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Termite fishing by wild chimpanzees: new data from Ugalla, western Tanzania

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Abstract Chimpanzees manufacture flexible fishing probes to fish for termites in Issa, Ugalla, western Tanzania. These termite-fishing tools are similar in size and material to those used by long-studied communities of chimpanzees in western Tanzania (*Pan troglodytes schweinfurthii*) and in West Africa (*P. t. verus*), but not central African populations (*P. t. troglodytes*). This report adds to the patchwork of evidence of termite-fishing tool use behaviour by chimpanzees across Africa.

Keywords Macrotermitinae · Tool use · Savanna chimpanzee · Material culture · Elementary technology

Introduction

Across all non-human taxa, only chimpanzees demonstrate habitual use of complex tools and tool kits in daily life (McGrew 1992). Over 50 years of field study of wild chimpanzees have revealed marked variation in tool type, form and function, both within and across populations (McGrew 1992; Whiten et al. 2001; Sanz et al. 2004; Schöning et al. 2008). Variation in tool diversity and complexity across chimpanzee communities is not easily explained by genetic or environmental differences, and cross-population analysis has suggested that patterns of tool use between communities represent different chimpanzee cultures (Lycett et al. 2011). Identifying and describing new occurrences and variants of tools and tool use behaviours, across a range of environmental conditions, are essential first steps to understanding environmental and cultural influences on intraspecific variation in tool use.

Across Africa, many chimpanzees consume insects. Termite consumption is widespread (McGrew 1992; Whiten et al. 2001; Sanz et al. 2004), but not ubiquitous (e.g. Fowler and Sommer 2007). However, use of tools to extract subterranean termites is not as widespread and is patchily distributed across the chimpanzee's range (McGrew 1992; Whiten et al. 2001; Sanz and Morgan 2007), and variation in the use of tools and behaviour to harvest termites has been described even between adjacent communities (Uehara 1982; McGrew and Collins 1985). Some differences are attributed to the environment (e.g. distribution of available prey), and others to culture (McGrew et al. 1979; Collins and McGrew 1987).

Interpreting geographical variation in the patterns of termite fishing behaviour between populations is difficult (McGrew et al. 1979; McGrew 1992; Sanz and Morgan 2007). Most research on chimpanzee termite fishing stems from populations in forested habitats of East and Central Africa, whilst reports from chimpanzees inhabiting different environments (e.g. savanna woodlands) are few. McGrew et al. (1979, 2005) described termite fishing in the Fongoli and Mt. Assirik chimpanzees, respectively, which inhabit a hot, dry, and open habitat dominated by open grasslands, in southeastern Senegal. More recently, Bogart and Pruetz (2008, 2011) reported termite fishing to occur regularly year-round in Fongoli, in contrast to marked seasonal peaks of consumption elsewhere (e.g. McGrew et al. 1979; McGrew and Collins 1985), which they

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propose may be an adaptation to living in such a marginal environment. Specifically, Bogart and Pruetz (2011) hypothesize that such a habitat may provide fewer protein sources, promoting chimpanzees to supplement their diet through termite consumption. Western Tanzania and southeastern Senegal share extreme seasonality, with lengthy dry seasons (>5 months) and less than 1000 mm of rain per annum (Moore 1992). Here we describe a new observation of termite fishing in a second savanna woodland chimpanzee population, with direct and indirect evidence from the Issa Valley, Ugalla, in western Tanzania.

Methods

Study site

Our study was conducted between October 2008 and March 2010 in the Issa Valley, Ugalla, in western Tanzania (S5.50, E30.56), one of the driest, most open habitats in which chimpanzees occur. Kano (1972) described the flora and fauna of Ugalla, including the chimpanzees that live there, and there are currently two on-going research projects: one at the Issa Valley (Hernandez-Aguilar 2009; Stewart et al. 2011), and one in Nguye (Ogawa et al. 2007). The Issa Valley, <100 km east of Lake Tanganyika, lies in the west of the Ugalla region (Fig. 1). Ugalla is a 3300 km^2 ecosystem consisting of broad valleys separated by steep mountains and flat plateaus ranging from 900 to 1800 m elevation. Ugalla vegetation is dominated by miombo woodland (*Brachystegia* and *Julbernardia*, Fabaceae), although it also includes swamp, grassland, as well as evergreen gallery and thicket riverine forests. There are two distinct seasons: wet (October–April) and dry (May–September), with dry months defined as having <100 mm of rainfall. Rainfall averages <1000 mm per annum (Hernandez-Aguilar 2009), and temperatures range from 11 to 35 °C (Stewart 2011).

Chimpanzees in Issa are unhabituated, and research focusses on an 85 km^2 study area. Genetic analyses have identified at least 67 individuals, 31 females and 27 males (and 9 individuals that could not be sexed definitively), in the Issa community (Rudicell et al. 2011). Previously reported technology of the Issa chimpanzees includes use of digging sticks for accessing underground storage organs (Hernandez-Aguilar et al. 2007) and *Strychnos* spp. fruit pounding behaviour (Carvalho et al. in prep).

Data collection

Tool use and diet were not foci of research during the study period, so observations of tool use emerged opportunistically, during reconnaissance walks or following fresh evidence of chimpanzees after hearing their vocalizations. When chimpanzees were observed near a termite mound, the surface of the mound was later checked for evidence of the ape's activity, including feeding remains and tools. When tools or tool use was observed, all tools were

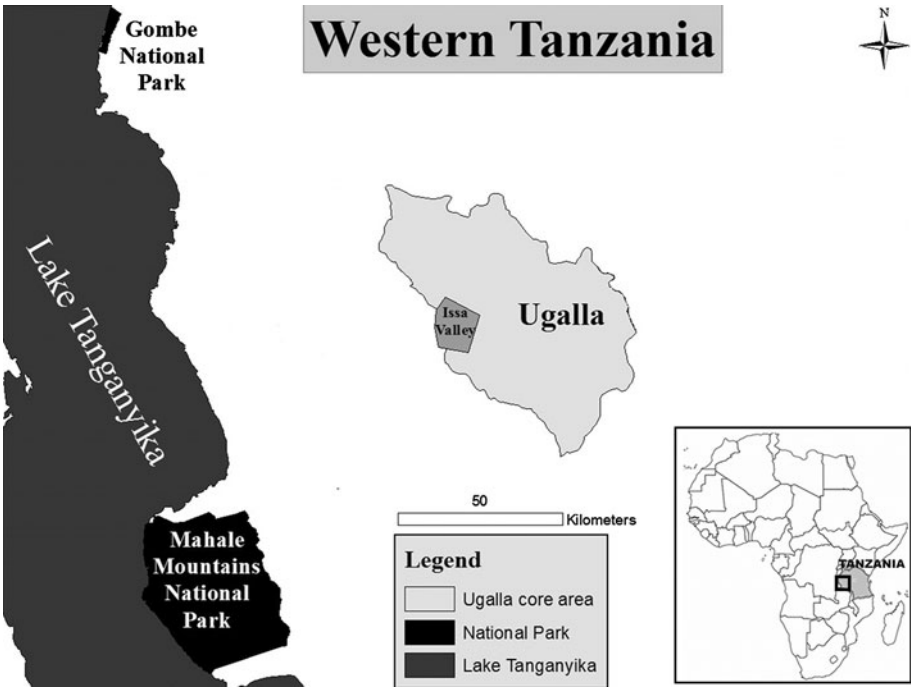

Fig. 1 Map of western Tanzania, indicating Issa, within Ugalla, and long-term research sites of Mahale and Gombe, next to Lake Tanganyika

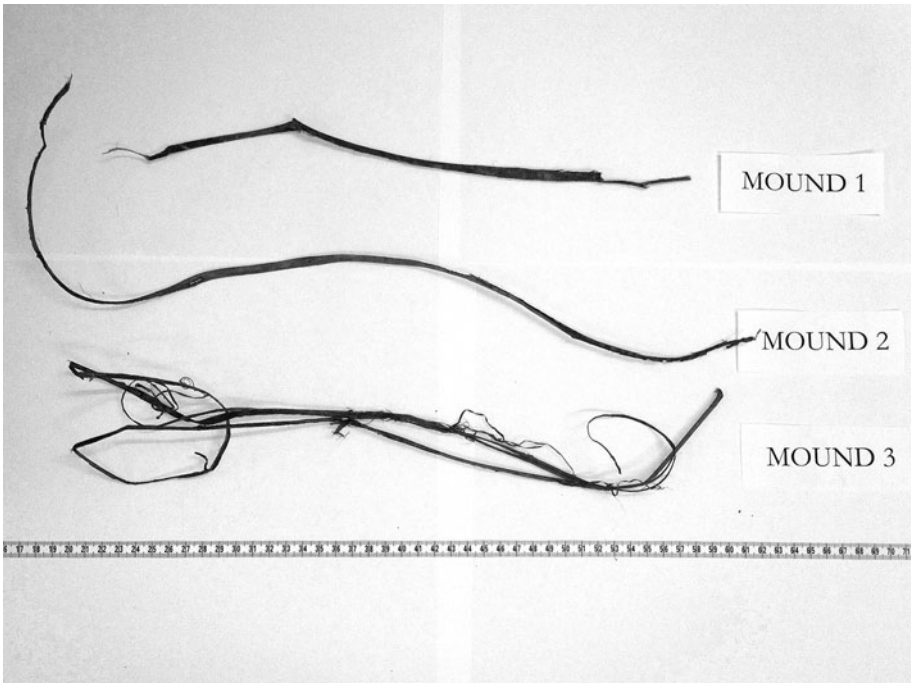

Fig. 2 Termite-fishing tools collected from mounds at Issa, Ugalla, western Tanzania

Table 1 Length and number of tools found at each mound

Mound	Number of tools	Mean length (cm)	SD
1	16	37.4	14.4
2	16	33.1	14.1
3	4	81.4	34.3
Total	36	40.4	23.0
Kruskal–Wallis test (two-tailed)	$H = 6.76$ $df = 2$ $p = 0.034$		

collected, photographed, and measured (length) using metric tape to the nearest mm.

For the duration of the study period, all fresh chimpanzee faecal samples were collected for dietary analysis following standard methods of sluicing faeces through a 1×1 mm^2 sieve and counting, or estimating the amount, of each food item present (McGrew et al. 2009). We recorded presence or absence of termites in faeces from the presence of exoskeletons. *Macrotermes* sp. termite heads were identified by their characteristic colour, size and shape, but have not yet been identified to species.

Total rainfall (mm) was calculated for each month of the study period. From November to December 2008, rainfall was recorded using a manual rain gauge read at 7 a.m. and 7 p.m. daily. From January 2009 to March 2010, rainfall data were recorded using a Hobo data-logging rain gauge (RG-3). However, due to a technical fault in the rain gauge, data were lost from October to December 2009.

Results

Observations

Chimpanzees were seen to fish for termites twice in 1 day, around 10 a.m. on 10 November 2008. Researchers first heard chimpanzee vocalizations early that morning and had separated into two teams, with one team surveying the east side of a target valley and the other approaching from the west side. Both research teams encountered a party of termite-fishing chimpanzees and recovered tools (Fig. 2). Each encounter was brief, with chimpanzees fleeing the area upon seeing researchers. In the first example, we watched a single fisher for 1 min, a juvenile female, and in the second, three adult males were seen fishing for 3 min before they fled. These observations correspond to 'mound 1' and 'mound 2', respectively, reported in Table 1.

On 30 November 2008, researchers opportunistically encountered a mound (mound 3, Table 1) with recent evidence of termite fishing and collected all tools found on the mound's surface.

Tool characteristics

Thirty-six termite-fishing tools were recovered from the three *Macrotermes* sp. mounds. At each mound, tools were found scattered on the surface of the mound, some tools were found partially inserted into the mounds and all tools had signs of use, e.g. soil stuck to the ends of the tools. Combined, the average tool length was 40.4 cm (SD 23 cm), which is similar to tools found at other research

Table 2 Length and material type of termite fishing probe tools reported across East, Central, and West Africa (modified from Sanz et al. 2004)

Study site and sub-species	Length (cm)	SD (cm)	Number of tools	Most frequently used tool type[a]	Proportion of tools of most frequently used type (%)	Reference
Pan troglodytes schweinfurthii						
Issa, Tanzania	40.4	23	36	Bark	100	This study
Gombe, Tanzania	30.7	–	145	Grass	48	McGrew et al. (1979)
Mahale K group, Tanzania	51.5	–	16	Bark	81	Uehara (1982)
Mahale B group, Tanzania	54.6	–	97	Bark	–	Uehara (1982)
Mahale B group, Tanzania	37.7	14.7	289	Bark	75	McGrew and Collins (1985)
Pan troglodytes troglodytes						
Goulougou, Republic of Congo	43.1	12.9	852	Herb	100	Sanz et al. (2004)
Guga, Republic of Congo	50.8	9.5	42	Herb	100	Suzuki et al. (1995)
Lossi, Republic of Congo	54.3	11.6	107	Herb	100	Bermejo and Illera (1999)
Bai Hokou, Central African Republic	50.5	17.5	62	Twig/stick	–	Fay and Carroll (1994)
Campo, Cameroon	30.5	–	4	Twig/stick	100	Sugiyama (1985)
Campo, Cameroon	44.4	5	16	Twig/stick		Muroyama (1991)
Belinga, Gabon	37.8	–	23	Twig/stick	96	McGrew and Rogers (1983)
Pan troglodytes verus						
Assirik, Senegal	32.5	–	173	Twig/stick	47	McGrew et al. (1979)
Fongoli, Senegal, 2002	30	–	58	Grass	59	McGrew et al. (2005)
Fongoli, Senegal, 2003	34	–	75	–	–	McGrew et al. (2005)

[a] Tool type definitions from McGrew et al. (1979), with the exception of 'Herb', which refers to tools made from terrestrial herbaceous stems. Sanz et al. (2004): twig/stick from woody parts of shrubs or trees; vine from segments of lianas or climbing herbs; bark stripped from woody parts of lianas, shrubs or trees; leaf/stalk from the compound leaves of shrubs or trees; 'grass' from blades of the plant family Gramineae

sites (Table 2). Mean tool length varied significantly between the mounds, however (Table 1). All the tools were made from bark that had been stripped from a similar species of plant (Fig. 2), but the source of the tools was not recorded.

Diet

Over the study, 635 chimpanzee faecal samples were collected and analysed for diet. Only the presence of termites in the faecal samples is reported here (Fig. 3). The number of faecal samples collected varied across months, with particularly few samples found during the wet season (October 2008, December 2008, January 2009, February 2009, December 2009, January 2010, March 2010). Termite consumption was most prevalent in the early (October, November) and late (February–April) wet season across all years. However, some termites were consumed during the dry season in June (Fig. 3). The proportion of faecal samples containing termites varied from year to year; For example in 2008–2009, termite consumption was higher in the months of October and November, but in 2009–2010, was highest in February (Fig. 3). Rainfall was highest in December 2008 to January 2009, and no correlation was found between the proportion of faecal samples containing termites and the amount of rainfall per month (Spearman's rank correlation; $r = 0.36$, $n = 12$, $p > 0.05$).

Discussion

The current report extends the database of chimpanzee communities known to fish for termites with slender probes (see Table 2). Issa represents the third dry habitat chimpanzee community to termite fish. Whilst both previous reports described termite fishing behaviour from southeastern Senegal (Mt. Assirik: McGrew et al. 1979; Fongoli: Bogart and Pruetz 2011), they differ in the purported role of seasonality in this behaviour. McGrew et al. (1979) reported seasonal fishing at Mt. Assirik, whilst Bogart and Pruetz (2008) show it to continue at higher levels year-round at Fongoli, only 50 km distant. Our results over a full annual cycle revealed termites to be eaten in 6 months out of the year, in the early and late wet season particularly, but occasionally during the dry season. The pattern of termite consumption described in Fig. 3 does not appear to be related

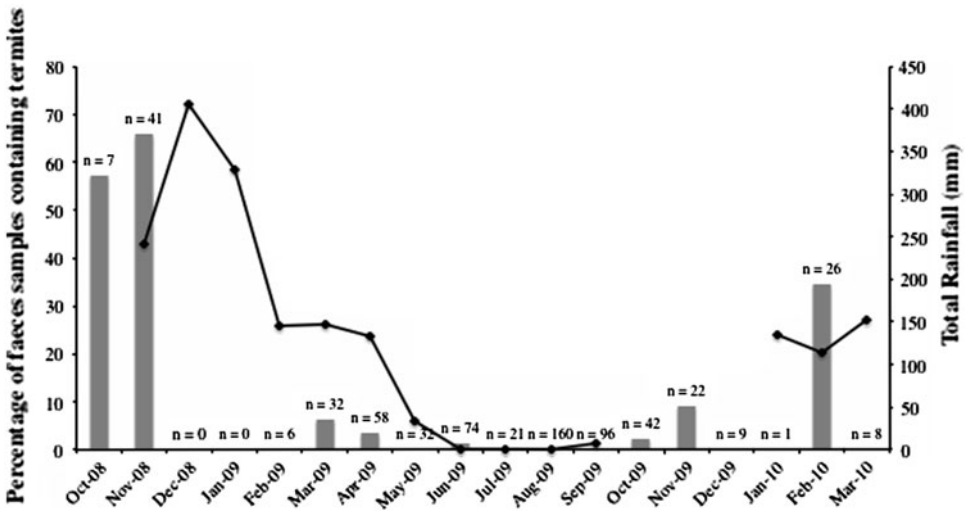

Fig. 3 Percentage of faecal samples collected each month containing termite remains (*bars* indicate percentage of faecal samples) and monthly rainfall (*line* indicates mm rainfall). Number of samples collected is noted above each month

to rainfall or season, but the number of samples found and limited rainfall data available may have influenced this pattern. The peak in Issa chimpanzees' consumption of termites during the late wet season is unusual in comparison with other populations in Tanzania (McGrew et al. 1979; McGrew and Collins 1985), suggesting that they may have a longer fishing season, or may not fish seasonally at all. This may be due to variation in termite ecology in this drier habitat, or the chimpanzees may continue to consume termites throughout the wet season, when the availability of other known food sources is lower than in the dry season (Hernandez-Aguilar 2006). Further data on the apes' diet are necessary across multiple years, to test whether the pattern of termite consumption in Ugalla more closely resembles that of other Tanzanian chimpanzees (McGrew et al. 1979; McGrew and Collins 1985), or other dry habitat chimpanzees (Bogart and Pruetz 2008, 2011).

All tools recovered from the three mounds were flexible probes made of bark, freshly stripped from woody plants. Despite such similarity in the material used for tool making, the tools found at one mound were significantly longer than those found at the other two mounds, and much longer than mean tool length reported from any other site (Table 2). However, this difference may be an artefact of the small sample size of tools found at this one mound, but could also be due to the size or structure of the mound. Alternatively, the difference in tool length might indicate another tool type, however, this seems unlikely given consistency across the mounds in the flexibility, and type, of material used. Future research is needed to determine whether such long tools are frequently used in Issa, and under which circumstances.

Such specificity in tool material is observed across sites where chimpanzee termite-fishing tools have been described, especially in the central sub-species (*P. t. troglodytes*; Table 2). Use of stripped bark is seen in both West and East Africa, but not in central chimpanzee populations, and only in East Africa is bark the most frequently used raw material (McGrew et al. 2005; Table 2). The mean length of Issa tools falls between those of previously reported bark probes used by chimpanzees in Mahale B group, K group (Uehara 1982; Collins and McGrew 1985) and Gombe (McGrew et al. 1979), and whilst at Gombe the most frequently used raw material is grass, all tools at Issa were made of bark, which is the most frequently used raw material at Mahale (Table 2). Similarity in tool type and morphology might be expected across these three sites, given their similarity in habitat and also the potential for cultural transmission as suggested by gene flow between Issa and Mahale (Inoue et al. 2012), and possibly also with Gombe (Piel et al. 2013). That Gombe differs in the predominant raw material used suggests that termite-fishing technology might vary with geographic distance and population connectivity. However, even neighbouring communities of chimpanzees differ in their termite predation technology (Nishida and Uehara 1980; McGrew and Collins 1985; Sanz et al. 2004). Environmental influences cannot be excluded without careful study, but in areas with continuous habitat between neighbouring communities, it seems likely that differences in tool type, morphology and use may have arisen through cultural processes (McGrew and Collins 1985; Sanz et al. 2004).

We continue research on the Issa chimpanzees' tool use, collecting tools throughout and across annual cycles. We are now analysing video footage from motion-triggered cameras deployed at termite mounds (sensu Sanz et al. 2004). Further, longitudinal study is necessary to determine if the type of tools used varies across the termite-fishing season in Issa (e.g. Uehara 1982) and whether or not the Issa chimpanzees' termite-fishing tool repertoire more closely resembles that of Mahale or Gombe, within the western Tanzania region.

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