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Nkala Forest: Introduction of a forest-savanna mosaic field site of wild bonobos and its future prospects

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INTRODUCTION

Bonobos are one of humans' two closest living relatives and display several remarkable similarities to us (Hare & Yamamoto 2015; 2017). To understand human evolution, it is essential to understand bonobos. However, compared to chimpanzees, research on bonobos is lacking. There are far fewer bonobo research sites, with far less environmental diversity.

In this article, we introduce our wild bonobo research site located at the southwest end of bonobos' range in the Forest Concession of Local Communities of the Mbali River (hereafter, "Mbali area", previously called "Malebo"), in Lac Tumba landscape, Mai-Ndombe province, Democratic Republic of the Congo (Figure 1). The site is unique for its forest-savanna mosaic environment, as previous studies on wild bonobos have mainly been conducted in rich tropical rainforests (Furuichi & Thompson 2010) such as Wamba (Kano 1992), Lomako (Badrian & Malenky 1984) and LuiKotale (Hohmann & Fruth 2003). Inogwabini *et al.* (2008) recently confirmed that wild bonobos inhabit a wider range of environments than previously thought, and since then much attention has been paid to wild bonobos in forest-savanna mosaic

environments (Inogwabini *et al.* 2013; Narat *et al.* 2015a, b, c; Pennec *et al.* 2016; Serckx *et al.* 2014, 2015, 2016). Wild bonobos in Mbali thus present a promising and novel research opportunity for understanding bonobo behavior from a broader species level.

Studies in forest-savanna mosaic environment are also important for theories of human evolution. Many researchers suggest that much of human evolution occurred in forest-savanna mosaic environments after divergence from a forest-dwelling ancestor, and it is therefore essential to study how savanna environments influence great apes' behavior and society. Such an approach has been taken to some extent with chimpanzees (*e.g.*, Pruetz & Bertolani 2009), however there are few studies with wild bonobos. Some research in forest-savanna mosaic environments has been conducted on local ecology (*e.g.*, Serckx *et al.* 2015; Trolliet *et al.* 2016; Pennec *et al.* 2016) and human-bonobo relationships (Inogwabini *et al.* 2013; Narat *et al.* 2015a) in the Mbali area, and also on conservation (Hickey *et al.* 2013) and genetics (Kawamoto *et al.* 2013; Takemoto *et al.* 2017) in Tshuapa-Lomami-Lualaba (TL2) in the eastern end of bonobo's range (Figure 1). However, studies on bonobos' behavior and society in forest-savanna mosaic environments are extremely limited (but see Druelle *et al.* 2020; Narat *et al.* 2015b).

GENERAL INFORMATION

Mbou-Mon-Tour (MMT), a local NGO for conservation, eco-tourism and community development, started habituating wild bonobos in the Nkala, Mpelu and Manzano sites in 2001. The first two sites have been technically and financially supported by WWF-DRC since 2006, and the third site, Manzano, has been supported by Bonobo-ECO since 2010. MMT has been operating daily monitoring of bonobos from their morning to night nests whenever possible. Since 2014, in collaboration with MMT and WWF-DRC, Kyoto University researchers have studied the Nkala group (named after the nearest village, 2°36'10"S, 16°27'17"E). Thanks to collaborative efforts of extensive habituation, we have been able to identify all bonobos in the Nkala group since 2016 and can observe them from a distance of approximately 10 to 20 m. This area includes old and young secondary forests, savanna, crop fields and villages (Figure 2). In the Nkala forest, we found direct or indirect evidence for 44 species of mammal including pangolins, civets, duikers, bonobos and other primates such as *Cercopithecus ascanius* and

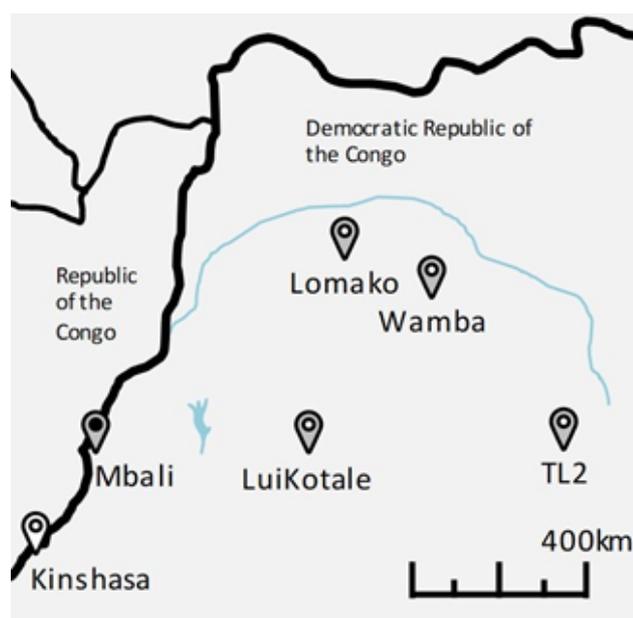


Figure 1. Map of bonobo research sites listed in this paper. The Nkala is one of the field sites in Mbali which is located in the Lac Tumba landscape.



Figure 2. Aerial photo of Nkala forest taken by a drone. (Photo taken by Ena Onishi)



Figure 3. Marantaceae forest. (Photo taken by Ena Onishi)

Cercopithecus neglectus (Shintaku *et al.* unpublished data). Direct evidence included live observation, hearing vocalizations and camera trap footage, while indirect evidence included hair, feces, footprints and reports from the local people.

COMPOSITION OF THE BONOBO GROUP

The Nkala group consisted of around 15 individuals until a drastic population decline in 2018. Table 1 shows the number of confirmed individuals at the end of each year from 2016 to 2019. In 2017, two females disappeared. An adult female was suspected to have died from natural causes and a juvenile female was suspected to have transferred to another group. In 2018, four adult and subadult males disappeared; one adult male disappeared in late March, two adult males disappeared simultaneously in early June, and another subadult male disappeared in late June. MMT research assistants did not detect any signs of disease or injury in their daily follows, and the infants survived, suggesting a disease epidemic is unlikely. We did not find dead bodies of bonobos during the study period. At the end of 2019, the population had only 10 individuals, including 4 juveniles and infants.

HABITAT USE

Since 2016, in collaboration with MMT local assistants, we have recorded bonobos' activity and habitat use every 30 minutes on full day follows whenever possible. We analyzed their habitat use throughout 2018; 280 days of data were collected (23.3 ± 5.0 days in a month on average) including 6997 data points. During observation, research assistants recorded bonobos' location with four categories: closed canopy forest, Marantaceae forest, inundated forest and savanna (Tutin *et al.* 1994). Marantaceae

forest refers to a forest type where Marantaceae plants predominate the landscape as shown in Figure 3.

Figure 4 shows monthly habitat use by the Nkala group. They spent 47.9% of the total time in closed canopy forest, 50.2% in Marantaceae forest, 1.4% in inundated forest and 0.5% in savanna environments. There was a significant difference in habitat use between the dry and wet season (dry season: February to March and June to August; wet season: April to May and September to January (Inogwabini *et al.* 2008); Fisher's exact test: p -value < 0.01). Multiple comparison with Holm correction revealed that bonobos significantly increased the ratio of savanna use in wet season (0.18% in dry season; 0.85% in wet season).

Crossing to a distant forest was the most common use of savanna in our observations (see Video 1 available online at <http://mahale.main.jp/PAN/2020/001.html>). We observed four complete savanna crossing events, each spanned less than 10 minutes. We have also observed longer stays (more than 2 hours) and foraging behavior in the savanna (see Video 2 available online at <http://mahale.main.jp/PAN/2020/001.html>; we could not identify the food item in the video).

CONSERVATION

Nkala villagers (Bateke people) have a strong traditional taboo against eating bonobos (Inogwabini *et al.* 2013). Due to the MMT's long-term efforts in the Mbali area (e.g. Narat *et al.* 2015b), the Nkala forest is protected by the community. Hunting of bonobos is strictly prohibited, though hunting of small animals with traditional methods is permitted. Unfortunately, during their regular patrolling of the forest twice a month, MMT forest rangers have found numerous banned metal-wire traps and cartridges. They found 38 traps and 57 cartridges between

Table 1. Group composition of Nkala group from 2016 to 2019

	adult/subadult male	adult/subadult female	juvenile male	juvenile female	infant	TOTAL
2016	5	4	2	1	2	14
2017	5	3	2	0	2	12
2018	3	3	0	0	3	9
2019	3	3	0	2	2	10

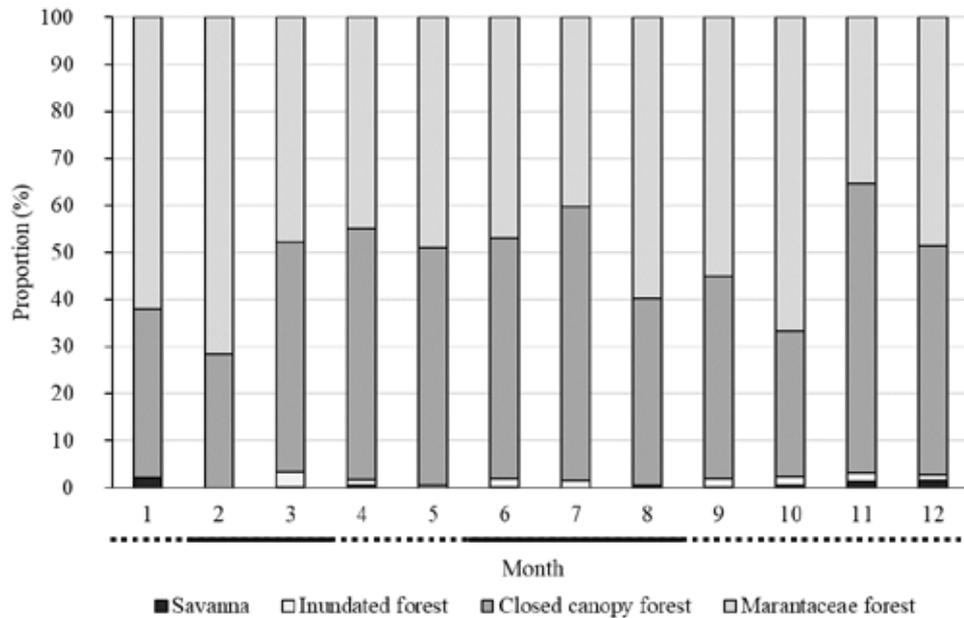


Figure 4. Habitat use by the Nkala bonobos in 2018. The black line along the x-axis represents dry season and the dotted line represents wet season.

July 2018 and May 2019 (Table 2). Suspected poachers with guns were also recorded by our camera traps.

DISCUSSION

Our preliminary survey and analyses on the Nkala bonobos’ habitat use shows constant and strong preference for forest and Marantaceae forest over inundated forest or savanna. Bonobos spent just 0–2.1% of time in savanna, despite the fact that 40% of their habitat by area is savanna (Inogwabini *et al.* 2008), suggesting that bonobos constantly and strongly avoid use of savanna. This is unsurprising considering the savanna has greater visibility, lower food availability and increased human activity. However, based on our observations, we can also predict that bonobos forage for plants or insects in the savanna which are not available or rare in the other habitat categories.

This perspective is supported by the differential time spent in the savanna between dry and wet seasons, though this should be investigated further. Future research, especially cross-site comparisons, can help reveal their adaptation to forest-savanna mosaic environments, which may prove insightful for understanding human evolution in similar environments.

Despite the evident scientific value of this field site, the Nkala group is at a critical risk of extinction. The traps and cartridges found in the forest indicate it is possible that the decline in group size was due to illegal poaching, though there is no direct evidence of bonobo hunting. Poaching for the commercial bushmeat trade is one of bonobos’ main threats (IUCN & ICCN 2012), and the situation in Nkala may be especially critical because the forest is directly beside a village. Thus, community development is key for conservation, and establishment of a sustainable economic alternatives to hunting activities is essential. Eco-tourism may be one of the most effective and sustainable strategies, thanks in part to the site’s close proximity to the country’s capital, Kinshasa (1-hour flight or 1-day boat trip). For this purpose, an international presence at this site must be established to attract tourists.

MMT has detected several other bonobo groups around the Nkala forest besides the Manzano and Mpelu groups, but intergroup relationships and migration patterns are not yet known. Green-corridor planting projects like those at Bossou-Nimba, Guinea (Matsuzawa *et al.* 2011) might help ensure connectivity and migration between forest fragments despite savanna, crop and grazing fields, and roads separating them. As scientific researchers, we would like to continue our efforts to study the wild bonobos in this area, promote their scientific importance, and acknowledge and support the local community that has made tremendous efforts to conserve the forest and the bonobos. We hope this report can help raise awareness of the conservation issues and the research possibilities in

Table 2. Number of traps and cartridges found in Nkala forest between July 2018 to May 2019

year	month	trap	cartridge
2018	July	1	8
	August	6	7
	September	3	7
	October	3	6
	November	1	4
	December	2	4
2019	January	0	7
	February	3	3
	March	2	4
	April	15	3
	May	2	4

Nkala.

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Cultural dietary stasis? Four decades on, Mahale chimpanzees still favour *Macrotermes*

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INTRODUCTION

Termite consumption by wild chimpanzees (*Pan troglodytes*) is widespread across Africa (McGrew 1992) but not universal (Fowler & Sommer 2007). When consumed, termites represent a valuable source of energy, fat, high-quality protein, minerals and vitamins (O'Malley & Power 2014). Frequency, acquisition techniques and choice of prey vary greatly among populations (Wondra *et al.* 2016). While some of these differences respond to the characteristics of the termite prey and ecological context, other aspects may more easily be attributed to social influences (Sanz *et al.* 2014). Of the 106 genera of soil-dwelling termites present in Afrotropical habitats (Krishna *et al.* 2013), only eight have been recorded as chimpanzee termite prey, with *Macrotermes* being the genus mostly eaten (Lesnik 2014).

Chimpanzees of Bilenge (B group) inhabiting the Mahale Mountains National Park in Tanzania were first reported to harvest *Macrotermes* with tools in 1975 (Nishida & Uehara 1980). Other termites such as *Odontotermes* and *Pseudacanthotermes spiniger* were more abundant but ignored (Collins & McGrew 1985).

Recent studies revealed that the B group has maintained their termite-fishing tradition for more than forty years (Pascual-Garrido 2017). However, if they continue to favour *Macrotermes* remains unknown. Here we document termite prey consumption by Mahale B group chimpanzees and compare with those reported decades ago (Collins & McGrew 1985). We discuss possible factors influencing this choice.

METHODS

The unhabituated chimpanzees (*Pan troglodytes schweinfurthii*) of B group live in Bilenge (6° 2' S, 29° 44' E; 772–1550 m elevation), the northwestern edge of the Mahale Mountains National Park in western Tanzania (Nishida & Uehara 1980). The dry season from mid-May to mid-October has virtually no rain. The rainy season generally has two peaks of rainfall in November and in March–April, with an average annual rainfall of about 1400 mm. Bilenge is mostly dominated by open grassy woodland, mainly *Brachystegia* (miombo), with vine tangles and forests only present in narrow strips along the valleys, and broad hilltops rising from the coastal plain (Collins & McGrew 1988). Termite-fishing though habitual, is highly seasonal, mainly taking place during the first half of the wet season (from October until at least February), which coincides with the annual and dispersal flights of the termites (Uehara 1982).

Three field seasons were conducted by APG assisted by one experienced Tanzanian field assistant (Nov 25th –

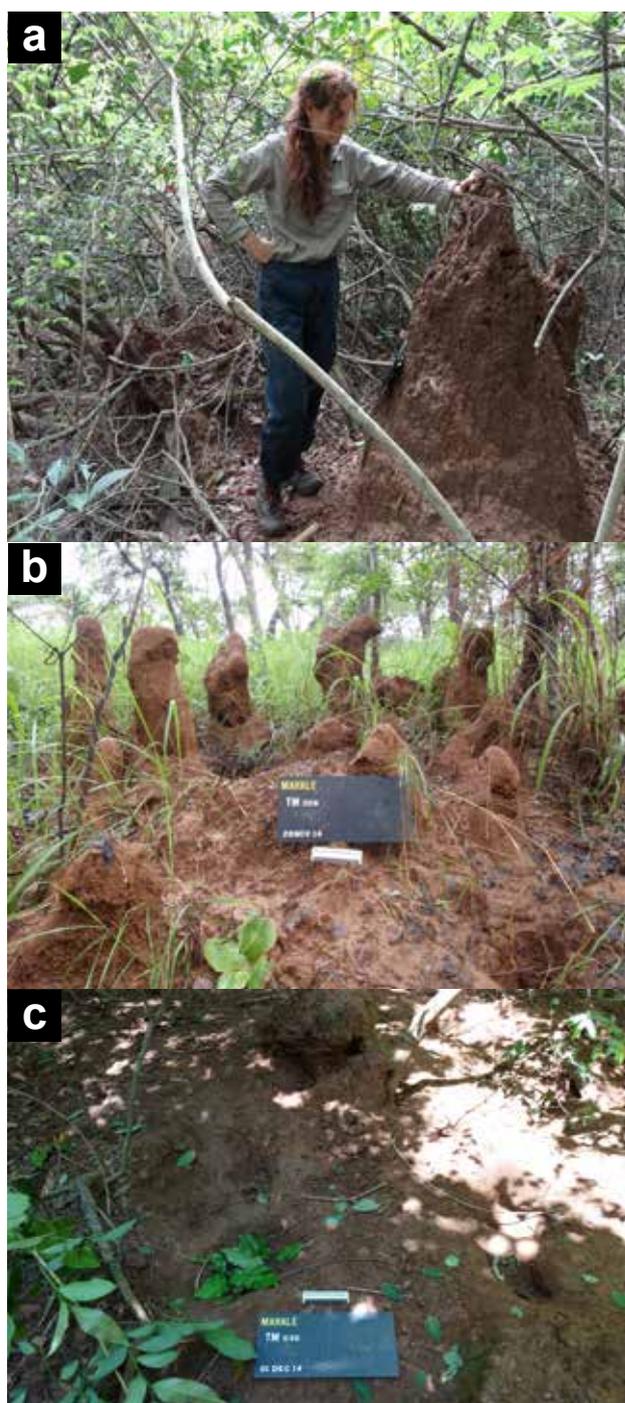


Figure 1. Termite genera in Bilenge. a) APG and a mound of *Pseudacanthotermes spiniger*; b) *Odontotermes*; c) *Macrotermes michaelseni* with recently abandoned termite fishing tools by chimpanzees (December 1st, 2014). Photo credits: Alejandra Pascual-Garrido.

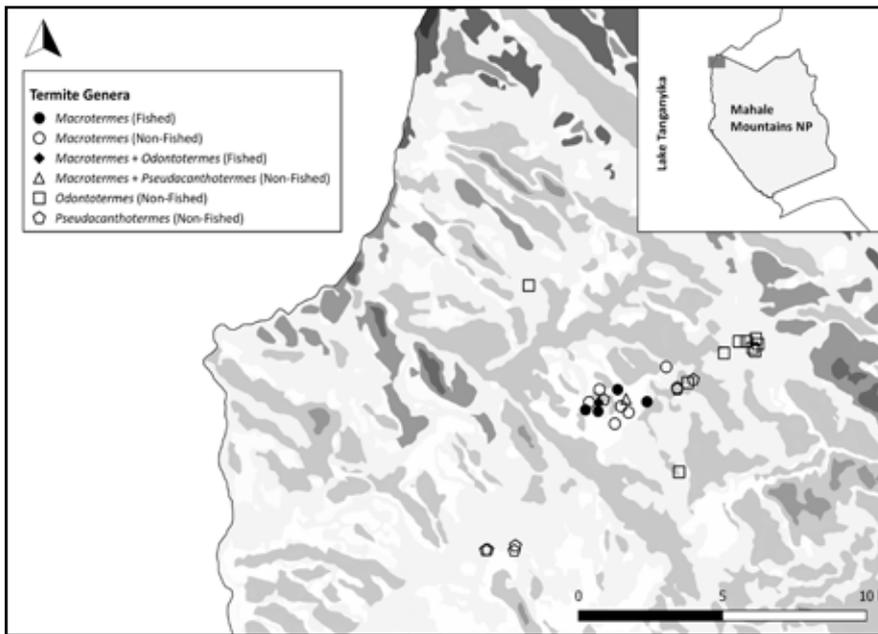


Figure 2. Map of the distribution of termite mounds surveyed at Bilenge. Mounds fished by chimpanzees are shown in black. Map credits: Katarina Almeida-Warren.

Dec 14th, 2014; Oct 20th–Nov 8th, 2015; Nov 21st–Dec 8th, 2016). During reconnaissance surveys, APG searched for mounds which could potentially have been fished by chimpanzees within B’s group range (Nishida & Uehara 1980). Mounds included broadly domed mounds, mounds with open ventilation holes and towers raised as chimney (Collins & McGrew 1985). Smaller mushroom-shaped mounds, typical of soil *Cubitermes*, were ignored given that they are not targeted with plant tools by chimpanzees (Collins & McGrew 1985; O’Malley & Power 2012) (though Bili-Uère chimpanzees use percussive technology to access them; Hicks *et al.* 2020). Data collected at each mound included GPS position and, based on archaeological methods (Pascual-Garrido 2018), evidence of each mound having been targeted by chimpanzees including: (a) tools, (b) plants sourced for tool material, (c) signs of damage (i.e. knuckleprints). For each mound, at least 10 termite specimens were collected, fixed in ethanol 80% and later identified by RS. Specimens collected included mostly soldiers. Workers and alates were collected when available.

RESULTS

A total of 36 mounds were sampled and identified. This included six genera and five species, with *Macrotermes*, *Pseudacanthotermes* and *Odontotermes* being the genera most represented (Figure 1). All mounds were occupied by a single resident species, except for four mounds where multiple occupants resided (Table 1). Soldiers were collected at all mounds, with alates only present at three *Macrotermes* mounds and at one *Odontotermes* mound. Only *Macrotermes michaelsoni* mounds showed signs of having been targeted by chimpanzees (n=5), one or multiple times (Pascual-Garrido 2017), and one also occupied with a second resident from the genus *Odontotermes* (Table 1; Figure 2). No evidence of chimpanzee predation was recorded for any other ter-

mite genera. Evidence of chimpanzee predation at mounds included tools (n=1), knuckleprints (n=1) and plants sourced for tool materials (n=5) (Pascual-Garrido 2017).

DISCUSSION

More than 40 years have passed and successive generations of Bilenge chimpanzees continue to fish *Macrotermes* mounds while ignoring other termites also common in the area (Collins & McGrew 1985). *Macrotermes* are preyed on by more populations of chimpanzees than all other termite taxa, being the best-documented insect genus for ape use of elementary technology in extractive foraging (Lonsdorf 2005). Given the high nutritional value, fishability, greater mass and less noxious taste of these fungus-

farming termites compared to other genera (Collins & McGrew 1985; O’Malley & Power 2014), it is therefore not surprising that Bilenge chimpanzees continue to fish them. But why do Bilenge chimpanzees still ignore other genera such as *Odontotermes* and *Pseudacanthotermes*? The absence of *Odontotermes*’ consumption, a genus not consumed by any wild chimpanzee population (except rehabilitated chimpanzees released in Rubondo Island in Tanzania; Moscovice *et al.* 2007), is not surprising: their distasteful defensive secretion makes them unpalatable for chimpanzees – and for humans too as corroborated by APG. More puzzling is the lack of ingestion of the highly nutritional and more abundant *P. spiniger* – a species habitually fished by the extinct neighbouring K group of Mahale (Uehara 1982) and by Issa chimpanzees living 114 km east of Bilenge (Stewart & Piel 2014; Pascual-Garrido, unpublished data). It may be that Bilenge apes fish *P. spiniger* later in the wet season (although Uehara’s (1982) analysis from faecal samples suggests that they do not). That we failed to find any evidence of termite-fishing at these mounds, including plants used for tool making which, unlike tools, remain detectable for years (Pascual-Garrido 2018), makes this unlikely. If members of the B group eat alates (and soil) of *P. spiniger*, as neighbouring (extinct) K group and M group do without tools (Uehara 1982) (though see Takahata 1982 for use of tools by two immigrant chimpanzees from K group termite fishing at *P. spiniger* mounds), we would have missed it, as this can only be evidenced by direct observation of the apes (not possible at Bilenge) or by faecal samples inspection (not included in this study). Still, at present we have no evidence for this – and certainly no signs at all that they fish them. The question therefore remains: Why do Bilenge chimpanzees focus their termite-fishing exclusively on *Macrotermes*, as do Gombe chimpanzees, while ignoring *P. spiniger* whose major soldiers are high in energy, fat and protein and fished by other chimpanzee communities

Table 1. Termite family, subfamily, genera and species surveyed at Bilenge. Mounds targeted by chimpanzees appear in grey.

Termite mound	Family	Subfamily	Genera	Species
MTM023	Termitidae	Apicotermittinae	<i>Alyscotermes</i>	<i>kilimandjaricus</i>
MTM030	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM050	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM054	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM051	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM063	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM063	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM018	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>bellicosus</i> ; <i>michaelseni</i>
MTM033	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM034	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM055	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM066	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM036	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM015	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM017	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i> ; <i>lilljeborgi</i> ; <i>bellicosus</i>
MTM002	Termitidae	Macrotermittinae	<i>Microtermes</i>	
MTM021	Termitidae	Macrotermittinae	<i>Microtermes</i>	
MTM006	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM005	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM010	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM007	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM008	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM009	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM012	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM011	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM014	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM038	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM033	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM031	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM042	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM013	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM016	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM025	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM026	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM041	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM040	Termitidae	Macrotermittinae		
MTM024	Termitidae	Termitinae	<i>Microcerotermes</i>	
MTM004	Termitidae	Termitinae	<i>Microcerotermes</i>	

(Uehara 1982; O'Malley & Power 2012)?

One possibility could be that the density of *Pseudacanthotermes* at Bilenge has declined during the last decades and chimpanzees are selecting their prey subject to their availability. However, earlier studies indicate this is not the case (Collins & McGrew 1985), but that *P. spiniger* are ignored because of the soldier's smaller size and less value on a per-foraging-unit basis compared to *Macrotermes* (O'Malley & Power 2012). However, an extended termite fishing session on *P. spiniger* could still provide a nutritional meaningful yield of energy, fat and protein (O'Malley & Power 2012). Previous research indicates that techniques and type of tools used to harvest insects, including termites, is partly influenced by the behaviour of the species preyed upon (Schöning *et al.* 2008; Sanz *et al.* 2014). If *Macrotermes* are more fishable than *Pseudacanthotermes* (i.e. grip on the tool with greater force) remains to be tested.

Another possibility, perhaps more difficult to test, is that chimpanzees may be reluctant to try new food choices. Adult chimpanzees are conservative regarding their feeding habits, which can act as a selective force against a new food (Nishida *et al.* 1983). Still, they may consume a variety of human (crop) foods if available (McLennan &

Hockings 2014). Furthermore, captive and wild chimpanzees show a marked persistence for initially adopted strategies related to the acquisition of food, even when a strategy stops being successful (Gruber *et al.* 2009; Hrubesch *et al.* 2009). Conservatism can create within-group behavioural homogeneity, while Whiten *et al.* (2005) attributed it to conformity. Chimpanzees are highly selective regarding their insect prey choices (Webster *et al.* 2014). That some chimpanzee communities prey on termites, while others do not (Fowler & Sommer 2007), and that harvesting techniques differ between (and within) communities (McGrew 1983; Boesch *et al.* 2020), highlights the importance of investigating the mechanisms behind these differences. Social influences on food preferences are barely contemplated in current studies of chimpanzee culture (but see Hicks *et al.* 2020) – maybe because variation in feeding behaviour is more parsimoniously explained by ecological differences (Byrne 2007). However, Boesch *et al.* (2006) suggested that variation in feeding time relative to fruit availability may reflect cultural differences, while Hicks *et al.* (2020) found no association between insect availability and consumption. Likewise, Nishida *et al.* (1983) and Sakamaki *et al.* (2007) reported that two neighbouring groups at Mahale consume different food items, despite their equal availability in both areas. Similarly, neighbouring chimpanzee communities living in the Budongo Forest Reserve, Uganda, vary in their preference for red duiker (*Cephalophus natalensis*) consumption despite no difference in prey distribution (Hobaier *et al.* 2017). Social learning plays a fundamental role in the acquisition of technological skills to harvest social insects, including food choices (Lonsdorf 2005; Schöning *et al.* 2008; O'Malley *et al.* 2012), and is key for the development and maintenance of cultural behaviours and traditions in primates (Schuppli & van Schaik 2019). Further research is warranted to establish if social learning in chimpanzees extends to their choice of termite prey.

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The New Chimpanzee: A Twenty-First-Century Portrait of Our Closest Kin

By Craig Stanford

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Craig Stanford, primatology professor at the University of Southern California, has a track-record of producing engaging and informative books about primates. Now comes his latest, and its subtitle tells us what it entails: A synthetic look at new findings about wild chimpanzees from the last two decades, across the board. Such an update is due, as field chimpology is in its sixth decade, and there are more habituated populations (12) and communities than ever. He delivers as promised: Of the 493 references in the bibliography, three-quarters come from 2000 onwards, and 41% come from 2010 onwards.

The 10 chapters cover the pertinent topics, after the first one devoted to a description of what is involved in studying wild chimpanzees and a history of the early days of field studies of *Pan troglodytes*. That is, sociality, diet, competition, collective agonism, sex and reproduction, ontogeny, hunting, culture and elementary technology, kinship, and implications for human evolution. Each chapter has super-scripted links to endnotes (12 pp). There are nine illustrations, but no photographs. Besides topics, the 10-page index includes individual researchers and chimpanzees, and study-sites.

Three of the chapters deserve special attention, as two of them reflect the author's committed interest in the topic. Previous books (e.g., Stanford 1999) reflect his longstanding interest in chimpanzee hunting, especially of red colobus monkeys. He focusses on four hypothesized answers to why chimpanzees hunt: for calories, protein, fat and trace nutrients. New data support the first three but not the fourth. (After all, carnivory is only one kind of faunivory, and invertebrates can provide the trace elements just as well as vertebrates.) He also outlines the factors that influence hunting, from forest structure to political and social aspects. Twenty-first century findings support the 'food-for sex' effect, whereby males share food with females who in the long-run favor those males in mating. However, no new evidence has emerged for cooperative hunting of the kind claimed for Tai's chimpanzees, so they apparently remain unique in that regard.

The extent to which chimpanzees provide a model for inferring the evolution of the ape and human lineages since the Last Common Ancestor remains a much-debated topic. Stanford (2003) has weighed in on this before,

especially with regard to Owen Lovejoy's rejection of any utility of living apes for understanding *Ardipithecus ramidus*. Stanford robustly rebuts Lovejoy's arguments (which is not surprising, as 'Ardi' is too young a taxon to be a candidate for the LCA). In contrast to reprising that well-trodden argument, he gives a more negative take on what apes might provide in the interpretation of purported cave interments of *Homo naledi*.

The author's chapter on culture cites progress in cultural primatology, especially new findings from field experimentation and primate archaeology. Important are recent studies of sub-cultures within populations, that is, comparing the habitats of neighboring communities of chimpanzees. However, Stanford restricts himself to material culture based on elementary technology, ignoring non-subsistence cultural traditions, e.g., in grooming or vocalizations. Meanwhile, exciting new evidence of collectivity is emerging, such as community-wide contrasts in prey choice (Hobaiter *et al.* 2017): Species of duiker at the same population densities are heavily hunted by one group but ignored by neighbours.

Stanford is especially good about citing the source of findings, both by authors and their institutions. The latter gives an interesting opportunity to see where recent field work on wild chimpanzees is based. Of the 79 institutions named, four stand out above all others (in order of frequency): Max-Planck-Institute for Evolutionary Anthropology (Leipzig), University of St Andrews (Scotland), Kyoto University and Harvard University. No other is mentioned more than six times.

Of course, there are some slip-ups. He states that chimpanzees have a 1 million-year history and that *Homo sapiens* dates from 300,000 years ago, both of which claims require evidence not cited (p. 1). His definitive table and map of chimpanzee study-sites older than 15 years omits Kalinzu (Hashimoto *et al.* 2001) (p. 12–13). He states that orangutans do not make nests, when he probably means to say gibbons (p. 33). He says that baboons were the first nonhuman primates studied in nature, somehow forgetting the earlier, pioneering work on Japanese macaques (p. 46). He lists only 17 species of mammal preyed upon by chimpanzees, while the actual number is much higher, perhaps because his sources are pre-2000 (p. 133). (Newton-Fisher 2014, listed 35.) He says that

besides humans there are no other mammalian bipeds, somehow forgetting about the terrestrial macropods (p. 194). But these flaws are few and trivial oversights in a work of this encompassing scope.

Perhaps the epigram best summing up the book is the cliché: “The more things change, the more they remain the same.” At the turn of the millennium, we knew not of the exploits of the savanna chimpanzees of Fongoli, Senegal: Their hunting skewers, cave-use, cooling-off baths, nocturnal travel, or dealing with bushfires. Yet, even with more than 120 study-sites, chimpanzee fission-fusion structure remains uniform, despite group sizes that vary by an order of magnitude. Good reasons for field chimpology to carry on, indeed!

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Bili-Uéré: A chimpanzee behavioural realm in northern Democratic Republic Congo

By Thurston C. Hicks, Hjalmar S. Küehl, Christophe Boesch, Paula Dieguez, Ayuk Emmanuel Ayimisin, Rumen Martin Fernandez, Donatienne Barubiyo Zungawa, Mbangi Kambere, Jeroen Swinkels, Steph B. J. Menken, John Hart, Roger Mundry and Peter Roessingh

Book review by *William C. McGrew*

Pan Africa News 26(2): 19–20 (2019)

There were several errors in this book review. The first, the preposition ‘of’ was missing between ‘Republic’ and ‘Congo’ in the book title. The second, the surname of author Hjalmar S. Kühl was incorrectly listed as ‘Hjalmar S. Kuehl’. The third, the following three lines were missing.

Folia Primatologica 90(1): 3–64.

Special Issue Editors: KAI Nekaris and Alejandra Pascual-Garrido

<https://doi.org/10.1159/000492998>

They should have been inserted between names of the authors and the reviewer. The errors have been corrected in the HTML and the PDF versions at <http://mahale.main.jp/PAN/2019/005.html>. We apologize for any inconvenience that it may have caused.

Behavioral responses toward a conspecific corpse of wild bonobos (*Pan paniscus*) at Wamba

Takumasa Yokoyama & Satoshi Yasumoto

Pan Africa News 26(2): 16–18 (2019)

Owing to a technical error, the affiliation and address of the second author was typed incorrectly as “The Center for African Area Studies, Kyoto University, Japan” instead of “Graduate School of Asian and African Area Studies”. This error has been corrected in the HTML and the PDF versions at <http://mahale.main.jp/PAN/2019/006.html>.