

Raw material procurement for termite fishing tools by wild chimpanzees in the Issa valley, western Tanzania

Katarina Almeida-Warren^{1,2}, Volker Sommer¹, Alex K. Piel^{3,4}, Alejandra Pascual-Garrido⁵

¹ Department of Anthropology, University College London, London WC1 E6BT, UK

² Institute of Cognitive and Evolutionary Anthropology, University of Oxford, Oxford OX2 6PN, UK

³ School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, UK

⁴ Ugalla Primate Project, PO Box 108, Uvinza, Tanzania

⁵ Leverhulme Trust Early Career Fellow, RLAHA, School of Archaeology, University of Oxford, Oxford OX1 3QY, UK

KEY WORDS: primate archaeology, plant tools, raw material selection, termites

CORRESPONDING AUTHOR: Katarina Almeida-Warren, Institute of Cognitive and Evolutionary Anthropology, 64, Banbury Rd., Oxford OX2 6PN, United Kingdom. Telephone number: +44 7491 871959. Email: katarina.almeida-warren@anthro.ox.ac.uk

GRANT SPONSORSHIP: UCL; The Leverhulme Trust; The Boise Trust Fund, University of Oxford; UCSD.

ABSTRACT

Objectives

Chimpanzee termite fishing has been studied for decades, yet the selective processes preceding the manufacture of fishing tools remain largely unexplored. We explored raw material selection and potential evidence of forward planning in the chimpanzees of Issa valley, western Tanzania.

Materials and Methods

Using traditional archaeological methods, we surveyed the location of plants from where chimpanzees sourced raw material to manufacture termite fishing tools, relative to targeted mounds. We measured raw material abundance to test for availability and selection. Statistics included Chi-Squared, two-tailed Wilcoxon, and Kruskal-Wallis tests.

Results

Issa chimpanzees manufactured extraction tools only from bark, despite availability of other suitable materials (e.g. twigs), and selected particular plant species as raw material sources, which they often also exploit for food. Most plants were sourced 1–16 m away from the mound, with a maximum of 33 m. The line of sight from the targeted mound was obscured for a quarter of these plants.

Discussion

The exclusive use of bark tools despite availability of other suitable materials indicates a possible cultural preference. The fact that Issa chimpanzees select specific plant species and travel some distance to source them suggests some degree of selectivity and, potentially, forward planning. Our results have implications for the reconstruction of early hominin behaviors, particularly with regard to the use of perishable tools which remain archaeologically invisible.

While there has been extensive research on hominin lithic technology, which has recently been dated to at least 3.3 mya (Harmand et al., 2015), few studies address plant-based implements, largely because direct evidence is lacking in the archaeological record (Carvalho et al., 2009). Still, there can be little doubt that technological industries of early hominins included plant tools (Schick and Toth, 2000; Panger et al., 2002; Hardy, 2016). This gap in our knowledge reaffirms the value of studying chimpanzees (*Pan troglodytes*) as referential models for the emergence and transmission of human technology (Carvalho et al., 2009; Toth and Schick, 2009; Sanz et al., 2014). *Pan* and *Homo* shared a last common ancestor around 7–8 mya (Langergraber et al., 2012), and extant chimpanzees are known for their versatile use not only of lithic, but also plant-based tools for foraging and other activities (Whiten et al., 1999; McGrew, 1992, 2004). Furthermore, one of the earliest known hominins, *Ardipithecus ramidus*, lived in environments comparable to those inhabited by some extant chimpanzee populations (cf. Moore, 1992, 1996; WoldeGabriel et al., 1994).

Thus, early hominins are expected to have consumed similar diets of fruits, nuts and invertebrates, and likely exploited them with similar technologies (Panger et al., 2002; Copeland, 2007; McGrew, 2014). The earliest tentative evidence for early humans harvesting social insects is a bone implement dating between 1.8–1.0 mya, thought to have been used to dig termite mounds (Backwell and D’Errico, 2001). However, wooden artifacts do not occur in the record until 0.8–0.4 mya (Goren-Inbar et al., 2002; Wilkins et al., 2012).

Studying plant-based tool use by non-human primates can therefore serve as a proxy to reconstruct such archaeologically invisible aspects of hominin behavior (McGrew et al., 1979; McGrew, 2004). However, explicit etho-archaeological research on perishable materials used as tools or for shelter is still rare (Stewart et al., 2011; Pascual-Garrido et al., 2012).

Plant-based implements by wild chimpanzees to “fish” for termites were first described half a century ago (Goodall, 1964). Termite fishing is now recognized as one of the

most widespread forms of chimpanzee technology (Whiten et al., 2001, 2009; Sanz and Morgan, 2011). Termites also feature in the contemporary human diet, suggesting that early hominins also ate them (Panger et al., 2002; Lesnik, 2014; O'Malley and Power, 2014). Techniques to extract termites vary regionally. For example, chimpanzees at Gombe (Tanzania) insert a plant probe into exit-holes on the surface of a termite mound to obtain the insects inside (Goodall, 1964). This simple technology is also recorded for chimpanzees in the Mahale Mountains (Tanzania), Mt. Assirik (Senegal), Okorobiko (Equatorial Guinea) and Belinga (Gabon), amongst others (McGrew et al., 1979; Nishida and Hiraiwa, 1982; McGrew and Rogers, 1983; McGrew and Collins, 1985). Simple plant probes are also used at the Issa valley (Stewart and Piel, 2014). In contrast, central African chimpanzees use different implements consecutively for the task (Bermejo and Illera, 1999; Deblauwe et al., 2006; Sanz and Morgan, 2009, 2011). Raw materials for tools differ as well. For example, at Gombe, virtually all tools are made from bark and grass. These plant parts are not used at Mt. Assirik. The absence of grass implements may reflect the rareness of suitable sources at the start of the wet season when termite fishing is most frequent, given that much grass is burned during the long dry season (McGrew et al., 1979). However, the lack of bark tools is difficult to explain as the raw materials are available. This suggests that differences between populations may extend beyond ecological factors.

To better understand the selective processes preceding the manufacture of fishing tools, including whether certain raw materials are preferred, we studied chimpanzees at one of the driest habitats – Issa valley, western Tanzania – where these apes habitually exploit termite mounds (Stewart and Piel, 2014). Using archaeological methods (Haslam et al., 2009), we investigated the following:

(a) Raw materials: From which types are termite fishing tools manufactured? How does this compare to general abundance?

(b) Taxonomy: Which species constitute sources of raw material and with which frequency? How does this compare to species density?

(c) Dimensions: What is the detachment height and thickness of sourced parts? How do these factors affect selection between and within the same species?

(d) Distance to targeted mound: From how far away are tools sourced? How are plant sources spatially distributed around the mound?

(e) Dietary connection: Are species used for tools also sources of food?

(f) Medicinal properties: Can tool source species be linked to health-giving qualities?

The complete *chaîne opératoire* (operational sequence) of tool use includes technical processes and social acts of the step-by-step production, use, and eventual disposal of artifacts (Carvalho et al., 2008). Typically employed for lithic tools, the concept can be applied to the steps of perishable technology, such as termite fishing, which include selection of plant raw material, its modification (e.g. removing leaves; cropping the tip) to produce a functional tool, the use of the implement to harvest termite prey, and discarding it afterwards.

Our research aims to reconstruct the commonly neglected initial stages of the *chaîne opératoire* (raw material selectivity and transport) that are nevertheless critical to understand subsequent steps of actual use.

MATERIALS AND METHODS

Study subjects and sites

Research was conducted on a population of *P. t. schweinfurthii* that lives in the Issa valley, Ugalla (S 5.50, E 30.56; 900–1800 m altitude), western Tanzania (Fig. 1; Hernandez-Aguilar, 2009; Stewart and Piel, 2014; Piel et al., 2015). Issa is one of the driest, most open and seasonal chimpanzee habitats, with broad valleys broken up by steep mountains and plateaus. The vegetation is mainly miombo woodland, dominated by *Brachystegia* and

Julbernardi, intersected by patches of swamp, grassland, as well as evergreen gallery and thicket riverine forest. A wet season (Nov–Apr) is followed by a distinct dry spell (May–Oct).

Following short-term studies since 2001, the Ugalla Primate Project established a permanent research base in 2008. Based on genetic analyses, the chimpanzee study community includes about 67 individuals, with a minimum home range of 85 km² (Rudicell et al., 2011). As of April 2016, the apes are now partially habituated, with 14 identifiable individuals. During the wettest months of the year (Nov–Feb), the Issa chimpanzees habitually harvest *Macrotermes* termites (Stewart and Piel, 2014). The chimpanzees also use perishable tools to obtain arboreal *Camponotus* ants (Wondra et al., 2016) and to dig for tubers (Hernandez-Aguilar et al., 2007).

Data collection

APG and KAW conducted three seasons of fieldwork for a total of 16 weeks, aided by Tanzanian field assistants (APG: 09Jan15–09Feb15; KAW: 17May15–27Jun15; KAW: 02Nov15–15Dec15). During the first season, 20 termite mounds were selected for study, 15 of which had been targeted by chimpanzees (Fig. 2a). Records included a unique identifier (ITMXXX), GPS location, nest dimensions (cross-section width and height) as well as habitat (open/closed forest, woodland, miombo woodland, savannah; cf. McBeath and McGrew, 1982; Pascual-Garrido et al., 2012). We established a Site Datum (cf. Carvalho et al., 2008) at a nearby tree to allow measurements within a standardized coordinate system, e.g., for the distance of a tool source to study mounds. Eight targeted mounds and their surroundings were selected for detailed study.

Based on previous research of chimpanzee termite fishing (e.g. McGrew et al., 1979; Nishida and Uehara, 1980; McBeath and McGrew, 1982), we considered the following potential categories of tool raw material: bark (the outermost layers of tissue overlaying the

wood of trees, shrubs and climbers or vines that can easily peel lengthways in strips); twigs (thin branches of woody plants); leaf stalks (mid ribs of large leaves of woody plants that can easily be removed from the blades); grass stems (the hollow vertical structural axes of grass plants that provide support for flowers at the top and leaves attached at the nodes).

The availability of raw material was ascertained for living plants growing within 5 m from a targeted mound's center (cf. McBeath and McGrew, 1982; Koops et al., 2013). Using cardinal orientations (N-S, E-W), the mound vicinity was divided into four quadrants numbered clockwise from north. The northwest quadrant, IV, was arbitrarily selected for scrutiny. If obstacles such as steep terrain prevented this, an adjacent quadrant was chosen. Recorded parameters included: number and species of plants suitable to provide raw material; growth type (tree, shrub, climber, grass); raw material type (twig, bark, leaf stalk, grass stem); and whether each plant was a known chimpanzee food source. Suitable raw materials were defined as long, thin and flexible pieces, capable of providing termite fishing probes, which a researcher could easily detach with hands or fingernails.

The surroundings of eight targeted mounds were surveyed for tool source plants (Fig. 2b–d), using signs of broken or removed parts as indicators, by walking back and forth from the mound in a clockwise fashion (cf. Pascual-Garrido et al. 2012). Traits of source plants were recorded as follows: position relative to targeted mound (Fig. 3); whether visible from mound or if vegetation or terrain contours obscured the line of sight; species; number of plants of same species within a 3-m radius; height; number of sourced and unsourced parts within the source plant; height at point of detachment; diameter of sourced parts at proximal, medial and distal points of detachment; medial diameter of unsourced parts. Used tools abandoned by chimpanzees were also recorded and classified according to raw material.

Herbarium samples of study species were collected and identified at the Botany Department, University of Dar es Salaam, Tanzania.

Tool source identification

The question of how to distinguish an assemblage of tools from a naturally occurring aggregation of plant fragments has been previously addressed by McGrew et al. (1979). Similar to stone tools, plant-based tools also acquire recognizable signs of use-wear. In the case of termite fishing implements, these included evidence of modification (e.g. peeled bark, stripped leaves) or wear from insertion into the mound (e.g. fraying at the tips) and termite bite marks. Plant parts with these characteristics are often associated with other signs of previous termite fishing activity, such as chimpanzee footprints, hairs, feces as well as discarded termite heads and freshly stripped leaves resulting from tool manufacture (cf. Nishida and Uehara, 1980; McBeath and McGrew, 1982; McGrew and Rogers, 1983; McGrew and Collins, 1985; Bermejo and Illera, 1999; Sanz et al., 2004, 2009; Deblauwe et al., 2006; Sanz and Morgan, 2011; Stewart and Piel, 2014).

Tool sources are more difficult to discern (McGrew et al., 1979; McBeath and McGrew, 1982; Pascual-Garrido et al., 2012) but can normally be distinguished from specimens that suffered breakage caused by other processes: (a) chimpanzees will often pluck multiple parts from a single source plant; (b) branch sections from where tool material has been removed are often also stripped of leaves and minor offshoots; (c) only a select number of species will show signs of breakage; (d) plants with breakage are concentrated around the mound periphery.

Statistics

Given non-normal distribution of our data ($p < 0.05$), we employed non-parametric statistics. Chi-squared tests compared proportions between groups (raw material classes; species), while two-tailed Wilcoxon (aka Mann-Whitney U test) were employed to compare means. When comparing two independent proportions between multiple groups, we

calculated individual p-values of paired groups via a Post-hoc Chi-squared analysis with Bonferroni correction. Kruskal-Wallis tests were used as a non-parametric equivalent to ANOVA to compare multiple groups (e.g. mounds, species). Pairwise Wilcoxon tests with Bonferroni correction were employed to ascertain the individual p-values of paired groups analyzed in the Kruskal-Wallis test. Linear regression analyses were used to arrive at linear correlation between numerical datasets. All analyses were performed in R (R Development Core Team, 2014). Level of significance was set at $p < 0.05$.

RESULTS

We identified 113 individual source plants, some of them having been exploited from multiple parts. This resulted in a combined total of 349 sourced parts belonging to 13 species from six families from which Issa chimpanzees manufactured termite fishing tools. We also recovered 140 fishing implements (Table 1).

[TABLE 1 about here]

Selection of raw materials

Approximately two thirds of plants within the surveyed 5 m radius quadrant in the vicinity of termite mounds could have provided one or multiple suitable raw materials (bark, twig, leaf stalk, grass stem) that are known constituents of termite fishing tools (cf. Table 1).

Overall, there were significant differences between the proportions of available raw material classes by individual plant unit (Chi-squared: $\chi^2 = 344.751$; $df = 3$; $p < 0.001$). The most abundant material sources were plants that afforded good twigs (94%), followed by bark (18%; i.e. bark that can easily be peeled off in long and flexible strips for termite fishing probes), whereas plants that could provide appropriate leaf stalks (12%) and grass stems (2%) were even rarer. However, only bark was actually sourced for tools (Table 2), both in terms of

parts sourced (Chi-squared with null-probability = 1/4: $\chi^2 = 1043.004$; $df = 1$; $p < 0.001$), as well as recovered tools (Chi-squared with null-probability = 1/4: $\chi^2 = 416.010$; $df = 1$; $p < 0.001$; cf. also Stewart and Piel 2014). Nevertheless, post-hoc experiments with twigs and grass demonstrated that these materials were also suitable as efficient termite fishing tools (Fig. 4).

[TABLE 2 about here]

Selection of plant species

While 66% of plants in the vicinity of targeted termite mounds were deemed suitable as tool sources, only 12% of these constituted species from which chimpanzees actually sourced material (Chi-squared with null-probability = 0.99: $\chi^2 = 2450.6$; $df = 1$; $p < 0.001$). The difference was equally significant when analyzing the proportions for each individual mound (Chi-squared for all individual tests with null-probability = 0.99; $p < 0.001$). Post-hoc Chi-squared tests aimed to determine which pairs of mounds were different in terms of species availability returned no significant results. This indicates that chimpanzees selected certain species from which to source tool materials.

Taxonomy of plant sources

Plant tool sources belonged to 13 species from six families (Table 3). More than four fifths (82%) of identified raw materials came from *A. collinus*, *Uvaria sp.*, *A. of FTEA*, and *C. polystachyus*. Compared to abundance, these plants were over-selected at a significant level (Chi squared for all individual tests: $p < 0.002$; Fig. 5).

[TABLE 3 about here]

However, mounds varied significantly with regard to the species sourced (Chi-squared: $\chi^2 = 260.350$; $df = 70$; $p < 0.001$). For example, *C. polystachyus* was only sourced at ITM004 and ITM006, *Grewia sp.* only at ITM006 and ITM016 and *D. burgessiae* only at ITM007 (cf. Table 3). Similarly, certain species were only over-selected at certain mounds. Thus, *A. collinus* was significantly over-selected at all mounds (Chi-squared for all individual tests: $p < 0.02$) except ITM004 (Chi-squared: $\chi^2 = 0.1599$; $df = 1$; $p = 0.689$) and ITM007, where no plants of this species were found within the surveyed area. *U. sp. A of FTEA* was only over-selected at ITM013 (Chi-squared: $\chi^2 = 6.182$; $df = 1$; $p = 0.013$) and ITM006 (Chi-squared: $\chi^2 = 4.069$; $df = 1$; $p = 0.043$). *C. polystachyus* was over-selected at both mounds where plants of this species were sourced, i.e., ITM004 (Chi-squared: $\chi^2 = 14.265$; $df = 1$; $p < 0.001$) and ITM006 (Chi-squared: $\chi^2 = 9.865$; $df = 1$; $p = 0.002$). The same applies to *D. burgessiae*, which was only recorded at ITM007 (Chi-squared: $\chi^2 = 8.874$; $df = 1$; $p = 0.003$).

Dimensions at point of detachment

Plant parts from which raw materials were sourced had a *diameter at point of detachment* of up to 27 mm, with 85% of values between 3–11 mm (Fig. 6). A comparison with non-sourced plant parts indicated a significant difference between the two groups (2-tailed Wilcoxon: $w = 50310.5$; $p < 0.001$). However, in absolute terms, the difference was only 1.0 mm (Table 4).

Plant parts were sourced from a mean height of 1.2 m (Table 4), with half from below 1 m (49%), a quarter from above 1.5 m (25%) and a maximum height of 3.8 m. Cross-species comparison revealed a significant difference between species means (Kruskal-Wallis: $\chi^2 = 62.833$; $df = 9$; $p < 0.001$). Thus, *U. welwetschii* and *C. polystachyus* were sourced from significantly higher than *U. sp. A of FTEA*, *A. collinus* and *A. monteiroae*. These findings could be an artefact of different plant heights (Table 4). To test this, we plotted height at point

of detachment against total height of plant (Fig. 7), which indicated a significant positive trend, albeit with poor goodness of fit ($p < 0.001$; $R^2 = 0.044$).

[TABLE 4 about here]

Distance of plant tool sources to targeted mound

To reveal potential spatial patterns of raw material procurement, we plotted the total number of sourced parts alongside the total number of sourced plants for every 1 m block (Fig. 8). 83% of plants were sourced 1–16 m away from the mound, with a maximum distance of 33.4 m. Only one pair of mounds differed significantly with respect to these distances, with plants sourced from approximately 7 m further away at ITM006 than at ITM004 (Kruskal-Wallis: $\chi^2 = 19.680$; $df = 7$; $p = 0.006$; Fig. 9).

We also investigated if sourcing distances differed between plant species, taking into account the number of times each species was individually sourced, and restricting the sample to species sourced more than once (Fig. 10). Thus, *A. garckeana* was sourced from nearest the mounds (mean 3.2 m), while *A. senegalensis* was sourced from the greatest distance (mean 13.4 m). An overall cross-species comparison yielded statistically significant results (Kruskal-Wallis: $\chi^2 = 42.207$; $df = 14$; $p < 0.001$).

Visibility of plant tool sources to targeted mound

If a source plant was not visible from the targeted mound (i.e., the line of sight was obstructed by dense vegetation or terrain contours), it seems likely that raw material was collected *en route*, rather than upon arrival at the mound. This applies to 21% of source plants (Table 5). These constituted about half (55%) of the 42 plants that were sourced from a distance of more than 10 m. Plants visible from the mound were more than twice as often sourced (3.5 times) than non-visible plants (1.6 times); and those that were within 10 m of the

mound were also sourced much more often (3.7 times) than encountered further away (2.0 times).

[TABLE 5 about here]

Food species as sources for tool material

Twelve out of 13 species sourced were also known chimpanzee food sources (Table 6). This is significantly different from a 0/1 ratio (Chi-squared with $np = 0.01$: $\chi^2 = 1004.5$; $df = 1$; $p < 0.001$).

[TABLE 6 about here]

Medicinal properties of plant sources

Of 13 identified tool source species, 10 (75%) are known to provide ingredients for traditional medicine in Tanzania and elsewhere, in the treatment of human ailments (Table 7).

[TABLE 7 about here]

DISCUSSION

Our research focuses on an under-researched component of the operational sequence of chimpanzee termite fishing: raw material selectivity and transport. Although not relying on direct behavioral observation, our results nevertheless reveal that rich information can be gleaned solely from indirect archaeological approaches.

Raw material classes

Consistent with initial findings (Stewart and Piel, 2014), bark was the only raw material sourced by Issa chimpanzees to manufacture their termite fishing tools (cf. Table 2).

Our results reveal that exclusive use of bark is not simply a corollary of availability. On the contrary, twig-providing plants are far more abundant, yet this material does not appear in tool assemblages. One might query the relatively rough quantification of available twig versus bark as derived from counts of potential source plants, without quantifying the actual amounts of raw material on plants of different sizes and growth types. However, the simple fact remains that Issa chimpanzees *only* source bark, and thus, clearly neglect twigs.

Bark is used by chimpanzees in East and West Africa, but not Central Africa, to harvest termites (Stewart and Piel, 2014). Bark is also a popular termite-extraction tool elsewhere in western Tanzania, albeit not the only material used (Uehara, 1982; McGrew and Collins, 1985). Gombe chimpanzees employ mostly grass for termite fishing (McGrew et al., 1979), although this might have changed during the last decades (but certainly since at least 2014, Pascual-Garrido, in prep.). While the absence of grass tools at Issa may be related to low abundance, the dearth of commonly available twigs is harder to understand. Ecological reasons are therefore not sufficient to explain the exclusive bark use. Given historical gene flow between the termite-fishing communities of Gombe, Issa and Mahale (Piel et al., 2013; Stewart and Piel, 2014), genetics are also an unlikely cause. Furthermore, other Issa tools, such as sticks to dig for tubers and tools to obtain arboreal *Camponotus* ants, are not exclusively made from bark (Hernandez-Aguilar et al., 2007; Wondra et al., 2016). This demonstrates that Issa chimpanzees are versatile in the type of raw material they use. It thus seems possible that the exclusive use of bark to fish for termites indicates a cultural preference at Issa, i.e., an arbitrary behavior not brought about by genetic or ecological factors (Boesch, 2003; Janson and Smith, 2003; McGrew, 2004).

Source species

Source plants for termite fishing tools have been identified at various sites (see Deblauwe et al., 2006, for review), but studies based on abundance are so far restricted to McBeath and McGrew (1982). Our research broadens this small database.

Accordingly, chimpanzees of the Issa valley sourced 13 plant species from six families for tool raw material (cf. Table 3). Three of these species also provide for termite fishing tools elsewhere, i.e., *A. monteiroae*, *U. angolensis* and *Grewia sp.* at Mahale (Uehara, 1982), as well as *Grewia sp.* at Mt. Assirik (McBeath and McGrew, 1982) and Fongoli (McGrew et al., 2005).

Issa chimpanzees did not use many plants with supposedly suitable raw material growing in the vicinity of targeted mounds, while species such as *A. collinus*, *C. polystachyus* and *Uvaria sp.* *A. of FTEA* were over-selected, as was *D. burgessiae* at individual mounds. The exploitation of other taxa (*A. garckeana*, *A. monteiroae*, *U. angolensis*, *Grewia sp.*) did not differ from what was expected by their general abundance. However, even these were probably not sourced opportunistically because one or more individual specimens were sourced multiple times (cf. Table 1). Except for *A. garckeana*, these species are also used at Gombe and Mahale (McBeath and McGrew, 1982; Uehara, 1982). Taken together, these findings imply some degree of selectivity.

Food species as tool sources

Chimpanzees are reluctant to interact with novel or unfamiliar items (Biro et al., 2003). The fact that 92% of tool source species at Issa were also exploited for food (cf. Table 6) suggests that – apart from physical characteristics such as being flexible (cf. Teleki, 1974; McGrew, 1992) – familiarity might also play a role in their selection. Frequent contact with species that provide nourishment (fruit, leaves, etc.) may conceivably trigger preferential sourcing of materials from these same species, not least because food acquisition is coupled

with haptic experiences. Alternatively, one might hypothesize that chimpanzees should avoid damaging food plants and therefore *not* source tools from them. However, most material is obtained from low heights where plants will generally not bear fruit (cf. Table 4). Furthermore, removing bark from a fruiting branch will have little or no detrimental effect for fruit production.

Medicinal properties of source plants

Many species sourced for tool material by chimpanzees possess medicinal properties, and are used by human populations in ethnomedicinal treatments (cf. Table 7). Conceivably, chimpanzees may prefer certain tool sources because the interaction with them may have health-giving side-effects (Pascual-Garrido et al., 2012; Huffman, 2015). For example, when Nigerian chimpanzees gather honey, they do this most frequently with tools from species that possess strong antibacterial properties (e.g. *Sorindeia warneckei*, *Chassalia kolly*). Furthermore, dental benefits that locals derive from chewing sticks of *S. warneckei* may also apply to Nigerian chimpanzees when they suck and bite on such sticks to ingest honey (Pascual-Garrido et al., 2012). While we cannot infer whether chimpanzees are actively selecting tool materials based on their medicinal properties, such benefits may nevertheless influence a preferred sourcing of certain species over others.

Physical properties of source plants

Not all parts of an individual tree nor all individuals of a certain species may be good sources of tool raw material. For example, some individual plants, or parts of them, may be too short, too thin or too thick for extracting long and flexible pieces of bark. One possible way of assessing whether chimpanzees are selecting for particular properties is to look at the

diameter and height of the sourced plant part at the point where raw material is detached (cf. Pascual-Garrido et al., 2012).

In our study, despite the fact that sourced and unsourced plant part diameters were significantly different, the absolute difference was just 1.0 mm (cf. Table 4). Similarly, at the level of absolute values, differences between sourced and unsourced parts at the species level and differences between species were minimal. It is therefore likely that all sourced species generally encompass the necessary dimensions for providing suitable termite fishing tools. A future task would therefore be to measure the properties of non-sourced species.

A quarter of plant parts were sourced from above 1.5 m, indicating that chimpanzees are climbing with some frequency to reach desired tool sources. The highest detachment point was at 3.8 m. However, we cannot exclude that some sources were too high to be detected by researchers from ground level. Only by using climbing equipment (cf. Stewart et al., 2011) would we be able to minimize this potential bias in our data collection.

Some plant species were sourced from higher points than others (cf. Table 4) and source height was positively correlated with absolute plant height (cf. Fig. 7). Thus, the number of potential source parts available at a certain height may play a role. This is likely the case for *C. polystachyus*, a tree that only branches higher up. Similarly, while *U. welwetschii* is best classified as a climber (Moscovice et al. 2007), its bark may only provide suitable fishing material above a certain height. This idea would need further exploration, as all *U. welwetschii* material came from a single specimen. Apart from active selection for particular properties, a simple depletion effect could be at work whereby Issa chimpanzees start to exploit the plants at ground level and move higher up into the trees when lower plant parts become unavailable.

Sourcing distances

The greatest distances between tool sources and the exploited termite mounds on which they were used reported from other sites are between 75–800 m (McGrew et al., 1979; Goodall, 1986; Sanz et al., 2004). However, these are exceptional distances recorded *ad libitum*. According to the only comparative study so far (McGrew et al., 1979), around 90% of tool sources at Mt. Assirik (Senegal) and Gombe (Tanzania) were within two meters from the mound, while at Okorobiko (Equatorial Guinea), most grew more than two meters away. Preferences for raw materials may influence this difference, because chimpanzees at Gombe and Assirik employ a wide variety of materials, while only twigs are used at Okorobiko.

Similar to Okorobiko, chimpanzees at Issa might need to acquire suitable material from relatively greater distances, given that only few species harboring adequate raw material for the exclusively used bark tools grew near mounds. Overall, Issa chimpanzees sourced plants growing up to 33 m from the mound, with half more than 10 m away and out of sight from the tool use area (cf. Table 5, Fig. 9). That chimpanzees at Issa acquire tool material from further away compared to other populations is conceivably linked to the drier and more open habitat of the Issa valley, with its correspondingly low plant density and scarcity of preferred raw material, while apes in forests with greater vegetation density and raw material abundance near mounds can source it from nearer to the mound (Pascual-Garrido et al., 2016).

Our study is the first to assess species-specific distances between sourced plants and termite mounds. Accordingly, at Issa, some plants were sourced from more than twice the distance than others (cf. Fig. 10). A greater sourcing distance might indicate a stronger preference for a certain species. However, we surveyed abundance only up to 5 m from the targeted mound, and can therefore not exclude that preferred species are more abundant outside this radius.

That said, chimpanzees are not exclusively sourcing plants in the immediate vicinity of the mound, and neither only from further away. A greater sourcing distance suggests that chimpanzees source plants *en route* before they actually see the subsequently targeted mound. Alternatively, an individual may opportunistically source raw material nearest to the mound, and once this is depleted, travel back and forth for a greater distance to obtain more. Direct behavioral observations are currently absent to confirm these assumptions. In any case, at the cognitive level, raw material sourced *en route* might indicate a degree of forward planning instead of pure opportunism.

Debates as to whether chimpanzees and other non-human primates are capable of foresight have persisted for decades (de Waal and Ferrari 2010). Recently, however, studies of populations both in captivity (Osvath and Osvath 2008) and in the wild (Byrne et al. 2013; Janmaat et al. 2014) have demonstrated that chimpanzees plan for the future. It would seem more likely, therefore, that they also plan ahead of their termite fishing sessions.

Conclusion

Studies of stone tool assemblages have provided insight into the ranging patterns of early hominins – whether they selected for specific raw materials, from how far away they sourced them, and what this may suggest about their cognitive abilities (Schick and Toth, 2006; Goldman-Neuman and Hovers, 2009; Harmand, 2009). However, the vast majority of such evidence is restricted to lithic artifacts. Research into chimpanzees is therefore a particularly valuable model for the reconstruction of early hominin behavior (Panger et al., 2002; Mikkelsen et al., 2005; Carvalho et al., 2009; Haslam et al., 2009; Haslam, 2012), as extant chimpanzees also use perishable tools that are typically lost in the archaeological record through processes of natural decomposition (McGrew et al., 1979; Panger et al., 2002; McGrew, 2004). Our study provides yet another piece in this puzzle.

ACKNOWLEDGMENTS

We are grateful to the Tanzanian Wildlife Research Institute (TAWIRI) and the Commission for Science and Technology (COSTECH) for permission to conduct research at Issa Valley. We greatly appreciate assistance in the field by Shedrack Lucas, Patrick Hassan, Godfrey Stephano, Mashaka Kalutwa, Busoti Juma, Mlema Juma, Msigwa Rashid, Sebastian Ramirez-Amaya and Eden Wondra. We are also thankful to Frank Mbago, Botany Department, University of Dar es Salaam, who kindly identified plants. KAW benefitted from a Daryll Forde studentship, Department of Anthropology of UCL. APG is supported by a Leverhulme Trust Early Career Fellowship and received further funding for fieldwork from The Boise Trust Fund, University of Oxford. Long-term support for research at Issa comes from the UCSD/SALK Institute Center for Academic Research and Training in Anthropogeny (CARTA).

LITERATURE CITED

- Arbonnier M. 2004. Trees, Shrubs and Lianas of West African Dry Zones. Paris: CIRAD.
- Backwell LR, D'Errico F. 2001. Evidence of termite foraging by Swartkrans early hominids. *Proc Natl Acad Sci* 98:1358–1363.
- Bermejo M, Illera G. 1999. Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. *Primates* 40:619–627.
- Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 6:213–223.
- Boesch C. 2003. Is culture a golden barrier between human and chimpanzee? *Evol Anthropol* 12:82–91.

- Bosch CH 2011. *Dombeya burgessiae* Gerrard ex Harv. Record from PROTA4U. In M. Brink & E. G. Achigan-Dako, (Eds.), PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale). Wageningen, Netherlands.
- Byrne RW, Sanz CM, Morgan DB. 2013. Chimpanzees plan their tool use. In: Sanz CM, Call J and Boesch C, editors. Tool Use in Animals: Cognition and Ecology. Cambridge: Cambridge University Press.
- Carvalho S, Biro D, McGrew WC, Matsuzawa T. 2009. Tool-composite reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? *Anim Cogn* 12:S103–S114.
- Carvalho S, Cunha E, Sousa C, Matsuzawa T. 2008. Chaînes opératoires and resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *J Hum Evol* 55:148–63.
- Copeland SR. 2007. Vegetation and plant food reconstruction of lowermost Bed II, Olduvai Gorge, using modern analogs. *J Hum Evol* 53:146–175.
- Deblauwe I, Guislain P, Dupain J, van Elsacker L. 2006. Use of a tool-set by *Pan troglodytes troglodytes* to obtain termites (*Macrotermes*) in the periphery of the Dja Biosphere Reserve, southeast Cameroon. *Am J Primatol* 68:1191–1196.
- Goldman-Neuman T, Hovers E. 2009. Methodological considerations in the study of Oldowan raw material selectivity: insights from A. L. 894 (Hadar, Ethiopia). In: Hovers E, Braun DR, editors. *Interdisciplinary Approaches to the Oldowan*. Dordrecht: Springer.
- Goodall J. 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* 201:1264–1266.
- Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behaviour*. Cambridge: Harvard University Press.
- Goren-Inbar N, Werker E, Feibel CS. 2002. *The Acheulian Site of Gesher Benot Ya'aqov, Israel, Vol. I. The wood assemblage*. Oxford: Oxbow Books.

Harmand S, Lewis JE, Feibel CS, Lepre CJ, Prat S, Lenoble A, Boës X, Quinn RL, Brenet M, Arroyo A, Taylor N, Clément S, Daver G, Brugal J-P, Leakey L, Mortlock, RA, Wright JD, Lokorodi S, Kirwa C, Kent DV, Roche H. 2015. 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521:310–315.

Hardy K. 2016. Plants as raw materials. In: Hardy K, Kubiak-Martens L, editors. *Wild Harvest. Plants in the Hominin and Pre-Agrarian Human Worlds*. Oxford: Oxbow Books. p 71–90.

Harmand S. 2009. Variability in Raw Material Selectivity at the Late Pliocene sites of Lokalalei, West Turkana, Kenya. In: Hovers E, Braun DR, editors. *Interdisciplinary Approaches to the Oldowan*. Dordrecht: Springer.

Haslam M. 2012. Towards a prehistory of primates. *Antiquity* 86:299–315.

Haslam M, Hernandez-Aguilar A, Ling V, Carvalho S, de la Torre I, DeStefano A, Du A, Hardy B, Harris J, Marchant L, Matsuzawa T, McGrew W, Mercader J, Mora R, Petraglia M, Roche H, Visalberghi E, Warren R. 2009. Primate archaeology. *Nature* 460:339–344.

Hernandez-Aguilar RA. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *J Hum Evol* 57:350–364.

Hernandez-Aguilar RA, Moore J, Pickering TR. 2007. Savanna chimpanzees use tools to harvest the underground storage organs of plants. *Proc Natl Acad Sci* 104:19210–19213.

Huffman MA. 2015. Chimpanzee self-medication: a historical perspective of the key findings. In: Nakamura M, Hosaka K, Itoh N, Zamma K, editors. *Mahale Chimpanzees: 50 Years of Research*. Cambridge: Cambridge University Press.

Hufford CD, Oguntimein BO. 1982. New dihydrochalcones and flavanones from *Uvaria angolensis*. *J Nat Prod* 45:337–342.

Janmaat KR, Polansky L, Ban SD, Boesch C. 2014. Wild chimpanzees plan their breakfast time, type, and location. *Proc Natl Acad Sci*. 111:16343-8.

Janson CH, Smith EA. 2003. The evolution of culture: new perspectives and evidence. *Evol Anthropol* 12:57–60.

Koops K, McGrew WC, Matsuzawa T. 2013. Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Anim Behav* 85:175–185.

Langergraber, KE, Prüfer, K, Rowney, C, Boesch, C, Crockford, C, Fawcett, K, Inoue, E, Inoue-Muruyama, M, Mitani, JC, Muller, MN. 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proc Natl Acad Sci* 109:15716–15721.

Lesnik JJ. 2014. Termites in the hominin diet: a meta-analysis of termite genera, species and castes as a dietary supplement for South African robust australopithecines. *J Hum Evol* 71:94–104.

McBeath NM, McGrew WC. 1982. Tools used by wild chimpanzees to obtain termites at Mt Assirik, Senegal: the influence of habitat. *J Hum Evol* 11, 65–72.

McGrew WC. 1992. Chimpanzee Material Culture: Implications for Human Evolution. Cambridge: Cambridge University Press.

McGrew WC. 2004. The Cultured Chimpanzee: Reflections on Cultural Primatology. Cambridge: Cambridge University Press.

McGrew WC. 2014. The “other faunivory” revisited: insectivory in human and non-human primates and the evolution of human diet. *J Hum Evol* 71:4–11.

McGrew WC, Collins DA. 1985. Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *Am J Primatol* 9:47–62.

McGrew WC, Rogers ME. 1983. Chimpanzees, tools, and termites - new record from Gabon. *Am J Primatol* 5:171–174.

McGrew WC, Tutin CEG, Baldwin PJ. 1979. Chimpanzees, tools, and termites: cross-cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man, New Series* 14:185–214.

McGrew, WC, Pruetz, JD, Fulton, SJ. 2005. Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatol* 76:222–226

Mikkelsen TS, Hillier LW, Eichler EE, Zody MC, Jaffe DB, Yang S, Enard W, Hellmann I, Lindblad-Toh K, Altheide TK, Archidiacono N, Bork P, Butler J, Chang JL, Cheng Z, Chinwalla AT, DeJong P, Delehaunty KD, Fronick CC, Fulton LL, Gilad Y, Glusman G, Gnerre S, Graves, TA, Hayakawa T, Hayden KE, Huang X, Ji H, Kent WJ, King M, Kulbokas III EJ, Lee MK, Liu G, Lopez-Otin C, Makova KD, Man O, Mardis ER, Mauceli E, Miner TL, Nash WE, Nelson JO, Pääbo, S, Patterson NJ, Pohl CS, Pollard KS, Prüfer K, Puente XS, Reich D, Rocchi, M, Rosenbloom K, Ruvolo M, Richter DJ, Schaffner SP, Smit AFA, Smith SM, Suyama M, Taylor J, Torrents D, Tuzun E, Varki A, Velasco G, Ventura M, Wallis JW, Wendl MC, Wilson RK, Lander ES, Waterston RH. 2005. Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature* 437:69–87.

Moore J. 1992. “Savanna” chimpanzees. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. DeWaal, editors. *Topics in Primatology, Vol. I: Human Origins*. Tokyo: University of Tokyo Press.

Moore J. 1996. Savanna chimpanzees, referential models and the last common ancestor. In W. C. McGrew, L. F. Marchant, & T. Nishida, editors. *Great Ape Societies*. Cambridge: Cambridge University Press.

Moriyasu M, Nakatani N, Ichimaru M, Nishiyama Y, Kato A, Mathenge SG, Juma FD, Chalo Mutiso PB. 2011. Chemical studies on the roots of *Uvaria welwitschii*. *J Nat Med* 65:313–321.

- Moscovice LR, Addressi E, Petrsekova KJ, Keuler NS, Snowdown CT, Huffman MA. 2007. Fruit availability, chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. *Am J Primatol* 69:487–502.
- Mustapha AA. 2013. *Annona senegalensis Persoon*: a multipurpose shrub, its phytotherapeutic, phytopharmacological and phytomedicinal uses. *Int J Sci Technol* 2:862–865.
- Neuwinger HD. 1996. African Ethnobotany: Poisons and Drugs: Chemistry, Pharmacology, Toxicology. London: Chapman & Hall.
- Nishida T, Hiraiwa M. 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *J Hum Evol* 11:73–99.
- Nishida T, Uehara S. 1980. Chimpanzees, tools, and termites: another example from Tanzania. *Curr Anthropol* 21:671–672.
- Nishida T, Uehara S. 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. *Afr Study Monogr* 3:109–130.
- O'Malley RC, Power ML. 2014. The energetic and nutritional yields from insectivory for Kasekela chimpanzees. *J Hum Evol* 71:46–58.
- Osvath M, Osvath H. 2008. Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Anim Cogn* 11:661–674
- Panger MA, Brooks AS, Richmond BG, Wood B. 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol Anthropol* 11:235–245.
- Pascual-Garrido A, Buba U, Nodza G, Sommer V. 2012. Obtaining raw material: plants as tool sources for Nigerian chimpanzees. *Folia Primatol* 83:24–44.
- Pascual-Garrido A, Sommer V, Almeida-Warren K. 2016. Raw material procurement for termite fishing tools in wild chimpanzees. *PeerJ Preprints* 4, e1844v1.

- Piel AK, Cohen N, Kamenya S, Ndimuligo SA, Pintea L, Stewart FA. 2015. Population status of chimpanzees in the Masito-Ugalla Ecosystem, Tanzania. *Am J Primatol* 10.
- Piel AK, Stewart FA, Pintea L, Li Y, Ramirez MA, Loy DE, Crystal PA, Learn GH, Knapp LA, Sharp PM, Hahn BH. 2013. The Malagarasi River does not form an absolute barrier to chimpanzee movement in western Tanzania. *PLoS ONE* 8, e58965.
- R Development Core Team, 2014. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Reynolds V. 2005. The Chimpanzees of the Budongo Forest: Ecology, Behaviour, and Conservation. Oxford: Oxford University Press.
- Royal Botanic Gardens, Kew. 1999. Survey of Economic Plants for Arid and Semi-Arid Lands (SEPASAL) database. Available at: <http://apps.kew.org/sepasalweb/sepaweb>. Last accessed, 15-04-2016
- Rudicell RS, Piel, AK, Stewart F, Moore DL, Learn GH, Li Y, Takehisa J, Pintea L, Shaw GM, Moore J, Sharp PM, Hahn BH. 2011. High prevalence of simian immunodeficiency virus infection in a community of savanna chimpanzees. *J Virol* 85:9918–9928.
- Ruffo CK, Birnie A, Tenganäs B. 2002. Edible Wild Plants of Tanzania, Technical Handbook No. 27. Dar es Salaam: REMLA.
- Russak S. 2013. Ecological role of dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*). Ph.D. Dissertation, Arizona State University.
- Sanz C, Call J, Morgan D. 2009. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol Letters* 5:293–296.
- Sanz C, Morgan D, Gulick, S. 2004. New insights into chimpanzees, tools, and termites from the Congo Basin. *Am Nat* 164:567–581.

Sanz CM, Deblauwe I, Tagg N, Morgan DB. 2014. Insect prey characteristics affecting regional variation in chimpanzee tool use. *J Hum Evol* 71:28–37.

Sanz CM, Morgan DB. 2009. Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. *Int J Primatol* 30:411–427.

Sanz CM, Morgan DB. 2011. Elemental variation in the termite fishing of wild chimpanzees (*Pan troglodytes*). *Biol Letters* 7:634–637.

Schick K, Toth N. 2000. Origin and development of Tool-making behavior in Africa and Asia. *Hum Evol* 15:121–128.

Schick, K, Toth, N. 2006. An overview of the Oldowan industrial complex: the sites and the nature of their evidence. In N. Toth & K. Schick (Eds.), *The Oldowan: Case Studies into the Earliest Stone Age* (pp. 3-42). Gosport: Stone Age Institute Press.

Stewart FA, Piel AK. 2014. Termite fishing by wild chimpanzees: new data from Ugalla, western Tanzania. *Primates* 55:35–40.

Stewart FA, Piel AK, McGrew WC. 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. *J Hum Evol* 61:388–395.

Tan KK, Wiart C. 2014. Botanical descriptions, ethnomedicinal and non-medicinal uses of the genus *Artabotrys* R.Br. *Int Curr Pharm J.* 6:34–40.

Teleki G. 1974. Chimpanzee subsistence technology: materials and skills. *J Hum Evol* 3:575–594.

Toth N, Schick K. 2009. The Oldowan: the tool making of early hominins and chimpanzees compared. *A Rev Anthropol* 38:289–305.

Uehara S. 1982. Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudocanthotermes spiniger*). *Folia Primatol* 37:44–76.

De Waal FB, Ferrari PF. 2010. Towards a bottom-up perspective on animal and human cognition. *Trends Cogn Sci* 14:201-207.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CE, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. *Nature* 399:682–685.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Wrangham RW. 2001. Charting cultural variation in chimpanzees. *Behaviour* 138:1481–1516.

Whiten A, Schick K, Toth N. 2009. The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. *J Hum Evol* 57:420–435.

Wilkins J, Schoville BJ, Brown KS, Chazan M. 2012. Evidence for early hafted hunting technology. *Science* 338:942–946.

WoldeGabriel G, White TD, Suwa G, Renn P, de Heinzelin J, Hart WK, Heiken G. 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, 371:330–333

Wondra EM, van Casteren A, Pascual-Garrido A, Stewart FA, Piel AK. 2016. A new report of chimpanzee ant-fishing from the Issa Valley, Tanzania. *Afr Primates* 11:1–18.

Wrangham, R.W., n.d. Kibale NP - Flora. Available at:
<http://pages.ucsd.edu/~jmoore/apesites/Kibale/KibaleFlora.html>. Last accessed, 15-04-2016.

TABLE 1 - Main parameters of vegetation cover within a quarter section of a 5 m radius circle of study mounds targeted by chimpanzees for termite fishing (abundance of plants suitable to provide raw material for termite fishing probes; identified individual tool source plants and sourced parts within the source plant; recovered tools that were abandoned by chimpanzees at the targeted mound).

Termite mound	Plants (n)							Near targeted termite mound		
	Total within quadrant	Suitable to extract raw material ^a	Potential sources of bark	Potential sources of twig	Potential sources of leaf stalk	Potential sources of grass	Plants of known tool sources species (n)	Individual tool source plants (n)	Sourced plant parts (n)	Recovered tools (n)
ITM004	39	39	6	38	4	0	1	15	45	21
ITM006	42	42	3	41	16	0	2	26	80	46
ITM007	74	4	0	4	0	0	0	1	14	21
ITM008	74	28	15	28	0	0	0	7	14	9
ITM009	45	28	7	17	1	6	6	22	50	3
ITM013	25	24	4	20	0	0	4	25	97	19
ITM015	25	25	5	25	11	0	1	12	36	6
ITM016	74	74	8	74	0	0	17	5	13	15
Sum	398	264	48	247	32	6	31	113	349	140
Mean	49.8	33.0	6.0	30.9	4.0	0.8	3.88	14.1	43.6	17.5
% relative to total plants	100.0	66.3								
% relative to plants suitable as raw material sources			18.2	93.6	12.1	2.3	11.7			

^a Note that the same plant may provide more than one type of raw material

TABLE 2 - Main classes of raw material sourced by chimpanzees to manufacture termite fishing probes relative to the average abundance of potential raw material sources near studied termite mounds.

	Raw material source				Total
	Bark	Twig	Leaf stalk	Grass	
Tools sourced (n)	140	0	0	0	140
Parts sourced (n)	349	0	0	0	349
Abundance of suitable raw material (mean of study mounds)	6.00	30.88	4.00	0.75	49.75

TABLE 3 - Percentage of plants sourced per species relative to the species' general abundance for each mound. TS = total sourced plants;
AB = abundance.

Family	Species	Type ^b	ITM004		ITM006		ITM007		ITM008		ITM009		ITM013		ITM015		ITM016	
			TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)
Annonaceae	<i>Annona senegalensis</i>	T											4					
	<i>Artabotrys collinus</i>	C	7		27				57	2	73	4	36	4	67	6	40	1
	<i>Artabotrys monteiroae</i>	C			8						9		4		25	4		
	<i>Uvaria angolensis</i>	C	7		4				14	3	5	4	12					
	<i>Uvaria sp. A of FTEA</i>	C	20	3	23	1			14				40		8	7		
	<i>Uvaria welwetschii</i>	C											4					
	<i>Monanthes buehneri</i> ^a	S																
Apocynaceae	<i>Saba comorensis</i>	C							14	3								
Euphorbiaceae	<i>Cleistanthus polystachyus</i>	T	67		35													
Malvaceae	<i>Azanza garckeana</i>	T															40	4
	<i>Dombeya burgessiae</i>	T					100											
Tiliaceae	<i>Grewia sp.</i>	C			4												20	1
Rubiaceae	<i>Rothmannia urcelliformis</i> ^a	T																
	Non-Sourced			97		99		100		92		92		96		83		94
	Total Plants (n)		15	39	26	42	1	74	7	74	22	45	25	25	12	25	5	74

^a Excluded from quantitative analysis as identified at two mounds that were not part of raw material availability studies

^b T = tree, C = climber, S = shrub

TABLE 4 - Plant species exploited by chimpanzees as sources for termite fishing tools and their main physical properties (diameter of sourced and unsourced parts of tool source species at point of detachment; height of sourced branch; total height of sourced plant).

Species	Type ^b	Diameter of sourced plant parts at point of detachment				Diameter of unsourced plant parts				Height of sourced plant parts at point of detachment (a)				Height of sourced plant			
		Mean (mm)	Min (mm)	Max (mm)	(n)	Mean (mm)	Min (mm)	Max (mm)	(n)	Mean (mm)	Min (m)	Max (m)	(n)	Mean (mm)	Min (m)	Max (m)	(n)
<i>Annona senegalensis</i>	T	5.1			1	8.5	3.3	2.7	6	1.1			1	2.2			1
<i>Artabotrys collinus</i>	C	7.0	2.6	19.9	137	8.9	1.6	69.9	88	1.0	0.0	3.5	145	2.6	0.8	2.3	47
<i>Artabotrys monteiroae</i>	C	6.6	4.2	12.7	18	7.3	2.0	30.9	32	0.9	0.4	1.8	19	2.5	1.7	2.1	8
<i>Azanza garckeana</i>	T	7.7	5.0	13.3	11	4.5	2.1	12.4	16	0.6	0.0	1.8	11	1.7	0.6	3.0	7
<i>Cleistanthus polystachyus</i>	T	6.9	2.8	20.5	78	8.0	1.8	29.3	56	1.0	0.0	2.6	78	2.1	0.9	4.0	24
<i>Dombeya burgessiae</i>	T	5.6	3.6	8.6	6					2.0	1.5	2.3	6	8.0			1
<i>Grewia sp.</i>	C	9.6			1									4.0			1
<i>Saba comorensis</i>	C	8.5	2.5	16.5	60	7.2	1.9	44.8	58	1.6	0.4	3.8	62	3.5	1.7	3.5	19
<i>Uvaria angolensis</i>	C	9.8	5.5	13.1	3	17.8	11.3	30.6	3	1.2	0.8	1.5	5	4.5	4.0	4.5	2
<i>Uvaria sp. A of FTEA</i>	C	10.0	4.1	19.0	11					1.4	0.3	2.3	14	2.0			1
<i>Uvaria welwetschii</i>	C	19.5	10.7	26.5	5	15.1	10.1	22.9	3	0.8	0.4	1.2	7	4.0	3.0	5.0	2
All species		8.7				9.7				1.2				3.4			

^a For species with more than one sourced part

^b T = tree, C = climber

TABLE 5 – Visibility of individual sourced plants from targeted mounds and sourced parts used to manufacture tools.

	Distance of source plants from targeted mound			Visible from targeted mound?		
	All plants	<10m	≥10m	Yes (all plants)	No (all plants)	No (plants sourced from ≥10m)
Plants (n)	113	71	42	89 (78.8 %)	24 (21.2%)	23 (54.8%)
Parts sourced (n)	349	266	83	311	38	37
Parts sourced per plant (n)	3.1	3.7	2.0	3.5	1.6	1.6

TABLE 6 – Tool source species that chimpanzees also exploit as food sources.

Species	Plant parts eaten by chimpanzees ^a	Eaten at Issa? ^b	Eaten elsewhere? ^b
<i>Annona senegalensis</i>	F, L, B	Yes (1)	Yes (3, 4)
<i>Artabotrys collinus</i>	F	Yes (2)	
<i>Artabotrys monteiroae</i>	F	Yes (2)	Yes (3)
<i>Uvaria angolensis</i>	F, L	Yes (1)	Yes (3, 4)
<i>Uvaria</i> sp. A of <i>FTEA</i>	F	Yes (6)	Yes (4)
<i>Uvaria welwetschii</i>	F		Yes (4)
<i>Monanthotaxis buchananii</i>	U	U	U
<i>Saba comorensis</i>	F, L	Yes (1)	Yes (4)
<i>Cleistanthus polystachyus</i>	F, W		Yes (5)
<i>Azanza garckeana</i>	F, Bl	Yes (2)	Yes (3)
<i>Dombeya burgessiae</i>	N		Yes (6)
<i>Grewia</i> sp.	F, L, Bl	Yes (1)	Yes (3)
<i>Rothmannia urcelliformis</i>	F		Yes (7)

^a F = fruit, L = leaves, B = bark, W = wood, Bl = blossom, U = unknown

^b Sources: 1 = Piel et al. unpublished; 2 = local field assistant; 3 = Nishida and Uehara, 1983; 4 = Moscovice et al., 2007; 5 = Reynolds, 2005; 6 = Russak, 2013; 7 = Wrangham, n.d.

TABLE 7 – Medicinal properties of chimpanzee plant tool sources.

Species	Medicinal properties (B = bark, L = leaves, R = roots, S = sap)	Reference
<i>Annona senegalensis</i>	Dermatosis (R, L), digestive and stomach disorders (R, B, L, F), intestinal worms (B), chest colds (R), toothache (B), respiratory infections (L), antidote for snake and scorpion venom (B, R), convulsions (L), fever (L), malaria (B), infertility (R), venereal diseases (R), seal and treat cuts and wounds (B, L, S)	Ruffo et al., 2002; Arbonnier, 2004; Huffman, 2015; Mustapha, 2013
<i>Artabotrys collinus</i>	Stomach disorders (R), antidote for snakebite (R)	Ruffo et al., 2002
<i>Artabotrys monteiroae</i>	Back aches (R), digestive and stomach disorders (R), malaria (R, B)	Tan and Wiart, 2014
<i>Azanza garckeana</i>	Digestive and stomach disorders (S, R), menstrual pains (R), fertility (R), urinary retention (R), venereal diseases (R), chest pain (R), ear pain (R, L), coughs (R), ulcers (R)	SEPASAL ^a
<i>Dombeya burgessiae</i>	Aphrodisiac (B), stomach pain (B), leprosy sores (L)	Bosch, 2011
<i>Grewia sp.</i>	Anemia (R), chest pains and colds (R), digestive and stomach disorders (R, L), constipation in domestic animals (L), female infertility (R), treatment of wounds (B, R), menstrual problems (R), pregnancy pains (R), snake bites (R)	Huffman, 2015; Ruffo et al., 2002
<i>Rothmannia urcelliformis</i>	Antidote to poisoning (R)	Neuwinger, 1996
<i>Saba comorensis</i>	Digestive and stomach disorders (R), vermifuge (R), jaundice (R), hepatitis (R), gonorrhoea (R), snake bites (R), aphrodisiac (R), splenosis (R), galactagogue for humans and cattle (S), abscesses (S), night blindness (S), hypertension (L), rheumatism and female infertility (B, R), applied on sores (S)	Ruffo et al., 2002; Arbonnier, 2004; SEPASAL
<i>Uvaria angolensis</i>	Antimicrobial and cytotoxic properties (B, R)	Hufford and Oguntimein, 1982
<i>Uvaria welwetschii</i>	Stomach disorders (R)	Moriyasu et al., 2011

^a SEAPASAL = online database of plants of arid and semi-arid lands developed by The Royal Botanical Gardens, Kew (1996)

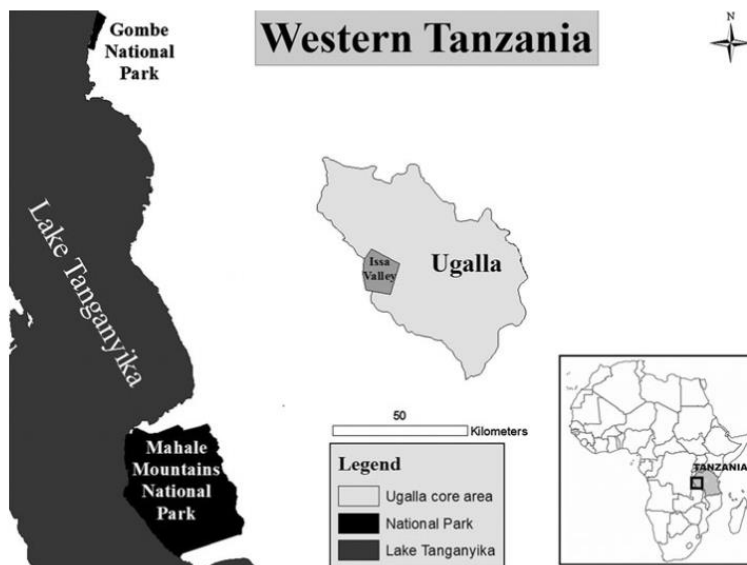


Figure 1 - Chimpanzee study site of Issa in West Tanzania relative to long-term study communities at Gombe and Mahale (Map: Stewart and Piel, 2014).

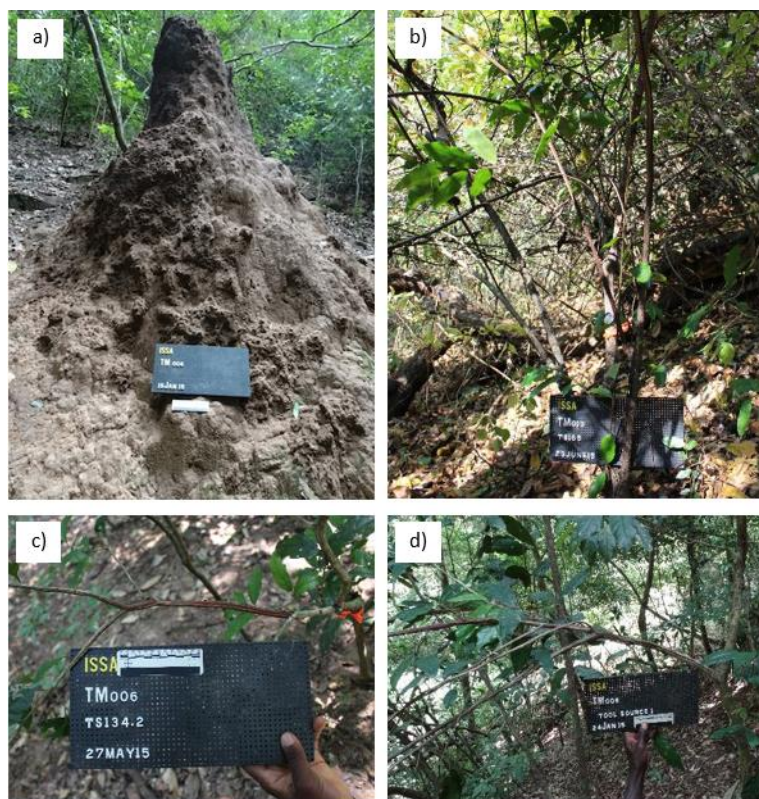


Figure 2 - Termite mound targeted by chimpanzees and plants sourced to obtain raw material for termite-fishing tools. (a) Mound ITM004; (b) Climber (*Uvaria* sp. A of FTEA) at ITM013; (c) Climber (*Uvaria* sp. A of FTEA) at ITM006; (d) Tree (*Cleistanthus polystachyus*) at ITM006. (Photos: APG - a, d; KAW - b, c).

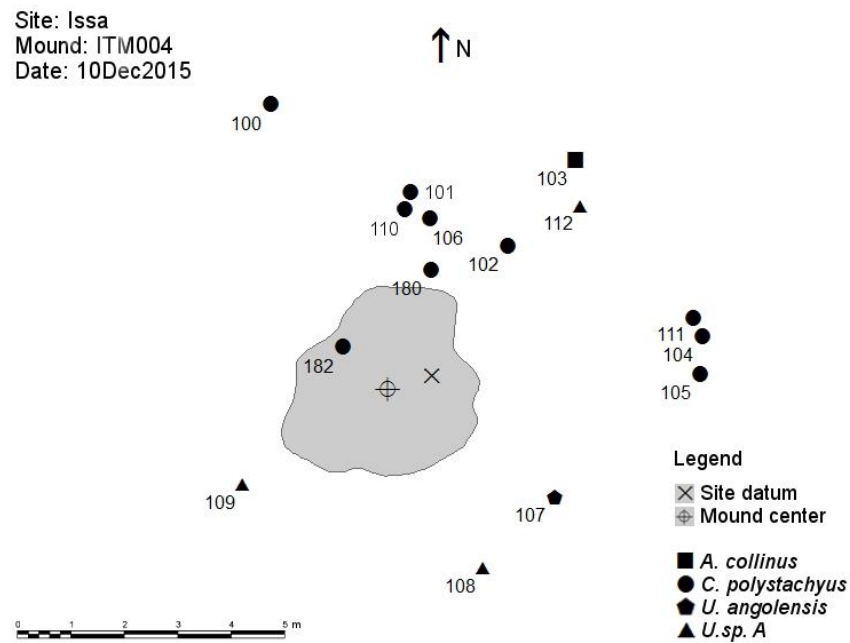


Figure 3 - Map of individual sourced plants (indicated by numbers) used by chimpanzees to fish at a termite mound (ITM004).



Figure 4 - Termites cling to a twig tool after an experimental fishing attempt by APG at mound ITM006. The tool was manufactured from the surrounding vegetation. (Photo: APG).

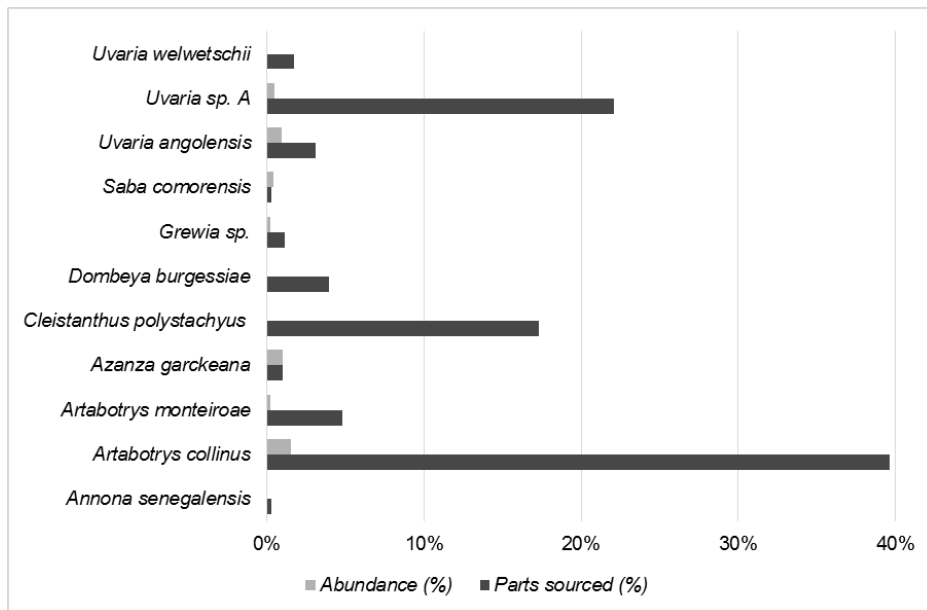


Figure 5 – Number of plant parts sourced by species used as tool sources relative to their general abundance. *M. buchananii* and *R. urcelliformis* are not included as they were identified at mounds that were not part of the raw material availability studies.

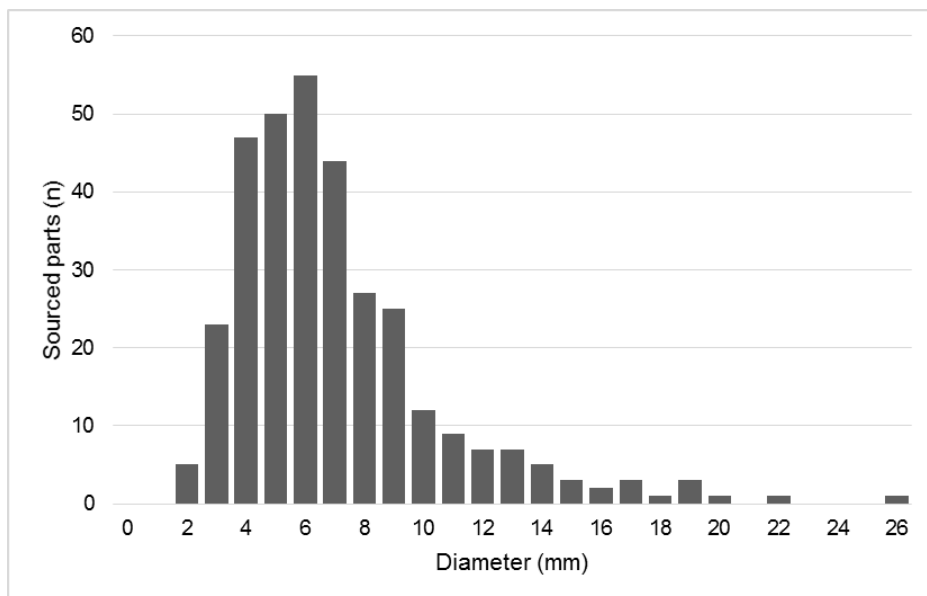


Figure 6 – Frequency distribution of diameters of sourced plant parts at point of detachment over 1-mm classes (0 = 0.0-0.9 mm; 1 = 1.0-1.9 mm; 2 = 2.0 mm; etc.).

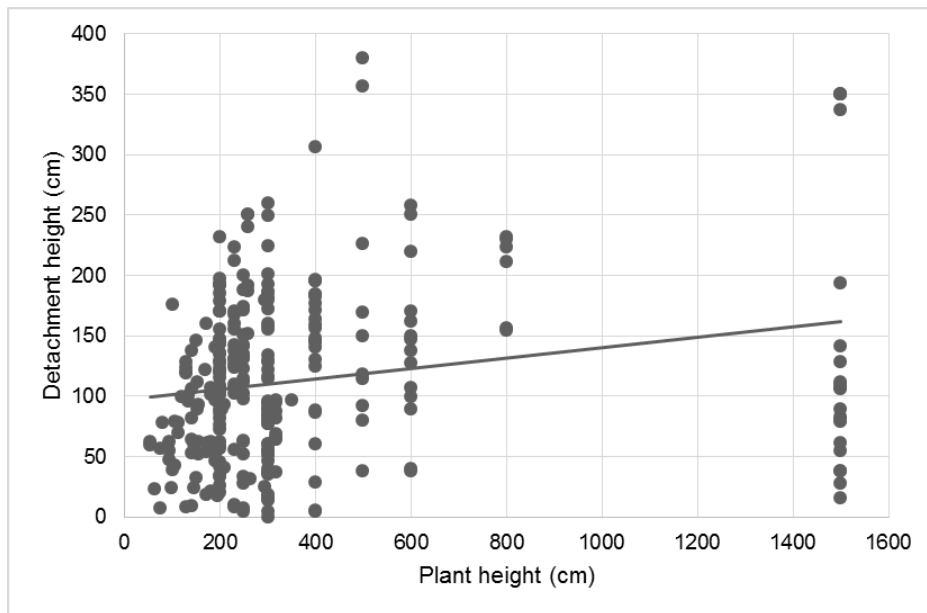


Figure 7 - Height at point of detachment relative to total height of source plant.

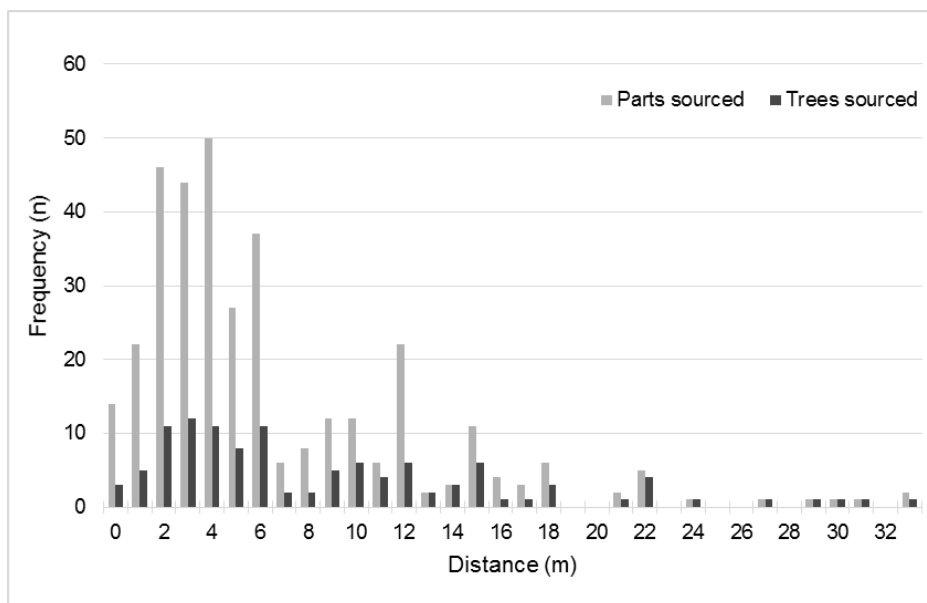


Figure 8 – Frequency distribution of distance of sourced plant parts and sourced trees over 1-m. classes (0 = 0.0-0.9 m; 1 = 1.0-1.9 m; 2 = 2.0 m; etc.).

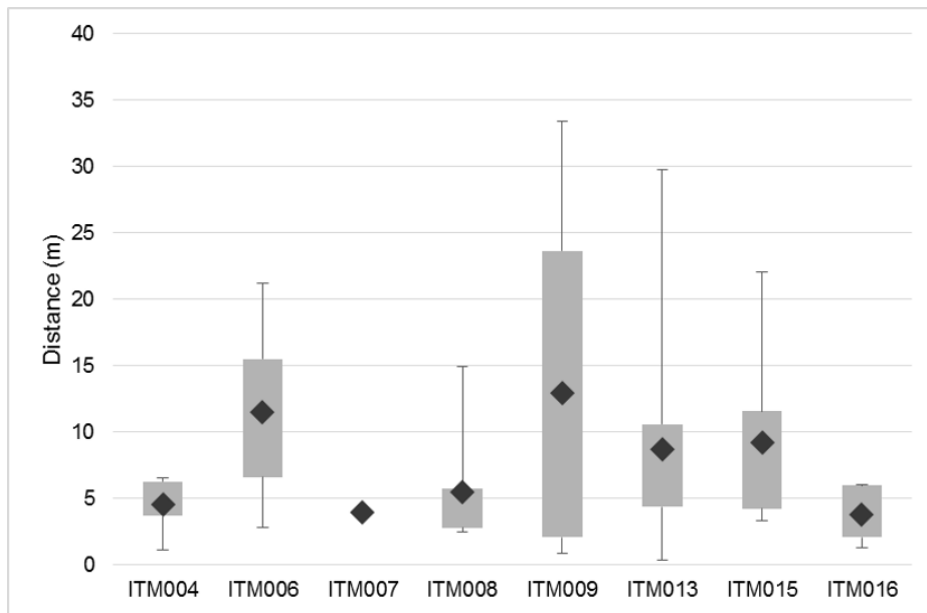


Figure 9 - Distance of sourced plants to termite mounds targeted by chimpanzees. Diamonds = mean values.

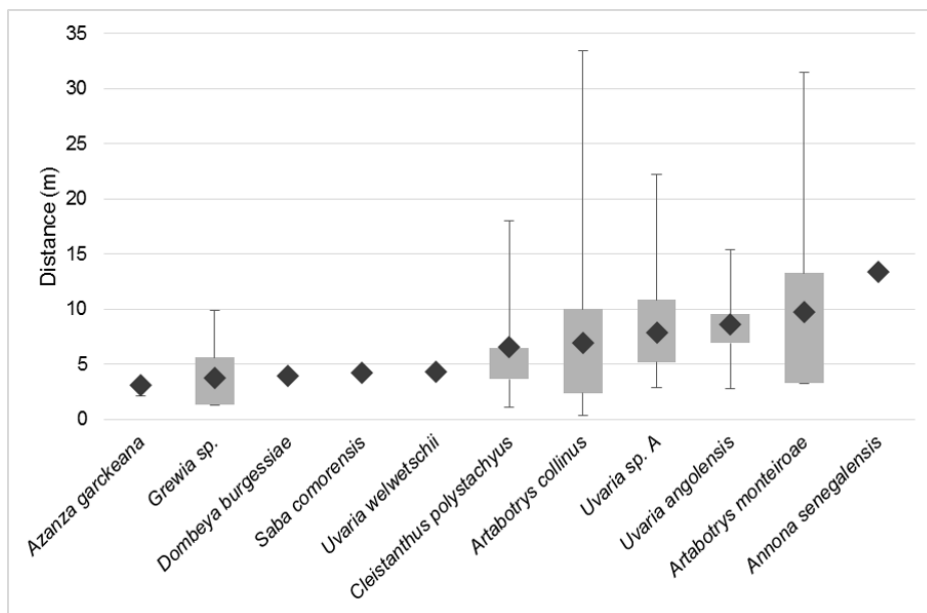


Figure 10 - Distance of sourced plants to targeted mounds by plant species. Diamonds = mean values. *M. buchananii* and *R. urcelliformis* are not included as they were identified at mounds that were not part of the raw material availability studies.