



Prospects for Bonobo Insectivory: Lui Kotal, Democratic Republic of Congo

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Abstract Chimpanzees (*Pan troglodytes*) are well-known to eat invertebrates, especially social insects, across Africa, but allopatric bonobos (*P. paniscus*) are not. Bonobo insectivory is sparsely documented and apparently sporadic. However, the availability to bonobos of social insect prey and raw materials with which to make tools to exploit them is unknown. Here, we test a set of hypotheses that relates to questions of presence, abundance, density, and distribution of taxa that *Pan* consume and of vegetation suitable for making extractive foraging tools. We worked at Lui Kotal, Democratic Republic of Congo, where unprovisioned bonobos live in intact forest, far from villages. We collected insect and fecal specimens, transected for prey and assessed raw materials, and monitored mounds of *Macrotermes*. All but 1 of the major taxa of relevant termites, ants, and (stinging) honey bees were present. The 3 main taxa of insects that chimpanzees elsewhere eat —*Macrotermes* (fungus-growing

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termites), *Dorylus* (*Anomma*; army or driver ants), and *Apis* (honey bees)— were abundant and widespread, and usually at densities exceeding those at well-known chimpanzee study-sites. Similarly, woody and nonwoody vegetation suitable for making fishing probes was common at mounds of *Macrotermes*. There is no obvious ecological reason why bonobos should not use elementary technology in extractive foraging, e.g., termite-fish, ant-fish, ant-dip, honey-dip, to obtain social insects.

Keywords elementary technology · extractive foraging · insectivory · *Pan paniscus* · *Pan troglodytes*

Introduction

We found no published report of habitual or customary insect-eating in bonobos (*Pan paniscus*). Instead, occasional and usually anecdotal evidence of consumption of invertebrates is the norm (Badrian and Malenky 1984; Badrian et al. 1981; Bermejo et al. 1994; Horn 1980; Kano 1983, 1986; Kano and Mulavwa 1984; Nishida 1972; Ono-Vineberg 1997; Sabater Pi and Veà 1994; Uehara 1990; White 1992). Further, only 1 report (Badrian et al. 1981) refers, obliquely, to use of tools to obtain invertebrate prey or their products, e.g. honey.

In contrast, chimpanzees (*Pan troglodytes*) eat invertebrates at almost all study sites across Africa (McGrew 1992). Chimpanzees typically use elementary technology in extractive foraging for social insects, especially Isoptera (termites) and Hymenoptera (ants and bees). Thus, regular and selective —if seasonal— insectivory is species-typical for chimpanzees, from Senegal to Uganda, and from savanna to rain forest (Bogart et al. 2005; McGrew et al. 1979, 2005; McGrew and Rogers 1983).

How does one explain the apparent specific difference in technological insectivory? One hypothesis is that chimpanzee field studies are greater in number, longer in duration, and have better habituated subjects. Thus, the apparent lack of regular invertebrate-eating in bonobos could be a false-negative result, reflecting the lack of close-range observational data versus that for chimpanzees. Even if once viable, the explanation is no longer tenable: 1) As with chimpanzees, fecal analysis of samples from unhabituated bonobos should reveal the chitinous exoskeletons of consumed arthropods, yet they rarely do; 2) As with chimpanzees, tools used to extract or process prey should be found as artifacts at feeding sites, even in the absence of the apes. In contrast, either tools or fecal remnants or both have shown insectivory to exist in ≥ 20 populations of wild chimpanzees not yet habituated to regular, close-range scrutiny. (McGrew will provide on request a list of sites and insect taxa.)

The aim of our study is to test an alternative hypothesis: Lack of availability of suitable prey or of raw materials for appropriate tools may preclude bonobo insectivory. That is, if the habitats of allopatric bonobos lack the pertinent insect taxa, or the taxa are inaccessible, or they are not sufficient in abundance, density, or distribution, then we should not be surprised at the absence of their exploitation.

The hypothesis leads to predictions to be tested at an apt field site:

- 1) Appropriate insects or raw materials are absent.
- 2) Taxa or materials amenable to *Pan*-style foraging techniques, including technology, are present but are inaccessible.

- 3) Taxa or materials are available but are so scarce as to be not worth exploiting.
- 4) Taxa or materials are at such low densities that they are not worth exploiting.

Suitability of insect taxa as potential prey for bonobos, thus needing investigation, comes from 2 existing knowledge bases: 1) Taxa reported to be eaten or likely to be eaten in other bonobo populations (Table I) and 2) Taxa eaten habitually by wild chimpanzees (McGrew 2001; Tables II and III). However, most data on prey-insects available to wild *Pan* are nominal only, i.e., present or absent (*cf.* Collins and McGrew 1985, 1987; Deblauwe *et al.* 2007; Schoening *et al.* 2007a, b). Further, most data on insect prey eaten by wild *Pan* do not elucidate their variation in space, e.g., habitat preferences, or time, e.g., periodicity. With few exceptions (*cf.* McBeath and McGrew 1982), the same constraints apply to the published literature on availability of raw materials. Another aim of our study is to provide such data, whenever possible.

We studied bonobos at Lui Kotal, on the southwestern edge of Salonga National Park, Democratic Republic of Congo, because: 1) Continuous field research on site had been underway for 4 yr, unlike at other sites where continuity had been broken by civil unrest or warfare; 2) Bonobos at Lui Kotal did not raid crops and were not provisioned, so their natural feeding ecology was minimally distorted; and 3) Background data on climate and vegetation, collected on a day-to-day basis over several annual cycles were available, unlike at other sites.

Methods

We collected data on social insects and their tools in Feb.–Apr., 2006, at the field site of Lui Kotal (02 45' 36.60" S, 20 22' 43.04" E) in Bandundu province, D.R.C. Research on bonobo ecology and ethology has been underway there continuously since 2002, where the community of *ca.* 30 individuals lives in mixed, evergreen

Table I Taxa of social insects reported to be preyed upon by bonobos

Termites	Ants	Bees	Source
2 spp. indet.	<i>Pachysema aethiops</i> 2 spp. indet.	Melliponid sp.?	Badrian <i>et al.</i> 1981
? <i>Microtermes</i> ? <i>Trinervitermes</i>	<i>Pachysima aethiops</i> 2 spp. indet.	Melliponid	Badrian and Malenky 1984
<i>Microceratotermes</i> <i>fascotibialis</i> <i>Nasutitermes</i> ? <i>Trichotermes</i> <i>Microtermes</i> <i>Trinervitermes</i>	<i>Tetraponera aethiops</i>	Meliponinae <i>Trigona</i>	Bermejo <i>et al.</i> 1994
? <i>Cubitermes</i> (soil)		Apidae <i>Dactylurina</i> <i>staudingeri</i>	Kano 1986
<i>Cubitermes</i> (soil)		2 spp. stingless bees	Kano and Mulavwa 1984
<i>Trichotermes</i> <i>Nasutitermes</i>	<i>Tetraponera aethiops</i>	<i>Trigona</i> (<i>Hypotrigona</i> , <i>Dactylurina</i>)	Sabater Pi and Vea 1994

Pachysima = *Tetraponera*; ? = identification unconfirmed

Table II Genera of termites sympatric with and eaten by *Pan*

Genus	Present(+)/Absent(-) at			Eaten/Not eaten (-) by	
	Lui Kotal	Gombe	Mahale	Bonobo	Chimpanzee
<i>Amitermes</i>	-	-	-	-	?Fongoli
<i>Basidentitermes</i>	-	+	+	-	-
<i>Coptotermes</i>	-	-	+	-	-
<i>Crenetermes</i>	+	-	-	-	-
<i>Cubitermes</i>	+	+	+	Soil at Wamba	Soil at Gombe
<i>Macrotermes</i>	+	+	+	-	Assirik, Bai Hokou, Belinga, Dja, Fongoli, Goulougo, Mahale, Nadakan, etc.
<i>Megagnathatermes</i>	-	-	+	-	-
<i>Microcerototermes</i>	+	-	+	Lilungu	-
<i>Microtermes</i>	+	+	+	Lomako	-
<i>Nasutitermes</i>	+	-	-	Lilungu	-
<i>Odontotermes</i>	-	-	+	-	-
<i>Orthotermes</i>	+	-	-	-	-
<i>Pericapritermes</i>	+	-	-	-	-
<i>Procupitermes</i>	+	-	-	-	-
<i>Promirotermes</i>	-	-	+	-	-
<i>Pseudacanthotermes</i>	-	+	+	-	Gombe, Mahale
<i>Schedorhinotermes</i>	+	-	+	-	-
<i>Termes</i>	+	-	-	-	-
<i>Thoracotermes</i>	+	-	-	-	-
<i>Trichotermes</i>	-	-	-	Lilungu	-
<i>Trinervitermes</i>	-	-	+	Lomako	Fongoli

? = identification unconfirmed

rain forest south of the Lokoro River (Fruth and Mohneke 2007; Hohmann *et al.* 2006; Hohmann and Fruth 2008).

In seeking to gauge the presence, abundance, distribution, and density of social insect taxa at Lui Kotal, we concentrated on taxa known or suspected to be eaten habitually by other populations of African apes. Thus we focussed on ants

Table III Genera of ants sympatric with and eaten by *Pan*

Genus	Present(+)/Absent (-) at			Eaten(+)/Not eaten (-) by	
	Lui Kotal	Gombe	Mahale	Bonobo	Chimpanzee
<i>Dorylus</i>	+	+	+	-	≥13 sites
<i>Camponotus</i>	+	+	+	-	Mahale
<i>Oecophylla</i>	+	+	+	-	Assirik, Gombe etc
<i>Pachycondyla</i>	+	+	+	-	Assirik, Gashaka
<i>Crematogaster</i>	+	+	+	-	Gombe, Mahale
<i>Monomorium</i>	?	?	+	-	Mahale
<i>Tetraponera</i>	?	?	?	Lomako Lulungu	-
<i>Tetramorium</i>	?	?	+	-	Mahale
<i>Pheidole</i>	+	?	?	-	-
<i>Odontomachus</i>	+	?	?	-	-
<i>Cataulacus</i>	+	?	?	-	-
<i>Polyrhachis</i>	+	?	?	-	-

? = unknown, as no systematic sampling

(Formicidae: *Camponotus*, *Dorylus* [*Anomma*], *Oecophylla*); termites (Termitidae: *Cubitermes*, *Macrotermes*, *Pseudacanthotermes*); and honey bees (Apidae: *Apis*). We collected specimens live, preserved them in 99% ethanol, and later sent them to specialists for taxonomic identification.

Transects

We noted all relevant taxa opportunistically but unsystematically whenever encountered anywhere in the study area, so the data denote only nonrandom presence or absence. A more systematic effort focused on *Dorylus*: once per day while walking in the study area for any reason, we monitored a segment of the trail system (types a and b) for army ants on the path in terms of rates in time and space. That is, if the observer walked 3000 m in an hour and encountered *Dorylus* 4 times, then we recorded a rate of contact per 15 min and 750 m for that day. Walking speeds varied, so the measure is crude. Whenever we found a bivouac (nest), we noted its longevity (length of occupation), albeit irregularly.

To gain quantitative data on relative abundance of prey, we also sampled via transects, which were of 3 types: 1) Trails cut by humans based on terrain features or preexisting animal paths; 2) Trails cut by researchers as straight lines in 1 of the 8 directions of 45° intervals on the compass (N, NE, E, SE, S, SW, W, NW); and 3) Lines cut *de novo* chosen from the same set of directions. We recorded 4 triplets of such transects, in approximate proportion to the composition of the study area and of bonobo sightings, totalling 6000 m (Fig. 1). Each of the 3 transects in a set originated from 1 point, and we preset each at 500 m length, although in 1 case the transect ended at swampy conditions that precluded terrestrial termites; we compensated by lengthening another set (Table IV).

Transecting methods are per Collins and McGrew (1987) to allow direct comparison with data collected elsewhere on termite resources accessible to chimpanzees. One person took compass bearings and wore a hip chain (Topometric Products Ltd., Vancouver) while walking the midline of the transect; another cut the transect ahead; 1 or 2 others searched on either side for termites. Strip width was 6 m, based on Collins and McGrew (1987), and we noted each mound, nest, or foraging trail encountered to the nearest meter along the transect. At that point, we noted the perpendicular distance from the transect line to the resource to the nearest 10 cm, to right or left. We sampled all transects in the evergreen forest typical of the site, and made no attempt to subdivide the vegetation into subtypes. For termite mounds, we recorded only the ones that were upright with intact tops. Collins and McGrew (1987) found that overall 30% of sampled mounds were unoccupied, and so had no potential as food for apes.

Productivity

To measure productivity (biomass) of termite colonies, we first defined the typical mound, which applied most precisely to *Cubitermes*, with insects above the substrate in a mushroom-shaped mound, but not to *Macrotermes*, with much of the colony subterranean, beneath an irregularly shaped, massive mound. For *Macrotermes*, we calculated the above-ground volume of the mound, via the formula for the volume of

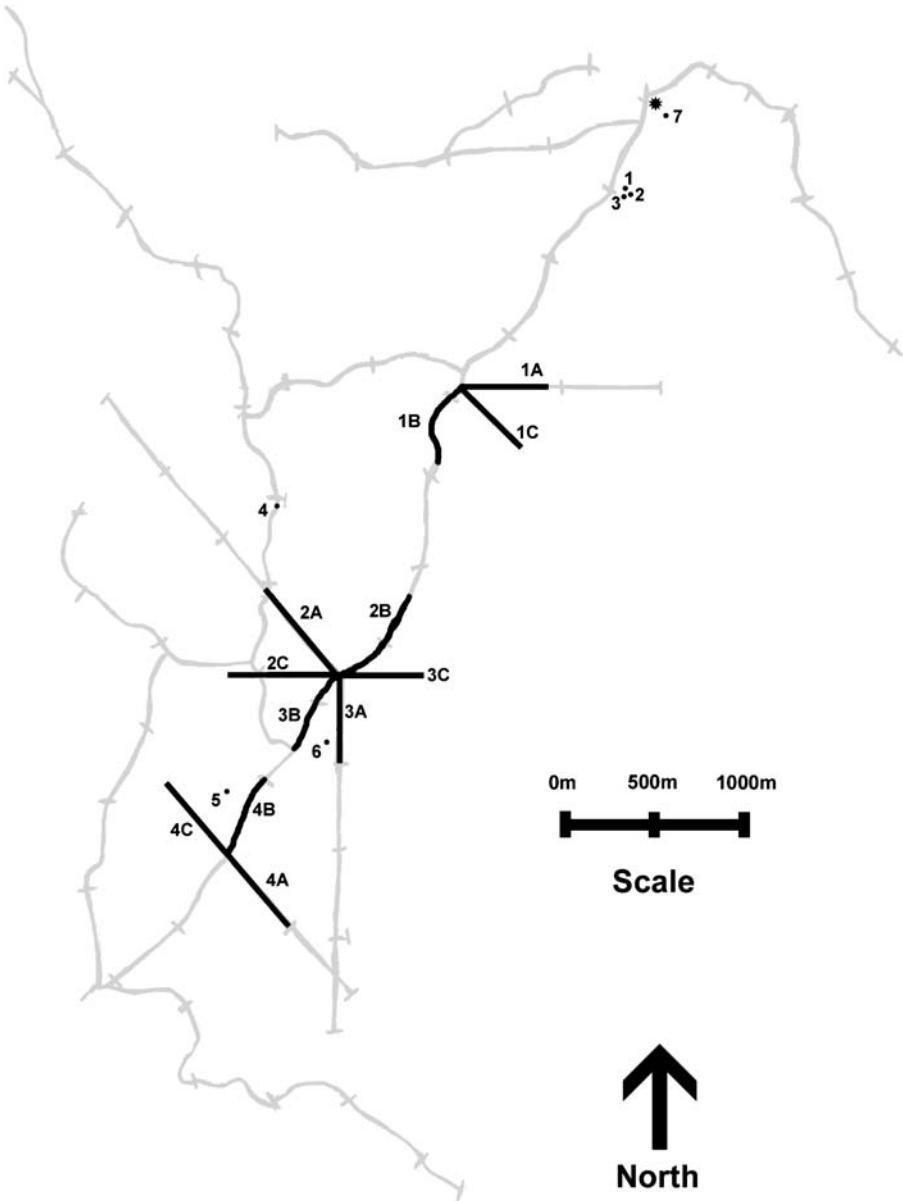


Fig. 1 Trail map of Lui Kotal study site. Numbers 1–7 denote monitored *Macrotermes* mounds; numbers 1A–4C denote transects; star denotes camp site.

a cone ($V = \Pi r^2 h / 3$, $N = 7$) from its height and widest girth (circumference at the widest point) to the nearest 10 cm. For *Cubitermes*, we took the same measurements, and used the formula for the volume of a cylinder ($V = \Pi r^2 h$). We took volumetric data on the first 30 mounds encountered on transect 1a, to sample for typicality, noting height and girth to the nearest cm. We counted only mounds that were intact, free-standing, and upright.

Table IV Abundance and distribution of social insects determined from 3 types of transects

Transect	Length (m)	Termite mounds	<i>Camponotus</i>	<i>Dorylus</i>	<i>Oecophylla</i>
1 A	393	61	2	0	0
B	393	79	2	1	0
C	393	47	0	1	0
2 A	607	141	0	2	0
B	607	148	2	2	1
C	607	79	1	0	0
3 A	500	96	3	1	0
B	500	130	2	0	0
C	500	108	4	3	0
4 A	500	94	2	0	0
B	500	116	1	2	0
C	500	54	1	1	0
Mean /transect	500	96	1.08	1.67	0.08

See text for details of transect types

To calculate the number of individuals in a typical colony of *Cubitermes*, we collected an intact mound by breaking it off at the base (at ground level), then enclosed it immediately in a sealed plastic bag. We then crushed the mound inside the bag with a hammer to chunks of about 1 cm³ and spread them evenly on a horizontal tarpaulin on the ground, over an area of about 2 m × 2 m. We quartered the area, and then quartered each quarter twice, yielding a matrix of 64 × [25 cm × 25 cm] squares. We decanted the contents of 4 randomly chosen squares into 4 stainless steel bowls and scrutinized each one, counting all termites, mature and immature, in a bowl. We multiplied the median score for all 4 bowls by 64 to obtain the total colony number.

Monitoring

We monitored 7 mounds of *Macrotermes* (cf. McBeath and McGrew 1982; McGrew and Collins 1985; Table V). At the first inspection, we cleaned the base of the mound (≤1-m apron around it) of all debris, e.g. leaf litter, dead twigs, taking care

Table V Characteristics of mounds of *Macrotermes* and surrounding vegetation suitable as tool sources

Mound no.	Height (cm)	Girth (cm)	Volume (m ³)	Type of vegetation			Total	Monitoring visits
				Twig	Vine	Other		
1	310	535	2.36	125	31	2	158	40
2	190	470	1.11	90	20	4	114	40
3	260	450	1.40	144	34	5	183	39
4	120	310	0.31	72	10	0	82	7
5	120	210	0.14	69	10	4	83	9
6	220	380	0.85	69	6	0	75	13
7	200	200	0.89	71	37	2	110	6
Mean	226	395	0.94	91	21	2.4	115	22

not to disturb any living vegetation bearing parts that could be made into termite fishing tools (Goodall 1964). Four mounds were close (<500 m) to the research camp, while 3 were further (>3000 m) away. We fished each mound with a Gombe-style fishing probe (Goodall 1968). We opened an exit-hole, inserted and withdrew a probe, and immediately fixed specimens of all castes —major soldier, minor soldier, worker— in ethanol in 5-ml vials.

On later visits, we checked each of the mounds of *Macrotermes* for signs of bonobo visitation —knuckle- or foot-prints, hair, feces, feeding remains, tools, debitage— or of termite activities: fresh building, exit-holes for alates, wings of alates, foragers. We noted other changes: giant pangolin excavation, other animal tracks, army ant raiding. We recleaned the apron when needed. We checked closer mounds more often than distant ones, but checked each at least weekly (*cf.* McGrew and Collins 1985).

Raw Materials

Per McBeath and McGrew (1982), we recorded the availability of raw materials, i.e. living plants, suitable for making fishing probes, at the 7 mounds of *Macrotermes* chosen for intensive study (Table V). Via a tape measure, we noted a circle of 5-m radius from the mound, then arbitrarily chose the NW 90° quadrant (270–0°) for scrutiny. We counted all individual plants in the quadrant capable of providing a tool and classified them as twig (tree or shrub), vine, or other (monocot or fern). We ignored plant size, so that a seedling counted the same as a mature tree; thereby the measure was of potential sources, not tools. (For mound 5, we used the NE quadrant instead because the NW quadrant was impenetrably overgrown, i.e., superabundant.)

Consumption of Insects

We collected fresh bonobo fecal specimens at nest-sites in the morning within min of them leaving the nests to begin daily activities. We collected whole samples in plastic ziplock bags and later sluiced them in 1-mm-mesh sieves in running water to retrieve undigested food remnants after the matrix was washed away.

Results

Prey Taxa

Table II contains the 21 genera of termites that researchers have found at sites with bonobos and chimpanzees. At only 3 sites —Gombe, Mahale, Lui Kotal— have researchers independently and systematically collected termites (Collins and McGrew 1985, 1987; this study), but none of the collections meets the more rigorous standards of termitologists (Eggleton *et al.* 1995; Wood *et al.* 1982). At other sites, researchers have collected termites only *ad hoc*, after apparent linkage with apes, so that comparisons are tentative and minimal.

Nine genera are eaten by chimpanzees ($N=5$) or bonobos ($N=6$), or both ($N=2$), but the extent and quality of data vary greatly (Table I).

More populations of apes eat *Macrotermes* than all other types of termites eaten by all known populations of apes combined. It is the only genus any ape species eats for which there are detailed ethological and ecological data, viz., customary consumption at Gombe (Goodall 1968). Also, it is the best documented genus of insect for ape use of elementary technology (termite-fishing, Goodall 1964) in extractive foraging (Lonsdorf 2005). The species at Lui Kotal, *Macrotermes muelleri*, is obtained via a tool-set by chimpanzees in Cameroon (Deblauwe *et al.* 2007).

Mahale's K-group habitually ate *Pseudacanthotermes (spiniger)* with fishing tools (Nishida and Uehara 1980; Uehara 1982) but M-group did not (Uehara 1999). At Gombe and Mahale, chimpanzees also eat *Pseudacanthotermes militaris*, but without tools (Goodall 1986).

All other records are anecdotal: *Microtermes* and *Trinervitermes* eaten by bonobos at Lomako (Badrian and Malenky 1984) and Lac Tumba (Horn 1980); *Microceratotermes*, *Nasutitermes*, and *Trichotermes* eaten by bonobos at Lilungu (Bermejo *et al.* 1994); *Cubitermes* mound soil (not insects) eaten by bonobos at Wamba (Kano and Mulavwa 1984) and by chimpanzees at Gombe.

Five of the 9 genera of termites are present at Lui Kotal, including the most commonly eaten genus, *Macrotermes* (Table II). As with the other sites of Gombe and Mahale, many other genera are also present but ignored by the apes.

Table III contains the 12 genera of ants that so far have been reported for sites where chimpanzees have been studied. However, only we collected ants independently, albeit in a highly selective manner, so few comparisons can be drawn. At most sites, researchers collected ants for identification only after apes had eaten them or they found ants in ape fecal specimens.

Chimpanzees eat 7 genera of ants, bonobos eat 1, and none ate the same genus (Table III), but the data vary greatly.

At least 13 populations of chimpanzee, across Africa from Uganda to Senegal, eat *Dorylus (Anomma)*, making army ants the most ubiquitous of all insect prey for apes, though ≥ 6 populations do not eat them (Schoening *et al.* 2007b). All consuming populations use elementary technology (ant-dipping, McGrew 1974), but it varies in form according to species of prey (Humble and Matsuzawa 2002). Chimpanzees eat the 3 species that are at Lui Kotal: *Dorylus rufescens* (Gashaka: Schoening *et al.* 2007a); *D. sjoestedti* (Dja: Deblauwe and Janssens 2007); and *D. wilverthi* (Kalinzu: Schoening *et al.* 2007b).

The chimpanzees of Mahale eat *Camponotus* daily, using probes to extract the wood-boring (carpenter) ants from their nests inside trees (ant-fishing; Nishida 1973; Nishida and Hiraiwa 1982).

Chimpanzees eat *Oecophylla* (weaver ants) patchily across Africa, from Senegal to Tanzania; 1 cosmopolitan species, *O. longinoda*, seems to be sympatric with *Pan* everywhere (McGrew 1983). Chimpanzees use no tool to harvest the ants, but process the leafy nests via a skilled technique (McGrew 1992).

Chimpanzees eat *Crematogaster* (ants) at Gombe (Goodall 1986) and Mahale, but no quantitative data are published.

Pachycondyla (formerly *Megaponera*) appear to be ubiquitous throughout the range of *Pan*; they often raid colonies of *Macrotermes* in predatory parties. Only 2 populations of chimpanzees eat them, at Assirik (McGrew 1983) and Gashaka (Schoening *et al.* 2007a).

All other records of ape ant-eating are anecdotal: *Monomorium* and *Tetramorium* by chimpanzees at Mahale and *Tetraponera* (formerly *Pachysima*) by bonobos at Lomako (Badrian and Malenky 1984) and Lilungu (Bermejo et al. 1994).

At least 5 of the 8 genera of ants eaten elsewhere by *Pan* are present at Lui Kotal, including the most commonly eaten genus, *Dorylus* (Table III), and many other genera of ants are there.

Apis mellifera, honey bees, are sympatric with *Pan* throughout Africa, and are commonly preyed upon by chimpanzees (Deblauwe 2006; Kajobe and Roubik 2006). They eat honey, honeycomb, larvae, pupae, and adults. There is no published record of bonobos eating *Apis*, but they consume ≥ 3 genera of stingless honey bees (Meliponini) at Wamba (Kano 1986) and Lilungu (Sabater Pi and Vea 1994). *Apis* are everywhere at Lui Kotal. We saw countless numbers daily but found only 1 hive. We did not survey other species of bees.

Abundance and Distribution of Prey Taxa

Table V contains details of 7 mounds of *Macrotermes* assessed and monitored at Lui Kotal. We found them opportunistically, at distances ranging from 100 to 5000 m from the research camp. We found none on a transect, but 4 of the 7 were within sight of a trail. We found another 24 mounds of *Macrotermes* throughout the study site but did not monitor them.

The average mound of *Macrotermes muelleri* was 2.26 m high (range 1.2–3.8) and had a girth of 3.95 m (range 2.1–5.35), giving a mean volume of 0.94 m³ (range 0.14–2.36). All yielded termites (workers and soldiers) ≤ 5 min in response to our use of standardized chimpanzee termite-fishing techniques, at the beginning of the study, and 4 of the 6 that we checked at the end of the study continued to do so.

On average, we checked the 7 mounds 22 (range 6–40) times between Feb. 25 and Apr. 24, or about once every third day. (We checked mounds closer to camp much more often.) All showed signs of predation by specialized termitophagic predators, aardvark (*Orycteropus afer*) or giant pangolin (*Manis gigantea*), but we found no sign of bonobo visits, i.e., no tool, foot- or knuckle-print, hair, wadge, food debris. Although we occasionally found fresh working of the soil by the insects, we saw no fresh exit hole for releasing alates, though old sealed exit-holes were visible and fishable.

In summary, bonobos at Lui Kotal seem to have access to ample numbers of *Macrotermes* within their home range, and the potential prey are accessible for harvesting.

We recorded on-trail encounters with *Dorylus* on 46 d. The median distance walked for monitoring them was 3800 m (range 500–7600; we used medians because of the highly nonrandom distribution of distances). Most of the time, a migration column was crossing the trail, but we rarely saw a foraging swarm. The average interval between encounters is 15 min (range 6–180) and the average distance is 692 m (range 360–3800). Thus, bonobos had ample opportunity to meet army ants as potential prey.

Table IV contains the results from the 3 kinds of transects, in terms of encounters with pertinent insect prey. Over 12 transects averaging 500 m in length, we found an average of 96 termite mounds (of all types), 1 or 2 trails of ?*Camponotus*, 1 trail

of *Dorylus*, but only 1 (total) trail of *Oecophylla*. We collected 1 sample of *Crematogaster* just off transect 3B. The termite mounds were terrestrial, and given that each transect strip was 6 m wide, this equates to a mound for every 32 m², or a mean density of 312.5 mounds/ha. We did not collect all of the 20 groups of ?*Camponotus*, so some identifications are not confirmed, but we collected almost all the ants on tree trunks or fallen logs. The *Dorylus* that we encountered were usually columns ($N=7$), but we also saw foraging swarms ($N=4$). *Oecophylla* were on living vegetation overhead, as is typical for weaver ants, while we took the wood-boring *Crematogaster* from the center of dead stems of *Haumania*.

For inter- and intratransect comparisons, only the termite mounds offer enough data for statistical analyses. Comparison across the 4 transect sets, once counts are corrected for the different lengths, shows no difference among them (Kruskal-Wallis analysis of variance, $N=12$, $k=4$, $\chi^2=2.40$, $p=0.50$). Thus, the frequency of encountering termite mounds does not differ across sets of transects originating at different points in the study area.

For comparison within transect sets, of the 3 types of transect, a significant difference in encounter rate emerges (Friedman analysis of variance, $N=4$, $k=3$, $\chi^2=6.50$, $p=0.04$). Type C transects, newly cut through intact forest for the purpose of the study, yielded fewer termite mounds.

Overall, bonobos at Lui Kotal seem to have ample opportunity to encounter termite and ant prey, although for some genera (*Crematogaster*, *Oecophylla*), the results are inconclusive.

Productivity of Mounds

On transect 1A, we found 178 termite mounds, occupied and vacant, of which 90 were assignable to mound types, based on shape. The remaining 88 were unassignable, due to damage or disrepair. Of the 90 mounds, 66 (73%) were characteristic mushroom-shaped mounds of *Cubitermes*, having a cylindrical stalk and a hemispheric cap. None of the other mound types amounted to >11% of the sample, so we did not analyze them further.

The first 30 mushroom-shaped (*Cubitermes*) mounds encountered averaged 38 cm in height (range 21–72) and 46 cm in girth (range 26–69); thus the average volume is 6288 cm³.

The average-sized mound of *Cubitermes* yielded 204, 234, 391, and 393 termites per 1/64 sample, thus a median of 312.5 termites per sample. When we multiplied the median number by 64, the calculated total number of termites in a typical mound was 20,000.

A bonobo choosing to eat *Cubitermes* or fragments of their mound would have plenty of both for a meal.

Availability of Raw Materials for Tools

Elementary technology of extraction of social insects by apes makes use of the vegetative parts of plants, woody and nonwoody: twig, branch, shoot, stem, stalk, leaf. These may come from trees, shrubs, vines, herbs, and grasses. All require some sort of processing to be transformed into tools: clip, strip, peel, split, tear, fray. Each

foraging task calls for a different type of tool suited to the antipredator strategies of the prey: termite-fishing and ant-fishing require slender and flexible probes that can be threaded into small holes and winding passages. Ant-dipping needs longer, straight and stiff wands or shorter rods with smooth surfaces for pulling through the hand or swiping through the lips. Perforating and digging into termite mounds require straight, sturdy sticks with blunt or pointed ends.

Table V contains the availability of sources for fishing probes at 7 mounds of *Macrotermes* with a quadrant area of 19.6 m². The average mound had 91 twig sources (range 69–144), 21 vine sources (range 6–37), and 2.4 other sources (range 0–5). In total, a mound on average yielded 115 tool sources (range 75–183) within easy access.

Bonobos at Lui Kotal would have no difficulty getting raw materials for fishing probes.

Bonobo Insect-Eating

We saw no bonobos eating insects, but collected 61 fecal samples for dietary analysis in 13 batches between Feb. 25 and Apr. 18, thus over an 8-wk period. We found no animal remains, invertebrate or vertebrate, in the samples.

Discussion

The results from Tables I, II, and III combine to show that Lui Kotal has several genera of edible ants and termites similar to those at other study sites with *Pan*. Among the Macrotermitinae, only *Pseudacanthotermes* was apparently missing. Given the *ad hoc* way that primatologists typically collect insects, there is more likelihood of false-negative results than false-positive ones. Clearly, more systematic social insect collection needs to be done, especially for taxa with cryptic nests or foraging habits, e.g. *Crematogaster*. Similarly, no systematic study seems to have been done on non-*Apis* honey-storing bees, i.e., the Melliponini, yet they are eaten widely by *Pan*.

The overall density of termite mounds at 320/ha at Lui Kotal is many times higher than comparable densities of mounds at Assirik ($x=10.75$ /ha, McBeath and McGrew 1982) or at Gombe ($x=5.6$ /ha) or Mahale ($x=13.3$ /ha; Collins and McGrew 1987). This is not surprising because the other sites are much drier and have correspondingly lower primary productivity than Lui Kotal. The most commonly found genera at other sites were *Microtermes* at Mahale and *Pseudacanthotermes* at Gombe; the former is present and the latter not at Lui Kotal, but the sample sizes of mounds encountered are much smaller at the Tanzanian sites, so comparison is difficult. Conversely, the most commonly found genus of termite at Lui Kotal, *Cubitermes*, comprised only 14.3% of mounds identified at Gombe, and was rarely found at Mahale (Collins and McGrew 1987).

The small number of mounds of *Macrotermes* at Lui Kotal is misleading: we found only 1 mound of the genus on a 2370-m transect at Gombe, and none on 10,122 m of transects at Mahale, yet chimpanzees regularly fished for termites at both places (Goodall 1968; McGrew and Collins 1985). In this sense, termite

mounds are no different from scattered yet energetically or nutritionally important plant resources, e.g., nut-bearing trees.

For *Dorylus*, Table IV shows no difference across the 3 transect types, so we pooled results, yielding an encounter with army ants every 462 m on average. Results from the walking surveys gave a comparable encounter rate of every 692 m. Authors of only 1 other study have recorded encounter rates with *Dorylus*: At Gashaka, Schoening *et al.* (2007a) saw *Dorylus* on average every 1300 m, in the wet season, using methods comparable to our latter one. The greater frequency of ants at Lui Kotal is not surprising, given its higher rainfall.

No systematic data on abundance of other taxa of ants or of bees seem to have been noted at any ape study site, but clearly this needs to be done for comparisons to be made.

For distribution of insects, quantitative comparisons across the 4 sets of transects that were (nonrandomly) scattered across the Lui Kotal study site show no difference in relative frequency of encounter with potential prey. However, even qualitative data for non-*Dorylus* ants are minimal, and researchers need to survey and systematically monitor them and bees.

For productivity, the monitored mounds of *Macrotermes* give a mixed picture: none was reproductively active, i.e., released alates, which at other sites is a sign of peak season termite-fishing by chimpanzees (Goodall 1968; McBeath and McGrew 1982). This suggests that our negative results for termite consumption are inconclusive, because we may have been at Lui Kotal at the wrong time of year. One can test the hypothesis only by year-round monitoring of mounds, to see if there are seasonal differences. However, the mounds were easily fishable, even by neophyte field workers, showing that there was an accessible resource to be harvested. Perhaps mounds of *Macrotermes* are more easily and productively fished at certain times of year.

Encounter rates with mounds of *Cubitermes* and army ant swarms were so high at Lui Kotal that the 2 common types of social insect could hardly be avoided. At 20,000 inhabitants, a mound of *Cubitermes* is well stocked; if each termite weighed 0.01 g (a notional figure), then a typical mound contained *ca.* 200 g of wet biomass; at 0.001 g per termite, it would be 20 g. Swarms of *Dorylus* number in the millions, and chimpanzees probably consume only hundreds or thousands in a typical feeding bout (the largest number of ant heads found in a chimpanzee fecal sample is 4636, at Gashaka; Schoening *et al.* 2007a), so only an infinitesimally small proportion of the total colony is eaten.

However, the difference in termite densities that emerged across transect types sounds a cautionary note. Freshly cut, random transects through intact forest yielded fewer termite mounds than well-established trails, whether randomly or non-randomly routed. The finding was unexpected, so we can but advance a speculation *post hoc*, that perhaps cleared areas with bare ground are somehow more attractive to dispersing alates seeking to found underground colonies.

For raw materials, only 1 previous study provided data for quantitative comparison: McBeath and McGrew (1982) recorded the abundance of plants suitable for tool-making at 40 mounds of *Macrotermes* at Assirik. They found an average of 37 raw material sources within a 5-m radius of a mound, giving a density of 2.12 per m². At Lui Kotal, the comparable density was 5.87 per m². Again, given

that Assirik is the driest site where chimpanzees have been studied, and Lui Kotal is one of the wettest for *Pan*, the higher productivity for the latter is not surprising.

Lack of evidence for consumption of social insects by the bonobos at Lui Kotal must be considered tentative: we collected few fecal samples and then only over 8 wk. We have few clear observations of their terrestrial feeding, given the thickness of the undergrowth. Year-round data from fecal specimens can yield high rates of insect consumption by chimpanzees: 42% of samples at Gashaka contained *Dorylus* (Schoening et al. 2007a); 27% of samples at Assirik contained *Macrotermes*; 24% contained *Oecophylla*; and 23% contained *Apis* (McGrew 1983). Conversely, even at long-term sites where close-range observational data on termite fishing are available, most months of the year yield no or few bouts of the behavioral pattern (Goodall 1986).

In conclusion, the bonobos at Lui Kotal have ample opportunity to prey upon the insect taxa most favored by congeneric chimpanzees. The prey and the means to exploit them are there. Whether or not the bonobos do so remains to be seen through further study.

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References

- Badrian, N., Badrian, A., & Susman, R. L. (1981). Preliminary observations on the feeding behaviour of *Pan paniscus* in the Lomako forest of central Zaire. *Primates*, 22, 173–181.
- Badrian, N., & Malenky, R. K. (1984). Feeding ecology of *Pan paniscus* in the Lomako forest, Zaire. In R. L. Susman (Ed.), *The Pygmy Chimpanzee. Evolutionary Biology and Behavior* (pp. 275–299). New York: Plenum Press.
- Bermejo, M., Illera, G., & Sabater Pi, J. (1994). Animals and mushrooms consumed by bonobos (*Pan paniscus*): New records from Lilungu (Zaire). *International Journal of Primatology*, 15, 879–898.
- Bogart, S. L., Pruetz, J. D., & McGrew, W. C. (2005). Termite de jour: Termite fishing by West African chimpanzees (*Pan troglodytes*) at Fongoli, Senegal. *American Journal of Physical Anthropology* (Suppl. 40):75 (abstract).
- Collins, D. A., & McGrew, W. C. (1985). Chimpanzees' (*Pan troglodytes*) choice of prey among termites (Macrotermitinae) in western Tanzania. *Primates*, 26, 375–389.
- Collins, D. A., & McGrew, W. C. (1987). Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates*, 28, 457–471.
- Deblauwe, I. (2006). New evidence of honey-stick use by chimpanzees in southeast Cameroon. *Pan Africa News*, 13, 2–4.
- Deblauwe, I., & Janssens, G. P. J. (2007). New insights into insect prey choices of chimpanzees and gorillas in southeast Cameroon: The role of nutritional value. *American Journal of Physical Anthropology*, in press.
- Deblauwe, I., Guislain, P., Dupain, J., & van Elsaker, L. (2007). 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.
- Eggleton, P., Bignell, D. E., Sands, W. A., Waite, B., Wood, T. G., & Lawton, J. H. (1995). The species richness of termites (Isoptera) under different levels of forest disturbance in the Mbal Mayo Forest Reserve, southern Cameroon. *Journal of Tropical Ecology*, 11, 85–98.

- Fruth, B., & Mohneke, M. (2007). Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, D.R.C.: Common methodology revisited. In T. Furuichi & J. Thompson (Eds.), *The Bonobos: Behavior, Ecology, and Conservation* (pp. 152–166). Springer.
- Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, *201*, 1264–1266.
- Goodall, J. v. L. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 161–311.
- Goodall, J. (1986). *The Chimpanzees of Gombe. Patterns of Behavior*. Cambridge, MA: Harvard University Press.
- Hohmann, G., Fowler, A., Sommer, V., & Ortmann, S. (2006). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: The abundance and nutritional quality of fruit. In G. Hohmann, M. Robbins, & C. Boesch (Eds.), *Feeding Ecology of Apes and Other Primates* (pp. 123–159). Cambridge: Cambridge University Press.
- Hohmann, G., & Fruth, B. (2008). New records of prey capture and meat eating by bonobos at Lui Kotal, Salonga National Park, Democratic Republic of Congo. *Folia Primatologica*, *79*, 103–110.
- Horn, A. D. (1980). Some observations on the ecology of the bonobo chimpanzee (*Pan paniscus* Schwarz, 1929) near Lake Tumba, Zaire. *Folia Primatologica*, *34*, 145–169.
- Humle, T., & Matsuzawa, T. (2002). Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, *58*, 133–148.
- Kajobe, R., & Roubik, D. W. (2006). Honey-making bee colony abundance and predation by apes and humans in a Uganda forest reserve. *Biotropica*, *38*, 210–218.
- Kano, T. (1983). An ecological study of the pygmy chimpanzee (*Pan paniscus*) of Yalosidi, Republic of Zaire. *International Journal of Primatology*, *4*, 1–31.
- Kano, T. (1986). *The Last Ape. Pygmy Chimpanzee Behavior and Ecology*. Stanford, CA: Stanford University Press.
- Kano, T., & Mulavwa, M. (1984). Feeding ecology of the pygmy chimpanzee (*Pan paniscus*) of Wamba. In R. L. Susman (Ed.), *The Pygmy Chimpanzee. Evolutionary Biology and Behavior* (pp. 233–274). New York: Plenum Press.
- Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in wild chimpanzees (*Pan troglodytes schweinfurthii*) of Gombe National Park, Tanzania. *Animal Behaviour*, *70*, 673–683.
- McBeath, N. M., & McGrew, W. C. (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, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution*, *3*, 501–508.
- McGrew, W. C. (1983). Animal foods in the diets of wild chimpanzees (*Pan troglodytes*): Why cross-cultural variation? *Journal of Ethology*, *1*, 46–61.
- McGrew, W. C. (1992). *Chimpanzee Material Culture. Implications for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew, W. C. (2001). The other faunivory: Primate insectivory and early human diet. In C. B. Stanford & H. T. Bunn (Eds.), *Meat-eating and Human Evolution* (pp. 160–178). Oxford: Oxford University Press.
- McGrew, W. C., & Collins, D. A. (1985). Tool-use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes heus*) in the Mahale Mountains, Tanzania. *American Journal of Primatology*, *9*, 47–62.
- McGrew, W. C., Pruett, J. D., & Fulton, S. J. (2005). Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatologica*, *76*, 222–226.
- McGrew, W. C., & Rogers, M. E. (1983). Chimpanzees, tools, and termites: New records from Gabon. *American Journal of Primatology*, *5*, 171–174.
- McGrew, W. C., Tutin, C. E. G., & Baldwin, P. J. (1979). Chimpanzees, tools and termites: Cross-cultural comparisons of Senegal, Tanzania, & Rio Muni. *Man*, *14*, 185–214.
- Nishida, T. (1972). Preliminary information of the pygmy chimpanzees (*Pan paniscus*) of the Congo Basin. *Primates*, *13*, 415–426.
- Nishida, T. (1973). The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. *Journal of Human Evolution*, *2*, 357–370.
- Nishida, T., & Hiraiwa, M. (1982). Natural history of a tool-using behaviour by wild chimpanzees in feeding upon wood-boring ants. *Journal of Human Evolution*, *11*, 73–99.
- Nishida, T., & Uehara, S. (1980). Chimpanzees, tools, and termites: another example from Tanzania. *Current Anthropology*, *21*, 671–672.
- Ono-Vineberg, E. (1997). Insect egg consumption by *Pan paniscus* at Wamba, Zaire. *American Journal of Primatology*, *42*, 138–139 (abstract).

- Sabater Pi, J., & Veà, J. J. (1994). Comparative inventory of foods consumed by the wild pygmy chimpanzee (*Pan paniscus*; Mammalia) in the Lilungu-Lokofe region of the Republic of Zaire. *Journal of African Zoology*, *108*, 381–396.
- Schoening, C., Ellis, D., Fowler, A., & Sommer, V. (2007a). Army ant availability and consumption by chimpanzees (*Pan troglodytes vellerosus*) at Gashaka (Nigeria). *Journal of Zoology*, *271*, 125–133.
- Schoening, C., Humle, T., Moebius, Y., & McGrew, W. C. (2007b). Chimpanzee predation on army ants: Can prey characteristics explain the diversity in the apes' behaviour? *Journal of Human Evolution*, in press.
- Uehara, S. (1982). Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). *Folia Primatologica*, *37*, 44–76.
- Uehara, S. (1990). Utilization patterns of a marsh grassland within the tropical rain forest by the bonobos (*Pan paniscus*) of Yalosidi, Republic of Zaire. *Primates*, *31*, 311–322.
- Uehara, S. (1999). Why don't chimpanzees of M group at Mahale fish for termites? *Pan Africa News*, *6*, 22–24.
- White, F. J. (1992). Activity budgets, feeding behaviour and habitat use of pygmy chimpanzees at Lomako, Zaire. *American Journal of Primatology*, *26*, 215–223.
- Wood, T. G., Johnson, R. A., Bacchus, S., Shittu, M. O., & Anderson, J. M. (1982). Abundance and distribution of termites (Isoptera) in a riparian forest in the southern Guinea savanna vegetation zone of Nigeria. *Biotropica*, *14*, 25–39.