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The nature of culture: Technological variation in chimpanzee predation on army ants revisited

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Abstract

Chimpanzee (*Pan troglodytes*) predation on army ants (*Dorylus*, subgenus *Anomma*) is an impressive example of skillful use of elementary technology, and it has been suggested to reflect cultural differences among chimpanzee communities. Alternatively, the observed geographic diversity in army-ant-eating may represent local behavioral responses of the chimpanzees to the anti-predator traits of the army ant species present at the different sites. We examined assemblages of available prey species, their behavior and morphology, consumption by chimpanzees, techniques employed, and tool lengths at 14 sites in eastern, central, and western Africa. Where army ants are eaten, tool length and concomitant technique are a function of prey type. Epigaeically foraging species with aggressive workers that inflict painful bites are harvested with longer tools and usually by the ‘‘pull-through’’ technique; species foraging in leaf-litter with less aggressive workers that inflict less painful bites are harvested with short tools and by the ‘‘direct-mouthing’’ technique. However, prey species characteristics do not explain several differences in army-ant-eating between Bossou (Guinea) and Taï (Ivory Coast), where the same suite of prey species is available and is consumed. Moreover, the absence of army-ant-eating at five sites cannot be explained by the identity of available prey species, as all the species found at these sites are eaten elsewhere. We conclude that some of the observed variation in the predator-prey relationship of chimpanzees and army ants reflects environmental influences driven by the prey, while other variation is not linked to prey characteristics and may be solely sociocultural.

Keywords: Army ants; Chimpanzee; Culture; Insectivory; Predation; Tool use

Introduction

Lacking direct access, paleoanthropologists seek to infer the origins and development of human technology in prehistory through a variety of indirect means. Paramount among these is the use of artifacts as the enduring products of ephemeral acts (e.g., Backwell and d’Errico, 2001). Unless we invent a time machine, we can never hope to know the behavior of making and using these artifacts, so we employ proxies in order to draw inferences (Goren-Inbar et al., 2002). One of these proxies is *Homo sapiens*’ nearest living relatives, the African great apes, and especially the chimpanzee, *Pan troglodytes*. The chimpanzee’s variety and complexity of elementary technology exceeds that of all other nonhuman species (McGrew, 1992, 2004).

Complicating this reconstructive exercise is the challenging phenomenon of culture, here operationally defined as a behavioral trait repeatedly transmitted through social learning among conspecifics (as opposed to environmentally determined,

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individual trial-and-error learning or genetic transmission). Typically, culture is manifest in variation across groups, whether these be lineages, communities, or populations. Such variation may be nuanced or gross, unique or ubiquitous, and continuously or discretely differentiated. Elucidating such transmission processes by observation in the uncontrolled setting of nature is difficult, and current debate is lively (Laland and Janik, 2006, 2007; Krützen et al., 2007). Here we propose to tackle these issues by focusing on a single kind of elementary technology, ant-dipping, used in extractive foraging by chimpanzees preying on army ants of the genus *Dorylus* (subgenus *Anomma*) (McGrew, 1974). Is behavioral diversity in ant-dipping an example of material culture?

Dorylus (Anomma) army ants form the largest single-colony insect societies on earth, with worker populations of up to nine million and an average total fresh mass of 40 kg (figures for *D. nigricans*; Leroux, 1982), so that their nests represent a highly concentrated food source. They nest in the soil and often choose the base of trees as a nest site. From their nests they conduct conspicuous, massive raids (in swarms often 20 m or more wide) in which they attack, kill, and retrieve an extremely diverse array of prey (Gotwald, 1995). At irregular intervals these army-ant colonies move to new nest sites (Raignier and van Boven, 1955; Leroux, 1982; Schöning et al., 2005a). Since *Dorylus (Anomma)* ants have only a nonfunctional sting, they defend themselves against predators by biting; their bites are painful and their falcate mandibles can easily pierce human skin.

Chimpanzees have been seen to eat army ants at Bossou (Guinea; Sugiyama et al., 1988), Fongoli (Senegal; P. Bertolani, pers. comm.), Gombe (Tanzania; Goodall, 1963), Goualougo (Republic of Congo; Sanz and Morgan, 2007), and Taï (Ivory Coast; Boesch and Boesch, 1990). At these sites, chimpanzees use modified, straight, thin stems or sticks (''wands'') as tools to gather and ingest the ants (''ant-dipping''; McGrew, 1974). These wands are stripped of twigs and leaves, sometimes peeled of bark, and have one or both ends clipped (for photographs, see McGrew, 1974). The tools are sometimes re-used, but raw materials are usually readily available. At Bossou, Gombe, and Taï, chimpanzees also harvest army ants without tools; brood and workers are taken directly by hand from the nest and transferred to the mouth (McGrew, 1974; Boesch and Boesch, 1990). When using tools, chimpanzees show two techniques: In the ''pull-through'' method (''ant-dip-wipe'' in Whiten et al., 1999), a chimpanzee typically holds the wand in one hand, dips it into the army-ant nest (or into a column or trail), waits for the attacking ants to stream up the tool, then withdraws it while sweeping off the ants with the other hand, and rapidly transfers the jumbled mass of ants into the mouth (McGrew, 1974). Sometimes the tool is transferred to and held in the foot before sweeping the length of the tool with the hand (McGrew, 1974). In the ''direct-mouthing'' technique (''ant-dip-single'' in Whiten et al., 2001), a chimpanzee dips for ants with one hand and then sweeps the wand directly between the lips or teeth (''swiping'') or nibbles the ants directly off the tool (''nibbling''; Boesch and Boesch, 1990). The direct-mouthing technique is practiced at Bossou, Gombe, and Taï, whereas the pull-through method used at Gombe and Bossou has not been seen at Taï (Boesch and Boesch, 1990; YM, pers. obs.).

Indirect evidence (abandoned tools at army-ant nests or *Dorylus* fragments in fecal samples) has been used to establish chimpanzee predation on army ants at 11 other sites where chimpanzees were not habituated to human observers (Fig. 1), namely Assirik (Senegal; McGrew et al., 1988), Bili (Democratic Republic of Congo; T.C. Hicks, pers. comm.), Bwindi

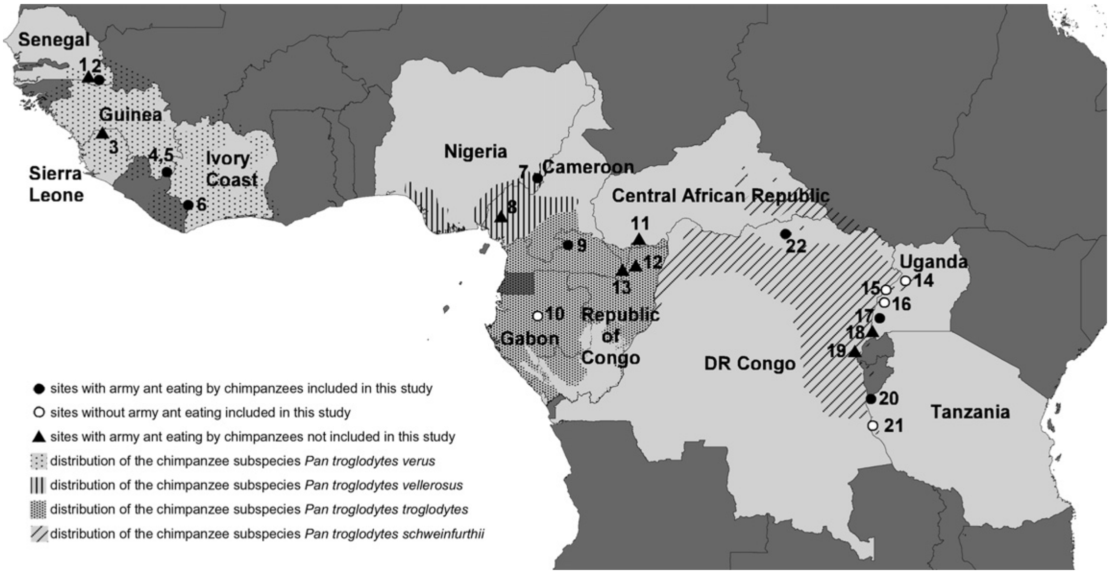

Fig. 1. Map of study sites and other sites where chimpanzees eat army ants: (1) Assirik, Senegal; (2) Fongoli, Senegal; (3) Tenkere, Sierra Leone; (4) Bossou, Guinea; (5) Seringbara, Guinea; (6) Taï, Ivory Coast; (7) Gashaka, Nigeria; (8) Ntale, Cameroon; (9) Dja, Cameroon; (10) Lopé, Gabon; (11) Ngotto, Central African Republic; (12) Ndakan, Democratic Republic of Congo; (13) Goualougo, Democratic Republic of Congo; (14) Budongo, Uganda; (15) Semliki, Uganda; (16) Kibale, Uganda; (17) Kalinzu, Uganda; (18) Bwindi, Uganda; (19) Kahuzi-Biega, Democratic Republic of Congo; (20) Gombe, Tanzania; (21) Mahale, Tanzania; (22) Bili, Democratic Republic of Congo.

(Uganda; Stanford and Nkurunungi, 2003), Dja (Cameroon; Deblauwe and Janssens, 2007), Gashaka (Nigeria; Fowler and Sommer, 2007), Kahuzi-Biega (Democratic Republic of Congo; Basabose, 2002), Kalinzu (Uganda; Hashimoto et al., 2000), Ndakan (Republic of Congo; Fay and Carroll, 1994), Ngotto (Central African Republic; Hicks et al., 2005), Ntale (Cameroon; Ingmanson, 1997), Seringbara (Guinea; Humle, 2003), and Tenkere (Sierra Leone; Alp, 1993).

The lengths of tools used for ant-dipping vary greatly across sites. Taï's tools are the shortest (mean ± SD = 23.9 ± 12.6 cm; $n = 28$; Boesch and Boesch, 1990), while Gashaka's average more than three times as long (83.8 ± 27.4 cm; range = 28–160 cm; $n = 72$; Fowler and Sommer, 2007) (Table 1). At Bossou (Humle and Matsuzawa, 2002), Gombe (McGrew, 1974), Ngotto (Hicks et al., 2005), and Goualougo (Sanz and Morgan, 2007), chimpanzees harvest army ants from their columns, while at other sites, ants are taken only directly at nests. Although the ants are available, chimpanzees do not eat them at the five long-term study sites of Budongo (Reynolds, 2005), Kibale (Wrangham et al., 1991), Semliki (Hunt and McGrew, 2002), Mahale (Nishida, 1990), and Lopé (Tutin et al., 1995).

Humle and Matsuzawa (2002) found that the antipredator traits of army ants influence the technique employed by chimpanzees at Bossou. In the field, they categorized army-ant species into two types based on coloration ("red" and "black") and showed that the two types differ in their functional characteristics as prey. Tool length correlated with ant prey type as well as with dipping technique. Tools used to harvest red ants were shorter than those used to gather black ants, and direct-mouthing was associated with the use of short tools (<50 cm). Moreover, context significantly affected tool length: tools used at nests were longer than those employed at columns.

These results emphasize that a meaningful and comprehensive comparison across populations of chimpanzee preying on army ants must include examination of the identity and characteristics of the prey species and of the precise context in which the army ants are harvested. As Laland and Janik (2006) and Yamakoshi and Myowa-Yamakoshi (2004) have pointed out, the substantiation of ecological parameters so far has been superficial, being based largely on the untested assumption that social learning alone explains the observed differences in chimpanzee predation on army ants (e.g., Whiten et al., 1999, 2001). The argument for a sociocultural explanation is only plausible if the environmental factors relevant to the behavior are the same or at least highly similar at all sites (cf. Möbius et al., in press; Humle et al., unpub. data). For example, if the army ants at one site are unpalatable or unavailable due to other characteristics or site-specific circumstances, the absence of army-ant-eating by the apes cannot be posited as evidence for cultural differences.

We therefore did a large-scale comparative study on army-ant-eating by chimpanzees. The aim was to assess which army-ant species are available, which species are consumed, in which contexts species are exploited, and whether or not the techniques and tools used to harvest the same species or

Table 1
Behavioral diversity in chimpanzee predation on army ants at 11 selected sites

	P. t. verus						*P. t. vellerosus*	*P. t. troglodytes*		*P. t. schweinfurthii*	
	Senegal		Sierra Leone	Guinea		Ivory Coast	Nigeria	Dem. Rep. of Congo	Cent. Afr. Rep.	Uganda	Tanzania
	Assirik	Fongoli	Tenkere	Bossou	Seringbara	Taï	Gashaka	Goualougo	Ngotto	Kalinzu	Gombe
Technique											
Direct-mouthing	Unknown	Unknown	Unknown	Yes	Unknown	Yes	Unknown	Yes	Unknown	Unknown	Yes
Pull-through	Unknown	Unknown	Unknown	Yes	Unknown	No	Unknown	Yes	Unknown	Unknown	Yes
Context											
Nest	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Trails	Unknown	Unknown	Unknown	Yes	Unknown	No	No	Yes	Yes	Unknown	Yes
Tool use											
With	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Without	Unknown	Unknown	Unknown	Yes	Unknown	Yes	Unknown	Unknown	Unknown	Unknown	Yes
Tool characteristics											
Mean tool length ± SD (cm)	72 ± 20	79 ± 28.2	79.8 ± 9.7	46.7 ± 15.9; 53.7 ± 21.01	62.3 ± 21.6	23.9 ± 12.6	83.8 ± 27.4	66.6 ± 17.6 (stem); 95.8 ± 31.8 (sapling)*	84.6 ± 32.6	79 ± 8	66; 63
Range	—	42–152	65.0–95.4	15.0–89.5; 23–154	21.4–120	11–58	28–160	—	—	60–90	15–113; —
n	48	24	7	60; 189	115	28	72	206 (stem + sapling)*	46	14	13; 30

References for each site are as follows: Assirik, McGrew et al. (2003); Fongoli, McGrew et al. (2005); Tenkere, Alp (1993); Bossou, Sugiyama (1995) and Humle and Matsuzawa (2002); Seringbara, Humle (2003); Taï, Boesch and Boesch (1990); Gashaka, Fowler and Sommer (2007); Goualougo, Sanz and Morgan (2007); Ngotto, Hicks et al. (2005); Kalinzu, Hashimoto et al. (2000); Gombe, McGrew (1974).

[*] Authors distinguished two types of ant-dipping tools (stems and saplings).

similar species differ across sites. Thus, we sought to test the hypotheses that the geographical differences in army-ant-eating by chimpanzees result from differences in the composition of army-ant communities, characteristics of the various army-ant species, or the chimpanzees' use of prey-specific harvesting strategies at the different sites. We also used our data to evaluate other potential environmental explanations for the observed geographic differences.

Methods

Study sites

Samples and data were collected at 14 sites (Table 2; Fig. 1). These covered all four currently recognized chimpanzee subspecies (*Pan troglodytes troglodytes*, *P. t. schweinfurthii*, *P. t. vellerosus*, *P. t. verus*; Grubb et al., 2003; Gonder et al., 2006). The authors and other researchers listed in Table 2 collected the samples and data.

Survey of available army ants

Currently six subgenera are recognized within the army-ant genus *Dorylus* (Bolton, 2003). Here, we consider only *Dorylus (Anomma)*, as it is the only subgenus so far reported to be preyed upon by chimpanzees. Samples of workers were collected with pitfall traps or from nests or columns encountered during opportunistic or transect walks. Specimens were stored in 70% ethanol.

Consumption of army ants

Worker samples were collected from nests or columns that chimpanzees were seen to exploit (Bossou, Gombe, Taï) or from nests where abandoned tools and widely dispersed ants around a nest indicated a recent attack shortly before the arrival of the researchers (Fongoli, Gashaka, Kalinzu, Seringbara). Fecal samples were examined for the presence of army-ant remains at Dja and Gashaka (Schöning et al., 2007; Deblauwe and Janssens, 2007).

Army-ant identification

The taxonomy of *Dorylus (Anomma)* is in disarray. Santschi (1912) and Raignier and van Boven (1955) provided the most recent keys to the worker caste of this subgenus. In this study, all specimens were identified by CS, who is currently undertaking a revision of *Dorylus (Anomma)* based on examination of all of the type specimens and on application of detailed morphometric analyses following Seifert (2002). The taxonomy and nomenclature of all species referred to here will be clarified elsewhere. Voucher specimens of all species are deposited in the collection of the Zoological Museum of the University of Copenhagen, Denmark.

Characteristics of prey species

All army-ant species found during surveys were classed as either "epigaeic" or "intermediate" (Schöning et al., 2005b). Epigaeic species hunt on the ground and up in the vegetation in large and conspicuous raiding swarms, while intermediate species hunt in the leaf litter but not up in the vegetation. When trails of epigaeic species are disturbed, the workers attack. In contrast, workers of intermediate species withdraw into tunnels underground or into the leaf litter when the exposed sections of their trails are disturbed.

We examined three morphological traits of the army-ant workers that are likely to be relevant in their interaction with chimpanzee predators. For morphometric analyses, about 100 uninjured workers were collected from at least three colonies (50 workers from a single colony in the case of *D. emeryi*) per study site; these were selected for each species so as to cover the entire size range found in the samples. The smallest workers were excluded because they are more similar across species and because the workers engaged in defensive tasks are predominantly large (Schöning et al., 2005b). Callow workers were also excluded. Not all samples met all criteria. All measurements were taken using an MS 5 Leica stereomicroscope fitted with an ocular micrometer, using methods recommended by Seifert (2002) to minimize measurement errors. The maximum possible magnification was used, while keeping a structure within the range of the ocular micrometer (6.3–64×). The definitions, abbreviations, and presumed functional significance of the characters under consideration are as follows:

Maximum head width (HWmax) = maximum measurable head width. Wider heads accommodate larger mandibular muscles and allow greater biting force (Paul, 2001).
Mandible length (ML) = distance between apex of the left mandible to the proximal point of the ventral ridge when fully opened with forceps. Longer mandibles may allow more painful biting.
Hind-leg length (HLL) = maximum length of left hind leg from trochanter to tarsal tips in dorsal view with the leg fully extended. Longer legs should be a good predictor of faster locomotion (Wehner, 1983) or climbing ability (Federle et al., 1997).

Dry mass (DM) was used as an indicator of overall size. Specimens were dried at 60 °C for 48 h and then weighed to the nearest 0.01 mg using an R 200 D balance (Sartorius GmbH, Göttingen, Germany).

Statistical analyses of the morphometric data followed Schöning et al. (2005b). In order to compare the relative sizes of body traits between workers of different species, we first established the best-fit model for raw linear data from all species combined over their common size range (0.48–5.44 mg) as a function of $DM^{1/3}$ by stepwise multiple regression. Higher-order polynomials were included if all coefficients were significantly different from zero ($p < 0.05$; Zar, 1996; Fraser et al., 2000). The goal of this multiple-regression

Table 2
Species of army ant sampled at 14 study sites

Country, site	Taxon	Habitat	Collector(s)	Number of samples (total/ consumed)	Epigaeic species								Intermediate species			
					D. burmeisteri	*D. nigricans*	*D. mayri*	*D. molestus*	*D. rubellus*	*D. sjoestedti*	*D. wilverthi*	*D. terrificus*	*D. opacus*	*D. emeryi*	*D. gerstaeckeri* complex sp.1	*D. kohli*
Senegal																
Fongoli	*P.t.v.*	WS	S. Bogart, J. Pruetz, WM	11/11	●											
Guinea																
Bossou	*P.t.v.*	F	TH, Y. Sugiyama	123/46	●	●	●							●	●	
Seringbara	*P.t.v.*	F	TH	14/3	○	●	○							●	○	
Ivory Coast																
Taï	*P.t.v.*	F	YM, T. Deschner	30/22	●	●	●							●	●	
Nigeria																
Gashaka	*P.t.vel.*	FS	D. Ellis, A. Fowler, CS, V. Sommer	133/59					●						○	○
Cameroon																
Dja	*P.t.t.*	F	I. Deblauwe	346/20			●			●	●		●	●		●
Gabon																
Lope	*P.t.t.*	F	K. Jeffrey, K. Abernethy, C. Tutin	7/0					○	○			○			
Dem. Rep. of Congo																
Bili	*P.t.s.*	FS	C. Hicks, J. Swinkels	6/4							●		○			●
Uganda																
Kibale	*P.t.s.*	F	CS, J. Mitani	25/0							○	○	○			○
Budongo	*P.t.s.*	F	CS, G. Muhumuza	9/0							○	○				○
Semliki	*P.t.s.*	FS	WM, K. Hunt	12/0				○								○
Kalinzu	*P.t.s.*	F	C. Hashimoto	27/6							●	●				
Tanzania																
Gombe	*P.t.s.*	FW	M. Wilson, WM	7/5				●								●
Mahale	*P.t.s.*	FW	S. Uehara	10/0				○								○

Abbreviations and symbols are as follows: *P.t.v.*, *P. t. verus*; *P.t.vel.*, *P. t. vellerosus*; *P.t.t.*, *P. t. troglodytes*; *P.t.s.*, *P. t. schweinfurthii*; W = woodland; S = savannah; F = forest; open circle indicates availability but no consumption by chimpanzees; filled circle indicates availability and consumption.

analysis was to develop a model that best predicts variation in the response. Thus, there was no need to know the particular relationships between the response and explanatory variables of different orders, and so any issues of multicolinearity could be ignored (Graham, 2003). The relative residuals (absolute residual divided by predicted value) from this common regression model were then compared using a nested ANOVA, with foraging style as a fixed factor and species as a random factor nested within foraging style.

While worker morphology strictly can be compared across species only over the common size range, the morphology of the largest ant workers is expected to be of particular relevance to a potential predator. Therefore, we also recorded the maximum worker size (i.e., DM) for each species.

Context, techniques, and tools

Observations by TH at Bossou (June 2003–April 2004, July–September 2005) and YM (July 2003–January 2004) and Tobias Deschner (December 2004–January 2005) at Taï, as well as published data, were used in the comparison of techniques and tool lengths among sites. We used only those observations for which the association between context, tool length, technique, context, and prey species (or at least prey-species category) could be established unambiguously.

Results

Availability and consumption of army ants

Table 2 lists the main results of the army-ant surveys. Sampling varied among sites in terms of sampling periods, duration, and effort. While commonly used species-richness estimators (Colwell and Coddington, 1994) indicate that sampling effort at Bossou, Dja, and Gashaka was sufficient to detect all occurring *Dorylus (Anomma)* species (data not shown), surveys at some other sites are probably incomplete. However, this does not affect the conclusions to be drawn, because we restrict interpretations of chimpanzee predatory patterns to the species known to be present. Overall, from one to six army-ant species available to chimpanzees are found at the sites.

Chimpanzees feed on army ants at nine of the 14 study sites. Army ants are consumed by all of the studied *P. t. verus* populations, as well as by the single *P. t. vellerosus* population. Army ants are not eaten at Lopé, but are preyed upon in the other *P. t. troglodytes* population at Dja. For *P. t. schweinfurthii*, consumption occurs at Bili, Gombe, and Kalinzu but not in the other four populations. All ant species collected at sites where army-ant consumption is absent are consumed elsewhere. For example, *D. wilverthi* is preyed upon at Dja, Bili, and Kalinzu but is ignored at Budongo and Kibale.

Characteristics of army-ant species as prey for chimpanzees

As the most detailed data on chimpanzee predation on army ants come from Bossou, we first examined the characteristics of prey species there. Humle and Matsuzawa (2002) classed the ants as black or red, as taxa could not be identified reliably in the field. We found the classification of black/red ants in their study to be largely concordant with the classification as epigaeic/intermediate. The proportion of correct classifications is 87%, with only *D. mayri* being classed inconsistently as either red or black.

In the comparisons of the three morphological traits across epigaeic and intermediate species over the common size range, workers of epigaeic species have longer mandibles (nested ANOVA: $p = 0.02$; Appendix A) and hind legs (nested ANOVA: $p < 0.001$; Appendix A) than those of intermediate species, while head width (nested ANOVA: $p > 0.8$; Appendix A) does not differ between the groups. The largest workers of intermediate species are not heavier than those of epigaeic ones (two-tailed unequal-variance *t*-test: $t' = 0.50$, $\mathrm{DF} = 5$, $p > 0.50$; Ruxton, 2006; Appendix B), and thus the differences in relative trait sizes are not counterbalanced by differences in maximum worker size. Visual inspection of the plots (Fig. 2) indicates that the differences in hind-leg length and mandible length between epigaeic and intermediate species are even more pronounced above the common size range (see also Schöning et al., 2005b).

Do chimpanzees use prey-type-specific methods when feeding on army ants?

When data of Humle and Matsuzawa (2002) were reanalyzed with the ants categorized and identified by CS, the pattern of tool-length differences found in black and red species is in the same direction and is highly significant when epigaeic and intermediate species are compared (Fig. 3). At Bossou, the tools used to harvest epigaeic species at nests are longer than those used at nests of intermediate species (Fig. 3). Similarly, we examined the lengths of tools used for dipping ants of the same categories and in the same contexts elsewhere. Kalinzu chimpanzees eat *D. wilverthi* and *D. terrificus* at nests (Table 2), both of which are epigaeic and have long legs and mandibles. Their tools are as long as the ones employed by Bossou chimpanzees to harvest epigaeic species at nests (Bossou data 2001–2005: mean = 72.3 ± 31 cm, range = 46–200 cm, $n = 25$; Kalinzu data from Hashimoto et al. [2000]: mean = 79 ± 8 cm, range = 60–90 cm, $n = 14$; two-tailed unequal-variance *t*-test, $t' = 1.02$, $\mathrm{DF} = 44$, $p > 0.20$). Gashaka chimpanzees use dipping tools to harvest the epigaeic *D. rubellus* at nests (*D. rubellus* was identified as *D. rufescens* by Schöning et al. [2007] because the relevant type material had not been examined at the time). These tools are as long as the ones employed by Bossou chimpanzees to harvest epigaeic species in the same context (Bossou data, see above; Gashaka data are from Fowler and Sommer [2007]: mean = 83.8 ± 27.4 cm, range = 28–160 cm, $n = 72$; two-tailed unequal-variance *t*-test, $t' = 1.59$, $\mathrm{DF} = 37$, $p > 0.10$). Tools used by Fongoli chimpanzees to dip for the epigaeic *D. burmeisteri* at nests are as long as the ones used by the Bossou chimpanzees for the same purpose (Bossou data for *D. burmeisteri* are from 2000–2005: mean = 67.9 ± 8.2 cm, range = 48.6–99.0 cm,

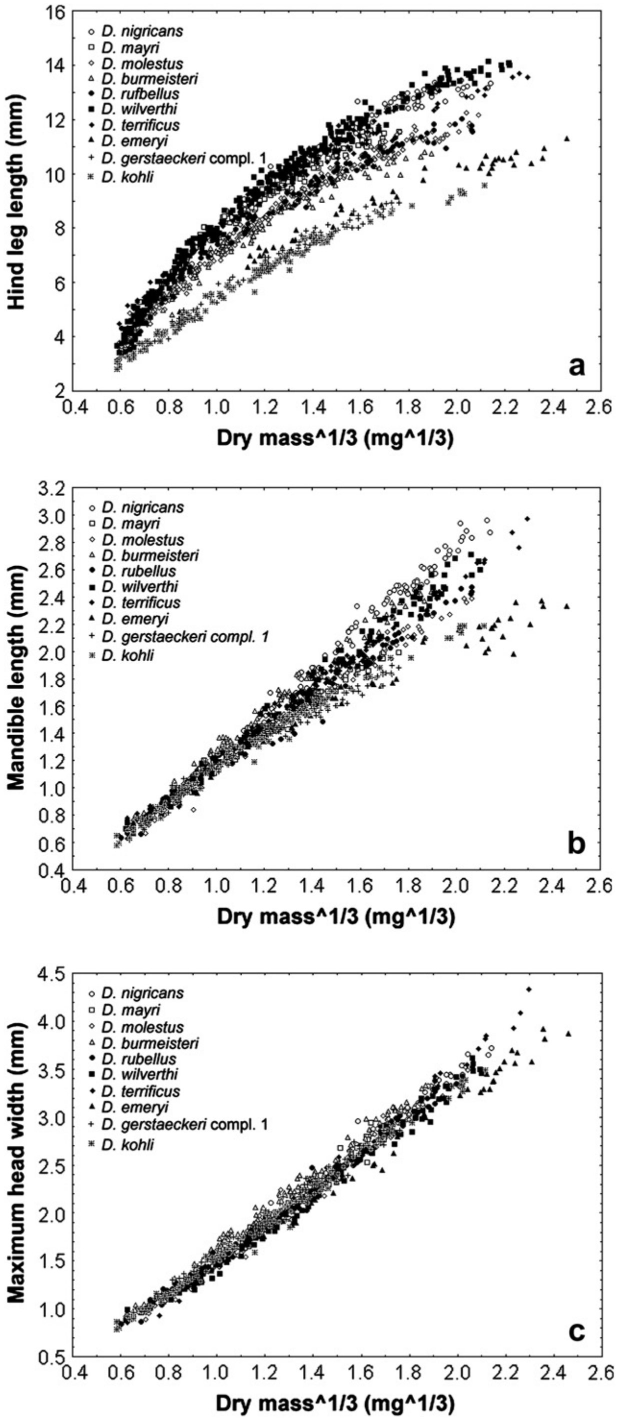

Fig. 2. Morphological features as functions of dry mass$^{1/3}$ for the ten *Dorylus* prey species included in the morphometric analysis: (a) hind-leg length, (b) mandible length, and (c) maximum head width.

$n = 15$; Fongoli data are from McGrew et al. [2005]: mean = 79.3 ± 28.2 cm, range = 42–152 cm, $n = 24$; two-tailed unequal-variance t-test, $t' = 0.30$, DF = 28, $p > 0.50$).

Bossou vs. Taï

At Bossou and Taï, the assemblages of available ant species are identical, and all available species are eaten at both sites (Table 2). However, there are five remarkable differences in the techniques employed by chimpanzees harvesting the same prey between the two sites (Table 3): (1) Taï chimpanzees use only the direct-mouthing technique, whereas chimpanzees at Bossou use both the direct-mouthing and pull-through methods; (2) adult Taï chimpanzees have never been seen to harvest ants from columns, while the chimpanzees at Bossou take army ants both from nests and columns; (3) Taï chimpanzees use tools that are shorter than at Bossou to harvest ants from nests of intermediate species (Bossou: mean = 56.5 ± 20.8 cm , $n = 32$; Taï [Boesch and Boesch, 1990]: mean = 23.9 ± 12.6 cm $n = 28$; two-tailed unequal-variance t-test, $t' = 7.44$, DF = 51, $p < 0.001$); (4) Taï chimpanzees have never been seen to use the swiping subtype of direct-mouthing, while chimpanzees at Bossou use either the swiping or the nibbling subtype of direct-mouthing; (5) Taï chimpanzees have never been seen to use tools to harvest epigaeic ants, but instead always open the nests of all three of the available epigaeic species and take out brood directly by hand. At Bossou the same ant species are harvested from nests either with or without tools.

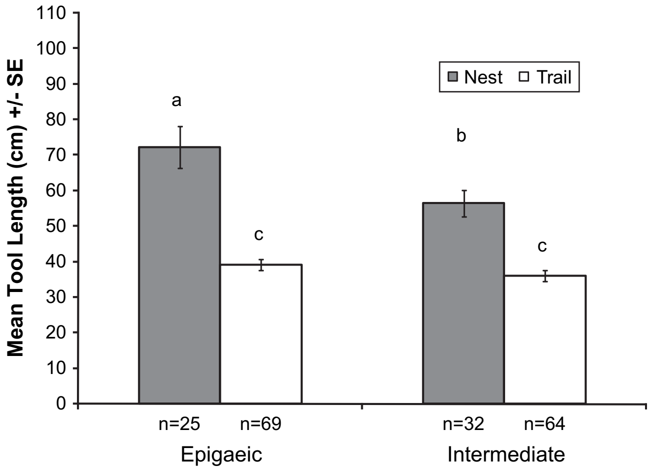

Fig. 3. Mean tool length (and standard error) employed by Bossou chimpanzees on army ants of both epigaeic and intermediate lifestyles at nest and trail. Data are from 2000–2005, when samples of prey species could be identified. Tool lengths differed significantly over the four categories (ANOVA: $F_{(3, 189)} = 33.06, p < 0.0001$). A post-hoc test (Tukey HSD) showed significant differences for all two-way comparisons, except for epigaeic vs. intermediate in the trail context.

Discussion

Army-ant characteristics and chimpanzee predation strategy

Worker morphology differs between intermediate and epigaeic *Dorylus (Anomma)* army-ant species: workers of epigaeic species have longer legs and mandibles over the common size range, and in the largest worker size classes above the common size range. Although the links between these morphometric traits and the running and biting performance of workers of different species have not yet been shown, we infer that workers

Table 3
Summary of chimpanzee predation on army ants at Bossou (Guinea) and Taï (Ivory Coast): relative proportions of types of activity, tool dimensions, and tool handling techniques

	Taï				Bossou			
	Epigaeic		Intermediate		Epigaeic		Intermediate	
	Nest	Trail	Nest	Trail	Nest	Trail	Nest	Trail
Activity								
Ant-dip only	0/20	—	4/6	—	7/26	18/18	3/5	16/16
Ant-dip but fail	0/20	—	0/6	—	2/26	0/18	0/5	0/16
Ant-dip and brood feed	0/20	—	1/6	—	2/26	0/18	2/5	0/16
Brood only (no tools)	18/20	—	1/6	—	15/26	0/18	0/5	0/16
Brood only but fail (no tools)	2/20	—	0/6	—	0/26	0/18	0/5	0/16
Tool length (cm)								
n	—	—	28	—	12	69	32	64
Mean	—	—	23.9	—	74	39.2	56.5	36.1
SD	—	—	12.6	—	43.5	12.8	20.8	12
Range	—	—	11–58	—	35–200	11.2–79.5	19.4–93.0	14.8–74.1
Technique								
Direct-mouthing (swiping)	—	—	No		Yes	Yes	Yes	Yes
Direct-mouthing (nibbling)	—	—	Yes		?	?	?	Yes
Pull-through	—	—	No		Yes	Rare	Yes	No

Data sources: Bossou: observations by TH between 2000 and 2005 for which prey samples were available and prey species identity could be ascertained. Taï: Boesch and Boesch (1990), new observations by YM and Tobias Deschner. Boesch and Boesch (1990) reported that, of 84 observations of predation on army ants, none took place on columns, and 14 of 84 involved tools, while 70 did not. *Dorylus nigricans* was always preyed upon without tools, while tools were used or not used in predatory episodes on *D. gerstaeckeri*. When using tools, technique was always "nibbling." In Boesch and Boesch (1990), ants identified as *D. nigricans* probably were three species: *D. burmeisteri*, *D. nigricans*, *D. mayr*i, while those identified as *D. gerstaeckeri* probably were *D. gerstaeckeri* complex sp. 1 and *D. emeryi*. The question mark (?) indicates unknown.

of epigaeic species probably run faster (and so attack predators sooner) and inflict more painful bites, with more impact in the largest workers. Extensive first-hand field experiences by the authors support this assertion.

At Bossou, chimpanzees use longer tools to harvest those ant species that have longer mandibles and legs, suggesting that workers of these species impose a greater cost on predators (Humle and Matsuzawa, 2002; Fig. 2). Chimpanzees at Bossou distinguish between epigaeic and intermediate forms and use specific strategies in response to prey characteristics. However, the morphometric data indicate that there is a continuum of relative sizes in the different features from intermediate to epigaeic species rather than a simple dichotomy (Fig. 2). Further analyses are needed to see if chimpanzees recognize different species and use prey-species-specific techniques. At other study sites, tools used for dipping epigaeic species at nests are similar in length to those used for the same purpose at Bossou. Therefore, some similarities across sites in army-ant-eating technology reflect the adoption of convergent strategies that are tailored to similar or the same prey.

Bossou vs. Taï

Although the chimpanzees at Bossou and Taï eat the same army-ant species, their strategies differ strikingly. Taï chimpanzees have never been seen to use the pull-through method. This difference reflects the finding that Taï chimpanzees use tools to prey only on intermediate species. At Bossou, direct-mouthing was the only technique seen with tools <50 cm long (Humle and Matsuzawa, 2002), and 96% of the tool lengths at Taï were below this value (reanalysis of data from Boesch and Boesch, 1990).

Adult Taï chimpanzees have never been seen to harvest ants from columns, while the chimpanzees at Bossou take army ants both from nests and columns. Two environmental factors may play a role here: harvesting ants from columns is less efficient in terms of ants gathered per unit time (Humle and Matsuzawa, 2002; Humle, 2006), so that chimpanzees may ignore columns at Taï and some other sites because they have generally easier access to other nutritious food sources, or, finding army-ant nests is easier at Taï. No data are yet available to test these hypotheses.

At Taï, chimpanzees use tools that are shorter than at Bossou to harvest ants from nests of intermediate species. This difference could be due to the relative frequencies with which the two intermediate species are targeted or to differential availability, so that further studies are needed to determine these frequencies. However, preliminary data (Table 3) indicate that there may be a similar association between tool length and technique within the direct-mouthing method (i.e., between short tools and nibbling [Taï] vs. longer tools and swiping [Bossou]) as has been found between tool length and direct-mouthing vs. pull-through (Humle and Matsuzawa, 2002). Taï chimpanzees seem to lack knowledge of techniques other than nibbling. Only shorter tools are efficient for nibbling because, when dipped, ants spread out along a longer tool, and some of them cannot be captured by the mouth and may then inflict bites on the dipper's face. This scenario may explain the shorter lengths of tools used at Taï and is consistent with the interpretation that ant-dipping is a socially transmitted behavioral pattern.

Taï chimpanzees always open by hand the nests of all three available epigaeic species and remove brood. The precise amounts of workers and brood gained during such quick "smash-and-grab" attacks are unknown, but they appear to be as great as the amounts harvested in a dipping episode of average length at Gombe (Boesch and Boesch, 1990). Moreover, only by opening up nests without tools can chimpanzees gain access to large numbers of defenseless, subterranean larvae and pupae that are rich in fat and protein and that lack indigestible chitin. Therefore, taking ants directly from the nest without tools may be both more efficient and more nutritionally rewarding. But then why do the Bossou chimpanzees sometimes use dipping-wands when feeding on epigaeic ants at nests (Table 3)? If manual access to the brood is hampered by roots, dipping still allows the harvesting of workers from the surface of such nests. As Taï chimpanzees seem to be restricted to nibbling only, they cannot dip at nests of epigaeic species, as this requires longer tools and the concomitant swiping or pull-though technique. When access to the nest interior is hampered by roots, Taï chimpanzees would be expected to abandon the nest, and this they sometimes do (Table 3).

Taï and Bossou chimpanzees do not always open nests of intermediate species by hand and take ants and brood, perhaps because the nest structure of intermediate species differs from that of the epigaeic species. The nests of epigaeic species are structurally similar across species (e.g., see Figures 3.27 and 3.28 in Gotwald, 1995; Figures 9–11 in Leroux, 1982). The whole colony clusters together in a central cavity, but in some species, there are also peripheral galleries and chambers. When a predator opens this type of nest, it thus gains direct access to a large clump of food. Although the corresponding nest structures of intermediate species have not been documented, it may be that dipping of workers emerging from the nest entrance may be more efficient than taking workers and brood by hand.

Geographic differences in army-ant consumption revisited

All *Dorylus (Anomma)* species collected in this study were eaten at least at one study site (Table 2). Although the chemical ecology of this subgenus is poorly known, this finding implies that no species produces noxious substances that completely deter chimpanzee predators. No clear geographic pattern emerges for the absence or presence of chimpanzee predation on army ants. Availability of prey species cannot explain the observed pattern. All the prey species that were found at the five sites where army-ant-eating has not been seen were eaten elsewhere, and field observations at these five sites are sufficiently long-term to dismiss the possibility that it has gone unnoticed (McGrew, 1992; Whiten et al., 1999; K. Hunt, pers. comm.).

Nor does chimpanzee subspecies identity elucidate the differences between populations: although present in all the studied populations in western Africa (*P. t. vellerosus* and *P. t. verus*), chimpanzee predation on army ants is both absent and present in *P. t. troglodytes* and *P. t. schweinfurthii*. Therefore, the observed geographic pattern of consumption does not match the subspecies pattern, rendering a population genetic basis for behavioral diversity relating to predation on army ants unlikely.

Although colony densities of epigaeic army ants are generally higher in forested than in savannah habitats (Leroux, 1982)—and so one might expect army-ant-eating to be absent at sites with lower availability of ants—habitat type does not explain the geographic pattern either. Three of the sites lacking army-ant-eating are in forested habitats, while the highest recorded occurrence of army-ant remains in fecal samples is in the mixed-habitat site of Gashaka (Schöning et al., 2007).

Even if army ants are exploited only at opportunistic encounters of conspicuous nests or columns (Sugiyama, 1995), predation rates can be high: 37.4% of chimpanzee fecal samples from Bossou contained *Dorylus* (Takemoto, 2000). So, why do chimpanzees in some populations ignore this easily and widely available prey even when they encounter it without search effort? Perhaps chimpanzees at these sites have other sources of animal protein available that can be exploited more efficiently than army ants. This idea is not supported by available data: for example, predation rates on mammals at Kibale, where army-ant-eating does not occur, are lower than at Gombe, where it does (Wrangham et al., 1991). There is clearly no simple correlation between predation on mammals and predation on army ants.

Army ants may be an important source of nutrients (minerals, trace elements, or vitamins) that might occur in high concentrations only in insect prey (Deblauwe and Janssens, 2007). If so, then ants, bees, and termites represent important and complementary food sources that can be exploited according to their relative availabilities and ease of access (McGrew, 2001). One might then predict that army ants are not eaten at sites where other social insects are consumed in large quantities and vice versa. For example, at Lopé, neither army ants nor termites are eaten, but other insect remains appear in 31% of fecal samples and remains of weaver ants alone occur in 20% of fecal samples (Tutin et al., 1995). However, at Semliki, Kibale, and Budongo, army ants are not eaten while other insects are eaten, albeit rarely (Wrangham et al., 1991; Newton-Fisher, 1999; Sherrow, 2005). Conversely, at Gombe, both army ants and termites are commonly eaten (Goodall, 1963; McGrew, 1992).

The use of twigs or sticks in elementary technology is ubiquitous across chimpanzee populations (McGrew, 1992). The absence of ant-dipping in any form at some sites is therefore unlikely to be caused by a lack of knowledge of the utility of raw materials. Chimpanzees at Mahale, Kibale, and Lopé, for example, do not eat army ants but do use woody vegetation to obtain other insects (Nishida, 1987; Tutin et al., 1995;

Sherrow, 2005). Even if this kind of knowledge were lacking in some populations, army ants could be exploited without the use of tools as they are elsewhere.

Limitation of the distribution of nut-cracking by impassable water barriers in chimpanzees and of tool use by orangutans, plus the absence of genetic and environmental explanations, has been invoked as strong evidence for a cultural basis of these behavioral patterns (Boesch et al., 1994; van Schaik and Knott, 2001). With the recent discovery of nut-cracking by chimpanzees in Cameroon, more than 1700 km east of the previously proposed riverine ‘‘information barrier’’ in Ivory Coast (Morgan and Abwe, 2006), Wrangham (2006) pointed out that disjunct present-day geographic distributions of behavioral variants may result not only from multiple independent innovations but also from extinction of chimpanzee populations or from secondary loss of a custom within populations. Comparative analysis of oil-palm use by neighboring chimpanzee communities in Guinea and Ivory Coast also suggests the possibility of a secondary loss or social constraints on the transmission of subsistence technology between communities (Humle and Matsuzawa, 2004). The observed patchy geographic pattern of army-ant-eating by chimpanzees suggests several independent innovations. However, we know little about the rate of invention of predation techniques, the conditions necessary for successful maintenance of these customs, the dynamics of cultural diffusion by dispersal, or even the historical biogeography of chimpanzee populations. Other scenarios of multiple secondary losses after an initial ubiquitous presence therefore cannot be ruled out. Thus, although the origin and ‘‘evolution’’ of army-ant-eating are obviously difficult to elucidate, our data contradict both genetic and environmental deterministic hypotheses for the observed variation.

Conclusion

In summary, we have examined alternative environmental hypotheses for across-site variation in army-ant-eating by chimpanzees. Our results show that the geographic pattern of presence/absence is not caused by availability of suitable prey species. Current data on the availability of alternative animal prey likewise seem not to explain this pattern. The similarities and differences in tool use, tool length, and technique are driven only partly by the identity and characteristics of the prey species. Our data do not show that variation in army-ant-eating is sociocultural, but our findings are consistent with the interpretation that army-ant-eating by chimpanzees varies culturally. This study exemplifies the need to document the essential circumstances of putative cultural diversity in great detail in order to test competing hypotheses invoking genetic and environmental factors.

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Appendix A.

Nested ANOVAs of relative residuals from regression models over common size range for three morphometric traits of ten *Dorylus* prey species included in the morphometric analysis.

(1) ANOVA results for synthesized errors: relative residual (all species ML common size range); DF error computed using Satterthwaite method MS type I

	Effect	DF	MS	DF	MS	*F*	*p*
Foraging style	Fixed	1	0.729	7.985	0.090	8.096	0.022
Species	Random	8	0.086	750.000	0.002	46.534	0.000

(2) ANOVA results for synthesized errors: relative residual (all species HWmax common size range); DF error computed using Satterthwaite method MS type I

	Effect	DF	MS	DF	MS	*F*	*p*
Foraging style	Fixed	1	0.002	7.990	0.074	0.022	0.885
Species	Random	8	0.071	750.000	0.001	69.229	0.000

(3) ANOVA results for synthesized errors: relative residual (all species HLL common size range); DF error computed using Satterthwaite method MS type I

	Effect	DF	MS	DF	MS	*F*	*p*
Foraging style	Fixed	1	11.636	8.003	0.354	32.836	0.000
Species	Random	8	0.387	982.000	0.001	428.863	0.000

Appendix B.

Size range and maximum values for three morphometric traits in worker samples of ten *Dorylus* prey species

Species	Category	DM range (mg)	Max. HWmax (mm)	Max. HLL (mm)	Max. ML (mm)
D. nigricans	Epigaeic	0.48–9.81	3.72	13.45	2.96
D. mayri	Epigaeic	0.32–5.44	2.94	11.61	2.07
D. molestus	Epigaeic	0.24–8.81	3.55	12.23	2.39
D. burmeisteri	Epigaeic	0.25–6.82	3.33	10.87	2.44
D. rubellus	Epigaeic	0.22–8.82	3.57	12.03	2.47
D. wilverthi	Epigaeic	0.24–9.24	3.62	14.13	2.71
D. terrificus	Epigaeic	0.21–12.09	4.33	13.68	2.97
D. emeryi	Intermediate	0.28–14.88	3.92	11.3	2.37
"*D. gerstaeckeri* complex sp. 1"	Intermediate	0.26–5.45	2.90	8.94	1.90
D. kohli	Intermediate	0.20–9.45	3.49	9.58	2.19

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