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

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

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ABSTRACT

Objectives

Chimpanzee termite fishing has been studied for decades, yet the selective processes preceding the manufacture of fishing tools remain largely unexplored. We investigate 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 Kruskall-Wallace 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 that remain archaeologically invisible.

[MAIN TEXT STARTS HERE]

While there has been extensive research on hominin lithic technology, which dates back 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 4.6–6.2 mya (Chen and Li, 2001), and extant chimpanzees are known for their versatile use not only of lithic, but also plant-based tools for foraging and social interactions (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 used to dig up termite mounds between 1.8–1.0 mya (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 used 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 in 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 km^2 (Rudicell et al., 2011). As of April 2016, the apes were 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: 09Jan–09Feb15; KAW: 17May–27Jun15; KAW: 02Nov–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: $\chi^2 = 344.751$; $df = 4$; $p < 0.001$). The most abundant material sources were plants that afforded good twigs (74%), followed by bark (14%; 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 (10%) 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 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 ($p < 0.002$; 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: $p < 0.02$) 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: χ^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: χ^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: χ^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 conceivable 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). Also, 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 (*Sorindeia warneckei*, *Chassalia kolly*) that possess strong antibacterial properties. 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. The 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), about 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 more raw material growing near mounds can source it from nearer spots (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 wider 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 cognition (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.

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FIGURE CAPTIONS

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; 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.

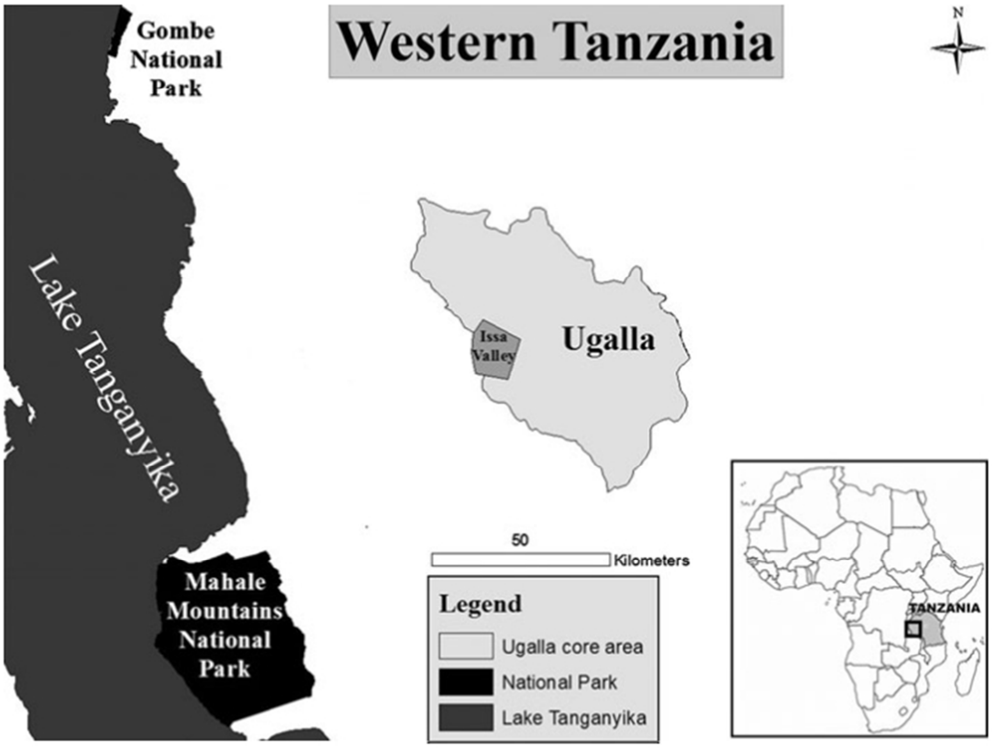

Figure 1 - Chimpanzee study site of Issa in West Tanzania relative to long-term study communities at Gombe and Mahale (Map: Stewart and Piel, 2014).
Fig. 1
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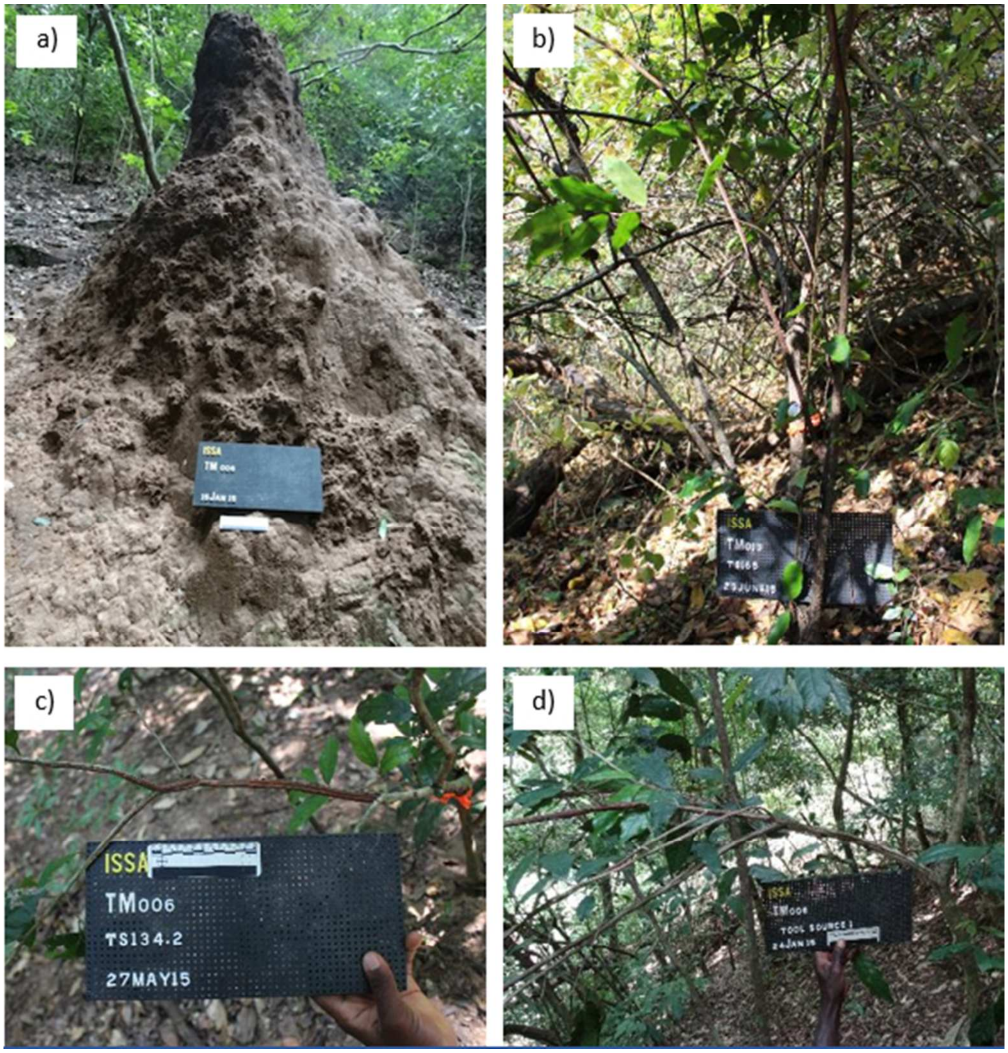

Figure 2 - Termite mound targeted by chimpanzees and plants sourced to obtain raw material for termite-fishing tools. (a) Mound ITM004; (b) Climber (Uvaria sp. A of FTEA) at ITM013; (c) Climber (Uvaria sp. A of FTEA) at ITM006; (d) Tree (Cleistanthus polystachyus) at ITM006. (Photos: APG - a, d; KAW - b, c).
Fig. 2
50x52mm (300 x 300 DPI)

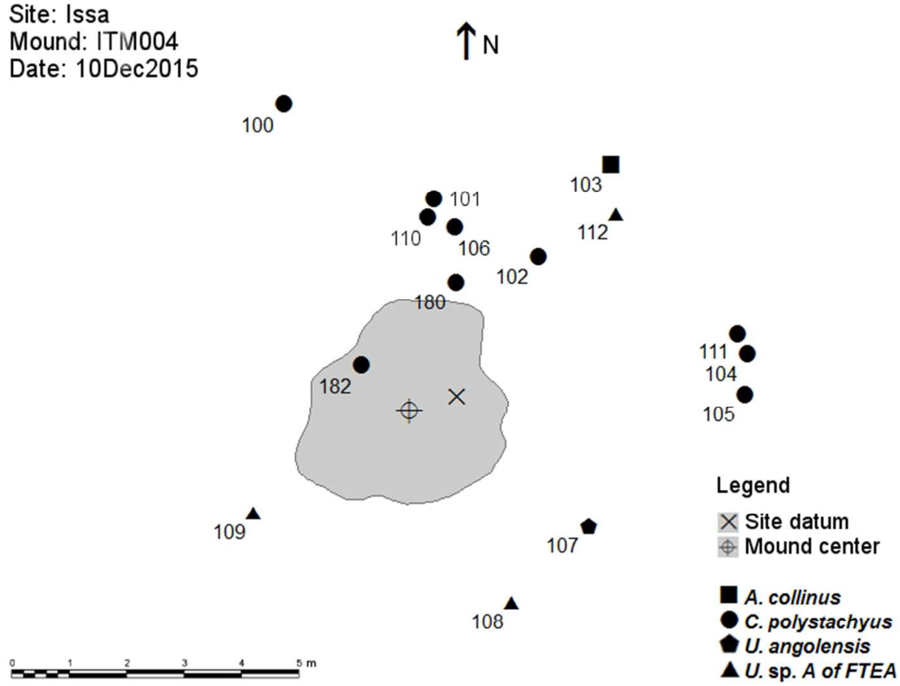

Figure 3 - Map of individual sourced plants (indicated by numbers) used by chimpanzees to fish at a termite mound (ITM004).
Fig. 3
68x51mm (300 x 300 DPI)

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).

	Plants (n)							Near targeted termite mound		
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	Specimens belonging to known tool source species	Individ-ual tool source plants (n)	Sourced plant parts (n)	Recove-red 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

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).
Fig. 4
105x150mm (300 x 300 DPI)

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				
	Bark	Twig	Leaf stalk	Grass	Total
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.

			ITM004		ITM006		ITM007		ITM008		ITM009		ITM013		ITM015		ITM016	
Family	Species	Type [b]	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)	TS (%)	AB (%)
Annonaceae	*Annona senegalensis*	T											4					
	Artabotrys collinus	C	7		27				57	2	73	4	36	4	67	6	40	1
	Artabotrys monteiroae	C			8						9		4		25	4		
	Uvaria angolensis	C	7		4				14	3	5	4	12					
	Uvaria sp. *A of FTEA*	C	20	3	23	1			14				40		8	7		
	Uvaria welwetschii	C											4					
	Monanthotaxis buchananii [a]	S																
Apocynaceae	*Saba comorensis*	C							14	3								
Euphorbiaceae	*Cleistanthus polystachyus*	T	67		35													
Malvaceae	*Azanza garckeana*	T															40	4
	Dombeya burgessiae	T					100											
Tiliaceae	*Grewia sp.*	C			4												20	1
Rubiaceae	*Rothmannia urcelliformis* [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

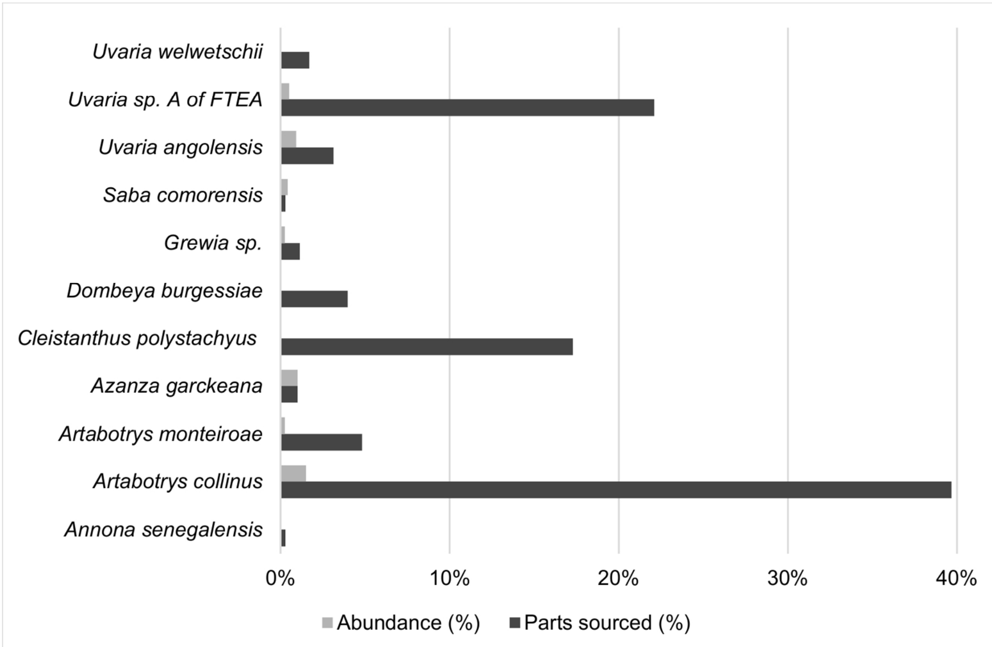

Figure 5 - Number of plant parts sourced by species used as tool sources relative to their general abundance. M. buchananii and R. urcelliformis are not included as they were identified at mounds that were not part of the raw material availability studies.
Fig. 5
153x99mm (300 x 300 DPI)

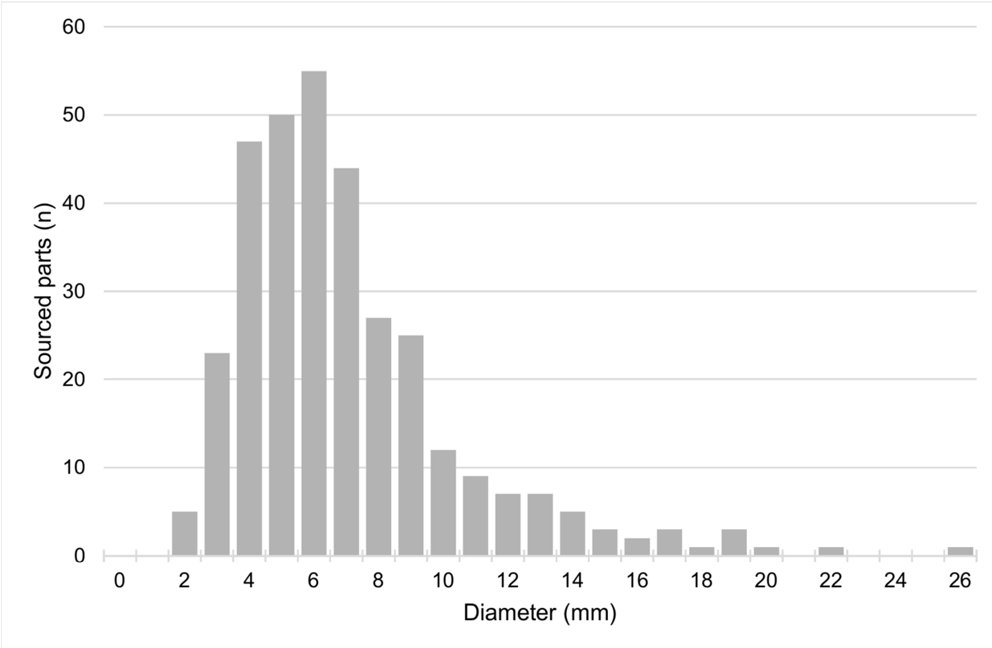

Figure 6 - Frequency distribution of diameters of sourced plant parts at point of detachment over 1-mm classes (0 = 0.0-0.9 mm; 1 = 1.0-1.9 mm; 2 = 2.0 mm; etc.).
Fig. 6
153x99mm (300 x 300 DPI)

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).

		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			
Species	Type [b]	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)
Annona senegalensis	T	5.1			1	8.5	3.3	2.7	6	1.1			1	2.2			1
Artabotrys collinus	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
Artabotrys monteiroae	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
Azanza garckeana	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
Cleistanthus polystachyus	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
Dombeya burgessiae	T	5.6	3.6	8.6	6					2.0	1.5	2.3	6	8.0			1
Grewia sp.	C	9.6			1									4.0			1
Saba comorensis	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
Uvaria angolensis	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
Uvaria sp. *A of FTEA*	C	10.0	4.1	19.0	11					1.4	0.3	2.3	14	2.0			1
Uvaria welwetschii	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

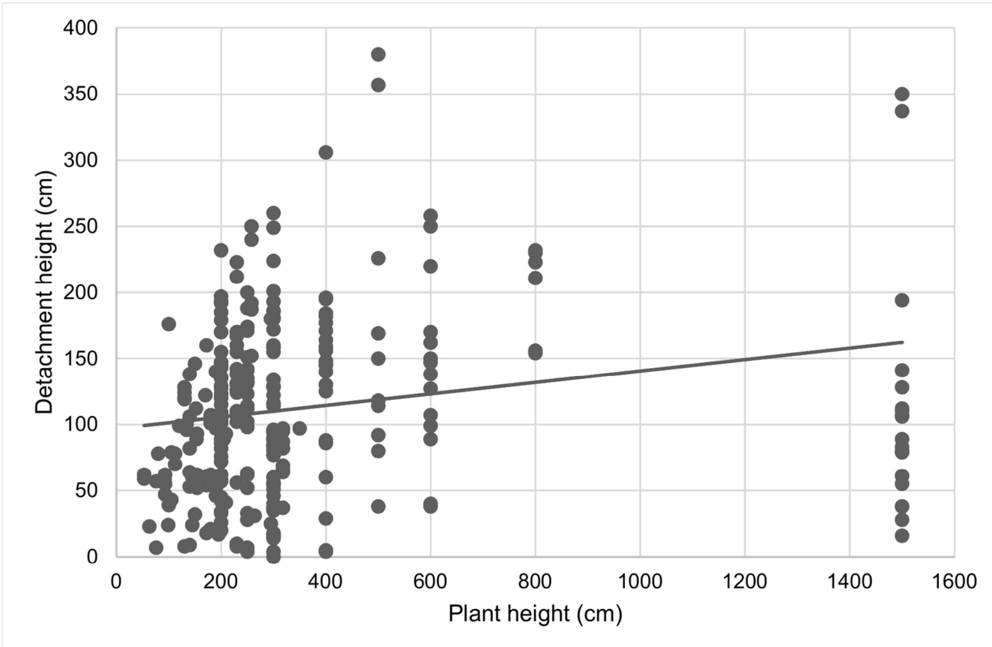

Figure 7 - Height at point of detachment relative to total height of source plant.
Fig. 7
153x99mm (300 x 300 DPI)

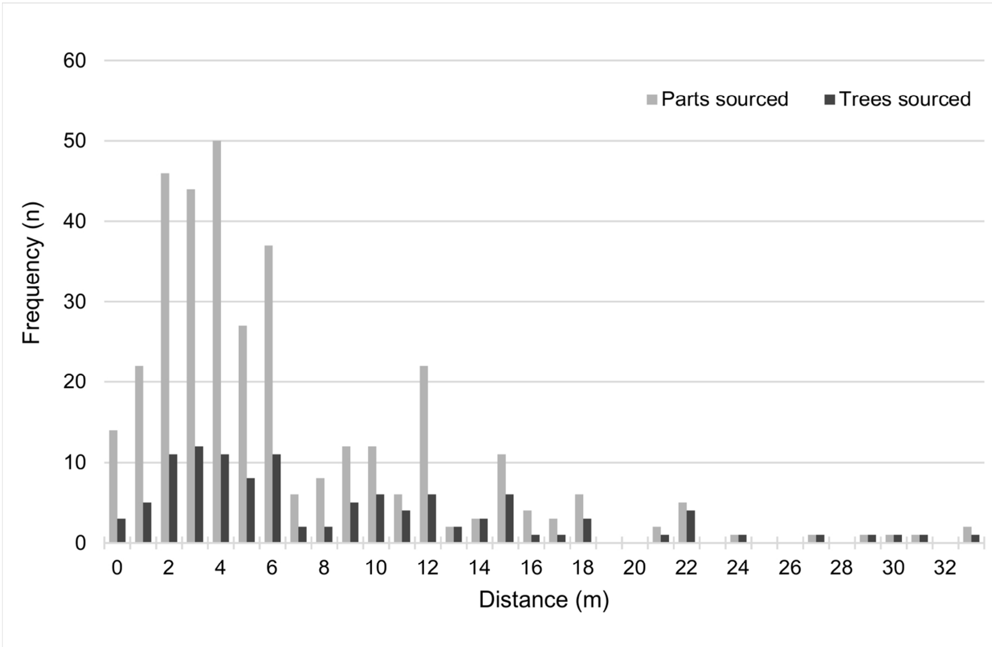

Figure 8 - Frequency distribution of distance of sourced plant parts and sourced trees over 1-m classes (0 = 0.0-0.9 m; 1 = 1.0-1.9 m; 2 = 2.0; etc.).
Fig. 8
153x99mm (300 x 300 DPI)

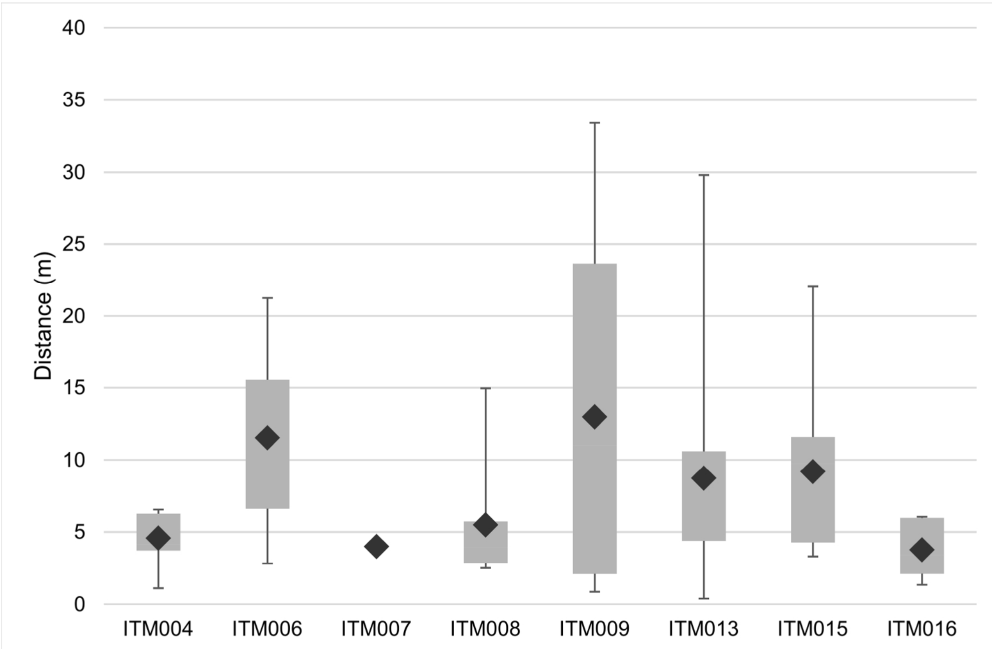

Figure 9 - Distance of sourced plants to termite mounds targeted by chimpanzees. Diamonds = mean values.
Fig. 9
153x99mm (300 x 300 DPI)

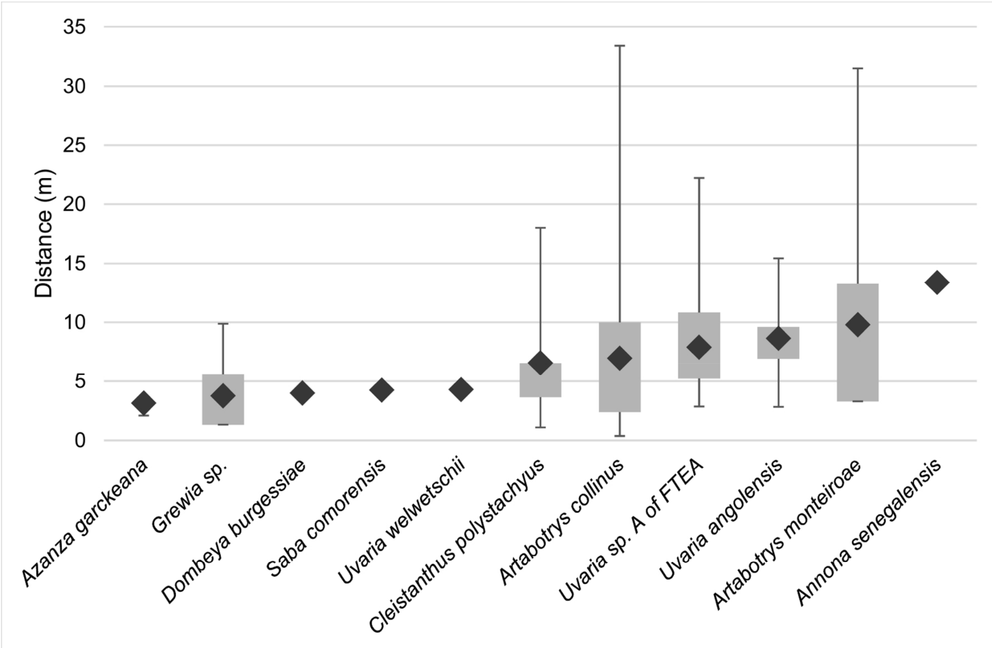

Figure 10 - Distance of sourced plants to targeted mounds by plant species. Diamonds = mean values. M. buchananii and R. urcelliformis are not included as they were identified at mounds that were not part of the raw material availability studies.
Fig. 10
153x99mm (300 x 300 DPI)

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]
Annona senegalensis	F, L, B	Yes (1)	Yes (3, 4)
Artabotrys collinus	F	Yes (2)	
Artabotrys monteiroae	F	Yes (2)	Yes (3)
Uvaria angolensis	F, L	Yes (1)	Yes (3, 4)
Uvaria sp. *A of FTEA*	F	Yes (6)	Yes (4)
Uvaria welwetschii	F		Yes (4)
Monanthotaxis buchananii	U	U	U
Saba comorensis	F, L	Yes (1)	Yes (4)
Cleistanthus polystachyus	F, W		Yes (5)
Azanza garckeana	F, Bl	Yes (2)	Yes (3)
Dombeya burgessiae	N		Yes (6)
Grewia sp.	F, L, Bl	Yes (1)	Yes (3)
Rothmannia urcelliformis	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
Annona senegalensis	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
Artabotrys collinus	Stomach disorders (R), antidote for snakebite (R)	Ruffo et al., 2002
Artabotrys monteiroae	Back aches (R), digestive and stomach disorders (R), malaria (R, B)	Tan and Wiart, 2014
Azanza garckeana	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]
Dombeyia burgessiae	Aphrodisiac (B), stomach pain (B), leprosy sores (L)	Bosch, 2011
Grewia sp.	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
Rothmannia urcelliformis	Antidote to poisoning (R)	Neuwinger, 1996
Saba comorensis	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), abcesses (S), night blindness (S), hypertension (L), rheumatism and female infertility (B, R), applied on sores (S)	Ruffo et al., 2002; Arbonnier, 2004; SEPASAL
Uvaria angolensis	Antimicrobial and cytotoxic properties (B, R)	Hufford and Oguntimein, 1982
Uvaria welwetschii	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)