for army ants in the chimpanzee diet, possibly as an important source of essential nutrients not available in the typical diet [McGrew, 2014; Rothman et al., 2014].

### Tool Use in Army Ant Predation

Seringbara chimpanzees ate the same species of *Dorylus* as chimpanzees at Bossou and Taï [Möbius et al., 2008]. At Bossou, chimpanzees use longer tools at nests of the more aggressive epigaieic species than at nests of intermediate species. Mean tool length at Seringbara was 64.2 cm, which falls in between tool lengths at Bossou used at nests of intermediate (56.5 cm) and epigaieic (74.0 cm) army ant species [Schöning et al., 2008a]. Taï chimpanzees dip only at nests of the less aggressive intermediate species and thus use shorter tools [23.9 cm; Schöning et al., 2008a]. So far, we have confirmed tools only at nests of two epigaieic (*D. mayri*, *D. nigricans*) and one intermediate species (*D. gribodoi*). Army ants often abandon their nests in response to a chimpanzee attack, rendering it difficult to obtain ant samples from exploited nests for identification. More extensive sampling is required to assess differences in tool lengths used for the different *Dorylus* species at Seringbara.

Seringbara chimpanzees used at least 51 plant species as raw material for tool manufacture, but showed a strong bias towards one particular woody species, *Alchornea hirtella*. Although *A. hirtella* was a common species in the study area, it was used more than expected based on availability. Other plant species may represent preferred tool material, too, but we could not test this due to the low use frequencies and the low availabilities. At Gashaka, chimpanzees used only 11 plant species for tool manufacture, but plant species availability and tool selectivity was not assessed [Pascual-Garrido et al., 2012]. At Seringbara, chimpanzees collected tool materials from *A. hirtella* more often at a greater distance from the ant nest (>8 m), which further suggests preferential use. Tool availability would ideally have been measured in a 12 m-radius area around nests, but we fixed the 5-m sampling distance at the start of data collection before knowing that chimpanzees go up to 12 m away to select suitable tools. Tool species selectivity in army ant predation has so far only been reported for dipping tools at Goulougo, where chimpanzees seem to prefer species of Marantaceae [Sanz et al., 2010]. In addition, tool-material selectivity has been found in termite-fishing, both in the Congo basin [Sanz & Morgan, 2007; Suzuki et al., 1995] and in Senegal [McBeath & McGrew, 1982]. At Seringbara, preferential use of *A. hirtella* may be linked to specific

characteristics of this small shrub, such as abundant straight and rigid branches available close to the ground. Further research in which relative toughness and straightness of all available plants is measured is required to reveal the exact basis of material selectivity, which in turn may shed light on the cognitive abilities of wild chimpanzees.

We investigated the use of tool sets at Seringbara. Previous research suggested the possible use of digging sticks to open army ant nests for dipping at Seringbara [Humble & Matsuzawa, 2001]. Our results showed that dipping and digging tools differed in width, but not in length. In addition, tool types differed in terms of a functional property, namely tool strength. Furthermore, we showed that tool type could be predicted statistically based on tool characteristics (i.e., width, strength), and tools with unknown function clustered together with digging tools. These findings suggest that ant-feeding tools fall into two categories, differing in tool width and strength, thus supporting a difference in function between tool types. Direct observation of army ant predation will be necessary to confirm the use of tool sets at Seringbara.

At nearby Bossou, only one case of digging stick use in army ant-feeding has been seen in over 30 years of research [Sugiyama, 1995]. Widespread use of a tool set in army ant predation has been reported for chimpanzees only at Goualougo [Sanz et al., 2010]. Some differences emerged between the “digging” sticks found at Seringbara and the “perforating” tools at Goualougo. The tools used at Goualougo to perforate ant nests were both thicker and longer than dipping tools, but no difference in length was found between tool types at Seringbara. Furthermore, Goualougo perforating tools often had attached leaves, whereas this was never found at Seringbara. Also, perforating tools were made of woody saplings and dipping tools of herb stalks at Goualougo. No distinction in tool material was found at Seringbara, where nearly all tools were manufactured from woody material. Most importantly, perforating tools at Goualougo seemed to function to entice ants to come out of the nest, while minimizing the ants’ aggressive response and disturbance of the nest [Sanz et al., 2010]. In contrast, all army ant nests exploited by chimpanzees at Seringbara were partly dug out and thus heavily disturbed, including those nests with potential “digging” tools present [Koops, unpublished data]. “Digging” tools at Seringbara may serve mainly to open up the subterranean chambers in the ant nest, which may be difficult to reach by hand. At Seringbara, all army ant nest cavities had a dense tangle of roots inside, which may render manual digging difficult.

Lastly, composite tool use in army ant predation was common at Seringbara. Chimpanzees constructed tree perches at 40% of the ant-feeding sites.

No comparative data on tree perch use is available from other chimpanzee study sites. Previous studies showed that chimpanzees moved off the ground in 74% of ant-dipping episodes at Gombe (Tanzania), in 64% of episodes in Bossou and in 60% of episodes in Goualougo [Humble & Matsuzawa, 2002; McGrew, 1974; Sanz et al., 2010]. Seringbara chimpanzees likely also used a variety of methods to position themselves above the ground (e.g., tree buttresses, lianas), and the proportion of army ant-feeding episodes perched above ant nests appears to be similar across sites.

To conclude, our findings highlight the interplay between army ant behavior and chimpanzee tool use strategies. Chimpanzees fed on army ant species according to the altitudinal distributions of both predator and prey. Moreover, chimpanzees were selective in their choice of tool materials, and invested more effort in collection of their preferred tool species. Lastly, chimpanzees used tool sets and composite tools in army ant predation. To fully understand the complex predator–prey interactions between chimpanzees and army ants, further comparative studies across chimpanzee study sites are essential.

## ACKNOWLEDGMENTS

We thank: Direction Nationale de la Recherche Scientifique and Institut de Recherche Environnementale de Bossou for research authorisation; Seringbara guides, K. Doré, F. Doré, F. Zogbila, P. Cherif, H. Camara, N. Doré, D. Zogbila, Y. Zogbila, C. Samy, and N. Gbouomy; research assistants, K. van Leeuwen, M. Reilly, M. Fitzgerald, P. Le Sommer, W. Edwards, J. Caraway, D. Montanari, N. James, I. Vélez del Burgo Guinea and D. Hassler, for help in the field; two anonymous referees for helpful comments. Research was supported by grants from Gates Cambridge Trust, Lucie Burgers Foundation for Comparative Behaviour Research (the Netherlands), Schure-Beijerinck-Popping Foundation (the Netherlands), International Primatological Society, St. John’s College, Homerton College and Newnham College (Cambridge) to K.K., by MEXT (#12002009, #16002001, #20002001, #24000001) and JSPS-U04-PWS grants to T.M., and by a Leverhulme Emeritus fellowship to W.C.M.

## REFERENCES

- Boesch C, Boesch H. 1990. Tool use and tool making in wild chimpanzees. *Folia Primatologica* 54:86–99.
- Boesch C, Head J, Robbins MM. 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution* 56:560–569.
- Brewer SM, McGrew WC. 1990. Chimpanzee use of tool set to get honey. *Folia Primatologica* 54:100–104.
- Deblauwe I, Janssens GPJ. 2008. New insights in insect prey choice by chimpanzees and gorillas in southeast Cameroon: the role of nutritional value. *American Journal of Physical Anthropology* 135:42–55.

- Deblauwe I, Guislain P, Dupain J, van Elsacker L. 2006. Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, Southeast Cameroon. *American Journal of Primatology* 68:1191–1196.
- Field A. 2005. *Discovering statistics using SPSS*. London: SAGE Publications.
- Hashimoto C, Furuichi T, Tashiro Y. 2002. Ant dipping and meat eating by wild chimpanzees in the Kalinzu Forest, Uganda. *Primates* 41:103–108.
- Hicks TC, Fouts RS, Fouts DH. 2005. Chimpanzees (*Pan troglodytes troglodytes*) tool use in the Ngotto Forest, Central African Republic. *American Journal of Primatology* 65:221–237.
- Hochberg Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* 75:800–802.
- 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 Primatologica* 72:57–68.
- Humle T, Matsuzawa T. 2002. Ant dipping among the chimpanzees at Bossou, Guinea, and comparisons with other sites. *American Journal of Primatology* 58:133–148.
- Koops K. 2011. Chimpanzees in the Seringbara region of the Nimba Mountains. In: Matsuzawa T, Humle T, Sugiyama Y, editors. *The chimpanzees of Bossou and Nimba*. Tokyo: Springer. p 277–287.
- Koops K, McGrew WC, Matsuzawa T. 2013. Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees (*Pan troglodytes verus*)? *Animal Behaviour* 85:175–185.
- Matsuzawa T, Yamakoshi G. 1996. Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In: Russon AE, Bard KA, Parker ST, editors. *Reaching into thought: the minds of the great apes*. Cambridge: Cambridge University Press. p 211–232.
- Matsuzawa M, Humle T, Sugiyama Y, editors. 2011. *The chimpanzees of Bossou and Nimba*. Tokyo: Springer.
- McBeath NM, McGrew WC. 1982. Tools used by wild chimpanzees to obtain termites at Mt Assirik, Senegal: the influence of habitat. *Journal of Human Evolution* 11:65–72.
- McGrew WC. 1974. Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution* 3:501–508.
- McGrew WC. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.
- McGrew WC. 2001. The other faunivory: primate insectivory and early human diet. In: Stanford CB, Bunn HT, editors. *Meat-eating and human evolution*. Oxford: Oxford University Press. p 160–178.
- McGrew WC. 2013. Is primate tool use special? Chimpanzee and New Caledonian crow compared. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368:20120422.
- McGrew WC. 2014. The 'other faunivory' revisited: insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution* 71:4–11.
- McGrew WC, Marchant LF, Beuerlein MM, Vrancken D, Fruth B, Hohmann G. 2007. Prospects for bonobo insectivory: Lui Kotal, Democratic Republic of Congo. *International Journal of Primatology* 28:1237–1252.
- McGrew WC, Marchant L, Phillips C. 2009. Standardised protocol for primate faecal analysis. *Primates* 50:363–366.
- McGrew WC, Rogers ME. 1983. Chimpanzees, tools and termites: new records from Gabon. *American Journal of Primatology* 5:171–174.
- 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. *Animal Behaviour* 76:37–45.
- Pascual-Garrido A, Umaru B, Nodza G, Sommer V. 2012. Obtaining raw material: plants as tool sources for Nigerian chimpanzees. *Folia Primatologica* 83:24–44.
- Pascual-Garrido A, Umaru B, Allon O, Sommer V. 2013. Apes finding ants: predator–prey dynamics in a chimpanzee habitat in Nigeria. *American Journal of Primatology* 75:1231–1244.
- 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. *Biological Conservation* 142:668–675.
- Rothman JM, Raubenheimer D, Bryer MAH, Takahashi M, Gilbert CC. 2014. Nutritional contributions of insects to primate diets: implications for primate evolution. *Journal of Human Evolution* 71:59–69.
- Sanz C, Morgan D, Gulick S. 2004. New insights into chimpanzees, tools, and termites from the Congo basin. *American Naturalist* 164:567–581.
- Sanz C, Morgan D. 2007. Chimpanzee tool technology in the Goulougo Triangle, Republic of Congo. *Journal of Human Evolution* 52:420–433.
- Sanz C, Morgan D. 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *International Journal of Primatology* 30:411–427.
- Sanz C, Schöning C, Morgan D. 2010. Chimpanzees prey on army ants with specialized tool set. *American Journal of Primatology* 72:17–24.
- Schöning C, Ellis D, Fowler A, Sommer V. 2007. Army ant prey availability and consumption by chimpanzees (*Pan troglodytes vellerosus*) at Gashaka (Nigeria). *Journal of Zoology* 271:125–133.
- 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. 2008a. The nature of culture: technological variation in chimpanzee predation on army ants revisited. *Journal of Human Evolution* 55:48–59.
- Schöning C, Gotwald WHJ, Kronauer DJC, Vilhelmsen L. 2008b. Taxonomy of the African army ant *Dorylus gribodoi* Emery, 1892 (Hymenoptera, Formicidae)—new insights from DNA sequence data and morphology. *Zootaxa* 1749:39–52.
- Shimada MK. 2000. A survey of the Nimba Mountains, West Africa, from three routes: confirmed new habitat and ant catching wand use of chimpanzees. *Pan Africa News* 7:7–10.
- Shumaker RW, Walkup KR, Beck BB. 2011. *Animal tool behavior: the use and manufacture of tools by animals*. Baltimore: The Johns Hopkins University Press.
- Sugiyama Y. 1995. Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates* 36:193–205.
- Suzuki S, Kuroda S, Nishihara T. 1995. Tool-set for termite-fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour* 132:219–235.
- Takemoto H. 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *American Journal of Physical Anthropology* 124:81–92.