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USE AND REUSE OF TERMITE-FISHING MOUNDS BY CHIMPANZEES IN TANZANIA:
AN ARCHAEOLOGICAL APPROACH TO PERISHABLE TOOL SITES

M.Sc. in Human Evolution and Biology Dissertation, supervised by Professor Paulo Jorge Gama Mota and Dr. Alejandra Pascual-Garrido, submitted to the Department of Life Sciences of the Faculty of Sciences and Technology, University of Coimbra.

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UMA ABORDAGEM ARQUEOLÓGICA A SÍTIOS DE TECNOLOGIA PERECÍVEL

Dissertação no âmbito do Mestrado de Evolução e Biologia Humanas, orientada pelo Professor Doutor Paulo Jorge Gama Mota e pela Doutora Alejandra Pascual-Garrido e apresentada ao Departamento de Ciências da Vida da Faculdade de Ciências e Tecnologia da Universidade de Coimbra.

Novembro de 2020

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Abstract

Chimpanzees have been the focus of numerous studies regarding tool-use. Because their flexible and regular use and manufacture of a diverse range of tools resemble the tool-using skills of early humans, they are considered relevant models for the understanding of our technological origins, likely invisible in the archaeological record. This study analysed data collected through archaeological methods to investigate site use and reuse by termite-fishing chimpanzees living in two distinct habitats in west Tanzania, akin to habitats where early humans are thought to have lived: Gombe and Issa. The results indicate that the Kasekela community of Gombe chimpanzees exploit termite mounds more intensively than the Issa population, likely due to constraints imposed by the differences between these two habitats. Contrary to Issa, termite-fishing at Gombe occurs throughout the whole year, albeit only sporadically during the dry season. Within each site, small variations in the intensity of tool-site use were detected. At Gombe, these could be influenced by mound-size, but the same doesn't seem to be true for Issa, probably because chimpanzee density is low at this site. Results also suggest that the discard of perishable utensils results in the creation of accumulation sites with higher concentrations of artefacts than stone tool primate sites, including early humans. This is the first detailed study of perishable tool-sites use and reuse, adding to the knowledge of processes of site formation and tool accumulation, and providing clues to the timescales, behaviours, and variability represented at known hominin sites.

Keywords:

Pan troglodytes; organic technology; tool accumulation; tool-site use; site formation.

Resumo

Os chimpanzés têm sido alvo de diversos estudos focados na utilização de ferramentas. Dado que a sua capacidade de fabricar e usar, de forma flexível e regular, uma vasta gama de utensílios pode ser comparada com as capacidades tecnológicas dos primeiros humanos, são considerados modelos relevantes para a compreensão das nossas origens tecnológicas. Este estudo analisou dados recolhidos através de métodos arqueológicos com o objetivo de investigar o uso e reuso de termiteiras por duas comunidades de chimpanzés em dois habitats distintos na Tanzânia, Gombe e Issa, semelhantes a habitats onde os primeiros humanos terão evoluído. Os resultados indicam que os chimpanzés da comunidade Kasekela em Gombe exploram termiteiras de forma mais intensiva que os seus congéneres de Issa, provavelmente devido às diferenças entre os dois habitats. Ao contrário do que sucede em Issa, a pesca de térmitas ocorre durante todo o ano em Gombe, apesar de ser esporádica durante a estação seca. Em ambos os sítios, foram detetadas pequenas variações na intensidade de exploração. Em Gombe, a dimensão das termiteiras pode influenciar estas variações, mas o mesmo não parece ser verdade para Issa, talvez porque a densidade da população de chimpanzés é baixa neste sítio. Os resultados sugerem também que o descarte das ferramentas perecíveis depois do uso dá origem à criação de sítios de acumulação com maior densidade de artefactos do que sítios de utensílios líticos explorados por primatas, humanos incluídos. Este é o primeiro estudo detalhado sobre a utilização e reutilização de sítios de ferramentas perecíveis, aumentando o conhecimento sobre processos de formação de sítios e acumulação de ferramentas, e fornecendo indicações sobre as escalas temporais, os comportamentos, e a variabilidade representados em sítios arqueológicos relacionados com a presença dos primeiros humanos.

Palavras-chave:

Pan troglodytes; utensílios orgânicos; acumulação de utensílios; uso de sítios; formação de sítios.

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1. Introduction

1.1. Primate Tool-use

Tool-use was once thought to be a defining human characteristic (Carvalho & McGrew, 2012; Haslam et al., 2009), believed to have led the evolution of our species through a path that separated us from the rest of the animal kingdom (Carvalho & Beardmore-Herd, 2019). This long-held view was challenged by the first scientific account of tool-use among non-human animals in the wild when Jane Goodall witnessed chimpanzees (*Pan troglodytes)* using plant utensils to harvest termites (Goodall, 1964).

Since then, several field studies have shown that tool-use, though rare in the animal kingdom, is present in nine different classes of animals (Biro, Haslam, & Rutz, 2013). For example, bottlenose dolphins (*Tursiops sp.*) use marine sponges on their rostra when foraging on the seafloor (Kopps & Sherwin, 2012), and Atlantic puffins (*Fratercula arctica*) use wooden sticks to scratch their bodies (Fayet, Hansen, & Biro, 2020). Tool-use is more prevalent in birds of the Passeriformes order, and Primates. The New Caledonian crow (*Corvus moneduloides*) is a well-known example of animal tool-use in the wild, making implements of leaves, twigs, and stems to fish for insect prey. These birds also distinctly shape some of the implements they use, producing hooked artefacts, and are capable of constructing compound tools, at least in a laboratory setting (Bayern, Danel, Auersperg, Mioduszewska, & Kacelnik, 2018; Hunt, 1996; Rutz & St Clair, 2012).

Non-human primates exhibit a great diversity in their tool-using behaviours: technology is used not only for foraging, but also for self-care and social interactions; primates manufacture various types of tools, use multiple types of tools to complete one task, and use one tool for multiple tasks (Musgrave & Sanz, 2018). Tool-use in the wild is rare among New World monkeys, being reported only for both genera of capuchin monkeys (*Cebus* and *Sapajus*), with the latter being habitual tool-users (Barrett et al., 2018; Musgrave & Sanz, 2018). Bearded capuchins (*Sapajus libidinosus*) tool-use is widespread and exhibits a great degree of complexity. At Serra da Capivara National Park (SCNP), they use stones and sticks to dig for tubers and probe for insects and honey (Barrett et al., 2018; Musgrave & Sanz, 2018). Multiple populations use stone hammers and anvils to crack hard-shelled foods (Fig.1), and at Fazenda Boa Vista (FBV) they have been reported to consider nut resistance, transport distance, and stone mass and hardness when selecting hammers (Fragaszy, Izar, Visalberghi, Ottoni, & De Oliveira, 2004; Musgrave & Sanz, 2018). Among Old World monkeys, occasional tool-use has been reported in wild baboons (*Papio*) and Barbary macaques (*Macaca sylvanus*), but the only habitual tool-user is the Burmese long-tailed macaque (*Macaca fascicularis aurea*) (Musgrave & Sanz, 2018). Populations of this species use stone hammers in a variety of ways to access at least forty-seven species of marine resources, like oysters, crabs, and molluscs (Malaivijitnond et al., 2007; Musgrave & Sanz, 2018) (Fig. 1).

Apes arguably exhibit the most complex tool-using behaviours of non-human primates (Musgrave & Sanz, 2018). Orangutans (*Pongo sp.)* use tools for physical comfort, subsistence, and communication. In the foraging context, orangutans use sticks to poke into tree holes to obtain social insects and their products, and to extract seeds from *Nessia* sp. fruits (Musgrave & Sanz, 2018; Van Schaik et al., 2003). Among apes, chimpanzees (*Pan troglodytes*) are the most prolific tool-users, making and using utensils in all settings, contrary to their sister species, bonobos (*Pan paniscus*), who occasionally use tools in social or self-care contexts, and gorillas, for whom only anecdotal events of tool-use in the wild have been reported (Breuer, Ndoundou-Hockemba, & Fishlock, 2005; McGrew, 1992; Musgrave & Sanz, 2018; Rolian & Carvalho, 2017). After humans, chimpanzees have the largest repertoires of tool-use and manufacture known among primates (McGrew, 2017). Across Africa, they engage in a variety of tool-assisted activities on a daily basis, including subsistence, sociality, and self-maintenance (McGrew, 1992). This includes the use of stone hammers and anvils for nut-cracking by the Western (*P. t. verus*) and the Nigeria-Cameroon (*P. t. ellioti*) chimpanzees (Boesch, 1978; Morgan & Abwe, 2006; Sugiyama & Koman, 1979) (Fig. 1). Plant-based implements are widespread amongst all subspecies of *Pan troglodytes*: twigs, sticks, vines, stems, and peeled bark are used in various foraging activities like termite-fishing, ant-dipping, and ant-fishing (McGrew, 2004); leaves are used as sponges to collect water and honey from tree holes (Lapuente, Hicks, & Linsenmair, 2017; McGrew, 2004); sticks are sharpened to hunt for bushbabies sleeping in tree hollows (Pruetz & Bertolani, 2007); more recently, chimpanzees in Comoé National Park, Ivory Coast, were reported to use modified sticks, with brush tips, to dip water from tree holes (Lapuente et al., 2017). The fact that most chimpanzee artefacts are made of plant-matter, means that the majority of chimpanzee tools are perishable, and quickly disappears from the material record (McGrew, 2004).

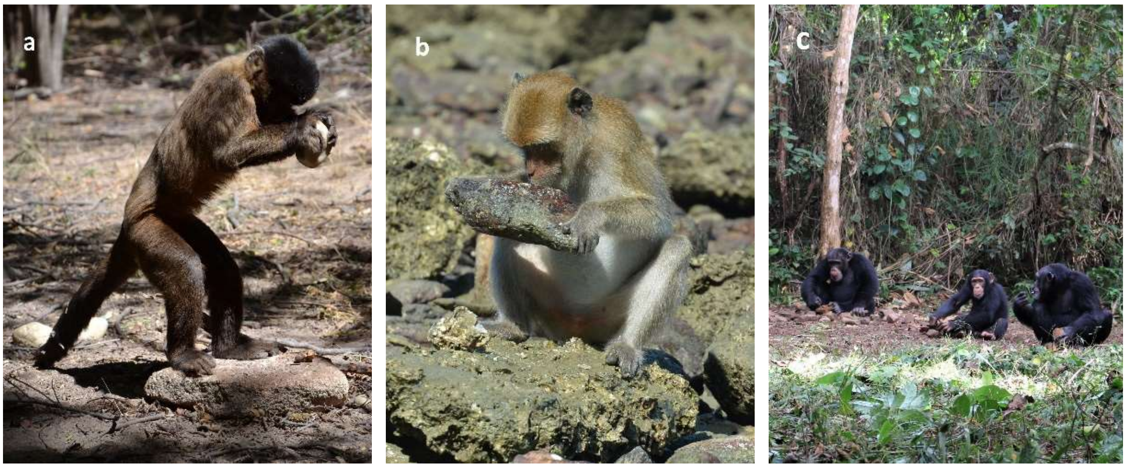

Figure 1 – Primate tool use. a) Capuchin nut-cracking at SCNP. Photo credit: Alejandra Pascual-Garrido; b) long-tailed macaque using stone hammer and anvil to access hard-shelled food. Photo credit: Amanda Tan; c) Nut-cracking chimpanzee at Bossou. Photo credit: Katarina Almeida-Warren.

Investigating animal tool-use is fundamental to understand its adaptive value and its evolution in the natural world, and can help us gain a better picture of the evolutionary trajectory of our species (Fayet et al., 2020). Although animal tool-use is not restricted to the primate order, the close relationship that non-human primates share with our species makes their study especially relevant to the understanding of early human behaviour in general, and the evolution of tool-use in our lineage in particular (Haslam et al., 2009; Panger et al., 2002). As Primates, humans share many features with other members of the Order primates, like morphology, physiology, life history, and also behavioural traits, and thus can serve as referential models to reconstruct certain aspects of human behavioural patterns (Boyd & Silk, 2009; Carvalho & McGrew, 2012). Research on monkey and ape behaviours has provided contributes to a better understanding of the evolution of human sexuality, language, morality, culture, and technology (Kappeler, Silk, Burkart, & Van Schaik, 2010).

Chimpanzees are particularly relevant to modelling human origins, and many studies have focused on topics such as their technology, diet, shelter, and ranging and foraging (McGrew, 2010). Although bonobos are as closely related to us as chimpanzees are, research on *Pan paniscus* hasn't produced, so far, data comparable in terms of depth and breadth, to chimpanzee data (McGrew, 2010; Rolian & Carvalho, 2017). Bonobos are also infrequent tool users in natural contexts, and so chimpanzees are the most pertinent referential models to understand the evolution of our technological behaviour (Carvalho & McGrew, 2012). To further understand this connection, the new discipline of primate archaeology combines archaeological methods with ethological observations to explore the adaptive contexts of primate technology (Haslam et al., 2009).

1.2. Primate Archaeology

Primate archaeology combines the use of archaeological methods with ethological approaches to study the technological behaviour of non-human primates (both extant and extinct) to arrive at models for early human tool-use behaviour (Carvalho & Almeida-Warren, 2019). This innovative approach has produced a large amount of information, allowing the reinterpretation of early archaeological records and identification of currently archaeologically invisible behaviours (Carvalho & McGrew, 2012; Haslam et al., 2017). For example, the excavation of a chimpanzee nut-cracking site in the Taï Forest in Côte d'Ivoire revealed that chimpanzees leave an archaeological record as a result of their tool-use which can be dated back for at least 4,300 years (Mercader et al., 2007; Mercader, Panger, & Boesch, 2002). This provided the first evidence that apes, like our human ancestors, are also capable of producing an archaeological record. This study, together with many others, has paved the way for the establishment of this new discipline (Haslam et al., 2009), kickstarted by the pioneering work of Carvalho, Sousa, and Matsuzawa (2007), surveying chimpanzee nut-cracking sites in Diecké Forest, Guinea (Carvalho, 2016). Thanks to Primate Archaeology, we now know that chimpanzees select the material and size of the stones they use to crack nuts (Carvalho, Cunha, Sousa, & Matsuzawa, 2008; Sirianni, Mundry, & Boesch, 2015), while analysis of use-wear (tool damage) on chimpanzee pounding tools revealed similarities with traces on archaeological percussive objects from the Early Stone Age (Arroyo, Hirata, Matsuzawa, & De La Torre, 2016).

More recently, primate archaeology has extended its scope to other non-human primates that use lithic tools (Carvalho & Almeida-Warren, 2019; Haslam et al., 2017). Research at FBV shown that bearded-capuchin monkeys select hammerstones based on material, size and weight (Visalberghi et al., 2009), and a study conducted in SCNP found that capuchin stone-on-stone percussion activities lead to the unintentional production of sharp-edged flakes, with conchoidal fractures, like early hominin tools (Proffitt et al., 2016). At the latter site, archaeological excavations of capuchin nut-cracking sites have shown that these primates have been using stone tools for at least 700 years (Haslam, Luncz, Staff, et al., 2016). Primate archaeology has also extended its research to Burmese long-tailed macaques' stone tools. Use-wear analysis of axes and hammers showed distinct damage patterns, that can be identifiable in the archaeological record (Haslam, Gumert, Biro, Carvalho, & Malaivijitnond, 2013). A subsequent study demonstrated that these monkeys hold on to utensils, transporting them and reusing them while foraging, before abandoning them near the location of the last use (Haslam, Pascual-Garrido, Malaivijitnond, & Gumert, 2016). These studies helped in guiding archaeological excavations of macaque tool-sites, and one such site was excavated in Thailand, resulting in the recovery of 65 years old stone artifacts of *M. f. aurea* (Haslam et al., 2016b). These studies have demonstrated that tool selection and transport, and the formation of sites to which archaeological techniques can be applied, is universal among stone-tool-using primates (Haslam et al., 2017).

However, archaeology and the emerging discipline of primate archaeology have a 'blind spot' related to non-lithic artefacts, that is, those made from organic materials (Haslam et al., 2017). Because plant-based substances decompose quickly, organic material that probably was employed long before stone tool-use first appeared in the archaeological record more than 3.3 million years ago is unlikely to have been preserved (Harmand et al., 2015; Panger et al. 2002). Although evidence from the use of plant materials in the paleolithic is rare, it nonetheless suggests plants were highly important in early humans' diet and technology (Hardy, 2018). In the rare instances where plant materials have survived in the early archaeological record, they represent 95% of recovered artefacts, comparable to chimpanzee tool-use, where plant-based materials strongly outweigh stone material (Hardy, 2018). Plant-based technology is not only the most common and diverse manifestation of primate tool-use but also the only tool source type that non-human primates modify intentionally before use (Whiten et al., 1999).

By looking at chimpanzee use of stone tools, Wynn et al. (2011) concluded that there is little that differentiates it from the Oldowan hominins technology, and it is likely that the same can be said about these early humans' plant-based technology (Hardy, 2018). The study of chimpanzee perishable technology can thus be used as a contribution to model the organic technology of our early ancestors (Hardy, 2018). Research *foci* and trajectories concerning organic implements employed by primates, both human and non-human, are still in their infancy (Hernandez-Aguilar, 2009; Hernandez-Aguilar, Moore, & Pickering, 2007; Sept, 1992; Stewart, Piel, & McGrew, 2011). However, in the last decade, studies on primate perishable technology employing archaeological methods have been expanding our knowledge about the selection and use of plant-based tools, and on patterns of landscape use and foraging strategies, creating a framework for reconstructing invisible aspects of our ancestors' behavior (Almeida-Warren, Sommer, Piel, & Pascual-Garrido, 2017; Carvalho & Almeida-Warren, 2019; Pascual-Garrido, 2018; Stewart et al., 2011).

1.3. Chimpanzee termite-fishing

Chimpanzees are our closest living relatives, having split from our lineage around 8-7 mya (Langergraber et al., 2012). Wild chimpanzees dwell primarily in evergreen forest, with some populations persisting in deciduous woodland and grassland biotopes interspersed with gallery forest (Matsuzawa, Humle, & Sugiyama, 2011). An endangered species, they can be found in 21 countries of tropical Africa, lying around the equator (Matsuzawa et al., 2011). The eastern chimpanzee subspecies (*Pan troglodytes schweinfurthii*) ranges from southeastern Central African Republic through northern Democratic Republic of Congo, to the western regions of east African countries and southeast Sudan (Plumptre et al., 2010).

Chimpanzees' diet consists mainly of fruits and leaves (Matsuzawa et al., 2011), but they also consume eusocial insects frequently, including *Isoptera* and *Hymenoptera*, often harvested with recourse to organic tools (O'Malley & Power, 2012). Tool-assisted insect foraging, particularly to eat termites, was first reported in 1964 by Jane Goodall (Goodall, 1964). Termite-fishing has gained considerable attention from the paleoanthropology community (Lesnik, 2014), especially since the discovery of termite foraging by *Paranthropus* (*Australopithecus*) *robustus* (Backwell & D'Errico, 2001). That the consumption of termites by chimpanzees and present-day modern humans is a well-documented phenomenon, posits the hypothesis that early hominins were also utilizing this resource (Lesnik, 2014; O'Malley & McGrew, 2014), and possibly with similar technologies as those used by modern chimpanzees (Sanz et al., 2014).

Chimpanzee's termite-fishing technology varies regionally. While central African populations use tool-sets - different implements used in succession - other populations, such as the one included in this study, use a much simpler technique which consists of the use of a single probe inserted into an exit hole to obtain the insects from inside the mound (Sanz et al., 2014) (Fig. 2). Tools are normally discharged at the tool use site (termite mound) after their use, sometimes left inserted in the mound surface. The manufacture of termite-fishing utensils includes the use of a variety of plant materials such as bark, herbs, grass, leaves, twigs, vines, petioles, and sedges (Fay & Carroll, 1994; McGrew & Collins, 1985; McGrew, Tutin, & Baldwin, 1979; Sanz, Morgan, & Gulick, 2004). Chimpanzees normally obtain these materials from near the termite mounds but also from further away when this option is not available. Distances of transport vary between a few meters to more than a kilometre (Almeida-Warren et al., 2017; McGrew et al., 1979; Pascual-Garrido, 2019; Sanz et al., 2004; Teleki, 1974), and preference exists for plant species and materials types used (Bermejo & Illera, 1999; Fay & Carroll, 1994; Sanz et al., 2014; Sanz et al., 2004). However, while local ecology, including raw material availability, is known to shape primate material culture (Carvalho et al., 2008; Koops, McGrew, & Matsuzawa, 2013; Koops, Visalberghi, & van Schaik, 2014; McBeath & McGrew, 1982; McGrew et al., 2019; Sanz et al., 2014), including humans (Andrefsky, 1994; Braun et al., 2008; Kimura, 1999), many determinants of chimpanzee termite fishing remain unknown. For example, much information could still be gleaned from analysing chimpanzee site selection and reuse, and the factors that influence these choices.

Figure 2 - Chimpanzee Tom uses a plant tool to fish termites at Gombe. Photo credit: Alejandra Pascual-Garrido.

Chimpanzee termite fishing offers a unique opportunity to investigate site-use and reuse. First, unlike the frequent relocation characteristic of other social insects habitually harvested with tools by chimpanzees (Pascual-Garrido, Umaru, Allon, & Sommer, 2013), *Macrotermes* termites reside in the same conspicuous terrestrial mounds for decades. This allows not only the easy recovery of artefacts at their place of discard (termite mounds) (McGrew & Collins, 1985), but also enables the systematic study of raw material availability and use near tool-use sites (Almeida-Warren et al., 2017; McBeath & McGrew, 1982; Pascual-Garrido, 2019).

Many studies on chimpanzee termite-fishing have reported on the accumulation of artefacts at tool-use sites. Based on the number of artefacts found, McGrew et al. (1979) showed that tool accumulation was higher at Mt. Assirik, Senegal than at Okorobiko, Equatorial Guinea, suggesting that tool-site use was more intensive at the former site, likely due to environmental differences, but some of the data were collected in a circumstantial way, and not on a mound by mounds basis. Another study conducted at the Mt. Assirik site looked at tool accumulation and concluded that chimpanzees, even within the same population, do not engage in termite-fishing equally throughout their range, concentrating their activities in specific habitat types (McBeath & McGrew, 1982). McGrew and Collins (1985) looked at tool accumulation at Mahale and reported differences in the sizes of tool assemblages across mounds, and also in the frequency of site use.

Other studies have looked at tool accumulation (Bermejo & Illera, 1999; Fay & Carroll, 1994; McGrew, Pruetz, & Fulton, 2005; McGrew & Rogers, 1983; Sanz et al., 2004; Sugiyama, 1985; Suzuki, Kuroda, & Nishihara, 2005). However, in many of these reports tool collection was done in an opportunistic or circumstantial fashion, was not done over the course of different seasons, or wasn't done on a mound by mound basis. Although these studies have enlarged the knowledge on termite fishing, looking at cross-cultural variations (Sanz et al., 2004), sex differences (Lonsdorf, 2005), and the effect of insect prey characteristics on termite-fishing strategies (Sanz et al., 2014), they haven't focused in detail on site use and re-use and the factors behind it. Only recently research on termite fishing has systematically applied archaeological methods, allowing for data to be collected in a way that will allow for detailed studies of use and reuse of perishable tool sites (Almeida-Warren et al., 2017; Pascual-Garrido, 2018, 2019; Pascual-Garrido et al., 2012).

1.4. Use and reuse of termite-fishing mounds

Site reuse is common in primate lithic technology. Early hominin stone-tool sites reveal high concentrations of tool materials, likely indicating repeated use (Toth & Schick, 2009). Variation in these sites could, however, reflect different types of site-use, including group size and duration of (re)occupation, and proximity to raw-material sources, among others constraints, and thus likely reflect different underlying behaviors (Schick & Toth, 2006). As the behaviour of our ancestors is invisible in the archaeological record, much could be learned by examining how the technological behaviours of living non-human primates, like using and discarding tools, creates a material record that can help in understanding site formation processes (Sept, 1998). However, until recently, research on chimpanzee site use, and its relationships with the localities of tool manufacture, use, and discard had not taken place (Sept, 1998).

One of the first studies to use archaeological methods to the study of tool-using primates, by Carvalho et al. (2008), applied the concept of *chaîne opératoire* to the study of primate material culture for the first time, studying the operational sequences of nut-cracking chimpanzees in Bossou, Guinea. The spatial analysis of tool distribution suggested that chimpanzee resource exploitation strategies reveal affinities with the Oldowan, including optimal use of resources with flexible, dynamic, opportunistic, and low-energy strategies to solve problems. This and further research explored how repeated events of tool and site use and reuse can create sites akin to early hominin ones (Carvalho, 2011; Carvalho, Biro, McGrew, & Matsuzawa, 2009). Looking at tool densities, Carvalho and McGrew (2012) suggested that site use could be explained by factors other than raw-material availability, like social constraints on individuals feeding at a tool site.

As with chimpanzees, research on capuchin spatial concentration of pounding tools, and repeated reuse of locations such as nut-tree sites, can form recognizable archaeological assemblages (Haslam et al., 2009), and discrete site formation seems to be universal among wild stone-tool using primates (Haslam et al., 2017). Although research on chimpanzee perishable technology has not focused deeply on site use, many studies have recorded old and new tools found together at termite-fishing sites (McGrew & Collins, 1985; Pascual-Garrido, 2018; Sanz et al., 2004), ant-dipping and honey/bee harvesting sites (McGrew et al., 2005; Pascual-Garrido et al., 2012), and also repeated use of sites in underground storage organs digging (Hernandez-Aguilar et al., 2007). Site reuse also happens in chimpanzee nesting behaviour (Sept, 1998). This will be the first detailed study of chimpanzee termite-fishing site (re)use, and the possible factors that might influence it.

The *chaîne-opératoire* of tool use, broadly speaking, can be represented as follows: raw material procurement and selection; transportation; modification; (re)use; discard. As the last step in the *chaîne-opératoire* of tool-use, discard can lead to artefact accumulation that can result in the formation of a site.

My research aims to study the use and re-use of activity areas by termite-fishing wild chimpanzees, by focusing on the last stage of the termite-fishing operational sequence. For this, I analyze the cumulative deposition of discarded artefacts at tool-use sites (termite mounds) from two communities of termite-fishing chimpanzees that live in two different habitats, to investigate possible factors influencing the use and reuse of sites.

I address the following questions: Does the accumulation of tools, and thus the intensity of site-use, vary between study sites? If so, can this be explained by the ecological differences between the two habitats? Issa is one of the driest habitats where chimpanzees live, and I expect that this influences the intensity of site-use. Does the intensity of site-use vary between termite mounds within each study site? If so, how does this compare with the general abundance of raw material available and activity site size? Are sites with more raw material available and/or bigger surface area used more intensively? Given that raw material availability influences stone technology in chimpanzees (Carvalho et al., 2008; Luncz et al., 2016) and early humans (Andrefsky, 1994; Braun et al., 2008; Braun et al., 2009; Kimura, 1999), I expect the availability of raw material to also be a determinant of perishable technology in wild chimpanzees. As to mound size, I expect bigger mounds to be more intensely exploited: the exploitation of resources by chimpanzees may be affected by social constraints imposed on the number of individuals feeding at the same time on a limited space (Carvalho et al., 2008), and bigger mound surfaces could possibly allow for more individuals to feed without being disrupted.

Additionally, I try to answer these questions: Does the use of termite-fishing utensils by chimpanzees create accumulation sites? If so, how do they compare with stone-tool densities described at other primate activity areas, including early human ones? Looking at the formation of tool sites in real-time may help understand how the intensity of tool-site use and reuse, through the repetitive deposition of artefacts, generates a recognizable pattern across the landscape, as is the case, for example, with chimpanzee nest building sites, that can be linked to the underlying behaviours (Haslam et al., 2017; Stewart et al., 2011; Sept 1992). Understanding the processes behind the formation of accumulation sites will thus shed new light at the timescales represented at known hominin sites (Haslam et al., 2017). As the low durability of perishable materials makes it difficult to identify this kind of sites in the archaeological record (Carvalho & McGrew, 2012), research on this topic can contribute to model the behaviour of our early ancestors, who were likely to also exploit eusocial insects as food, probably with the use of similar tools as those used by chimpanzees (Carvalho & McGrew, 2012), and who likely lived in habitats like the ones studied here.

2. Materials and Methods

2.1. Study sites and subjects

As part of an ongoing study led by Dr. Alejandra Pascual-Garrido (APG), Primate Models for Behavioural Evolution Lab, Institute of Cognitive & Evolutionary Anthropology, University of Oxford, research has been conducted in two sites in western Tanzania, where local communities of eastern chimpanzees (*Pan troglodytes schweinfurthii*) habitually engage in tool-assisted termite fishing. The study sites (Fig. 3) correspond to two different types of habitat where early humans might have lived too: thicket and open forest woodland / Gombe and open miombo-woodland with small patches of forest / Issa (Pascual-Garrido, 2018).

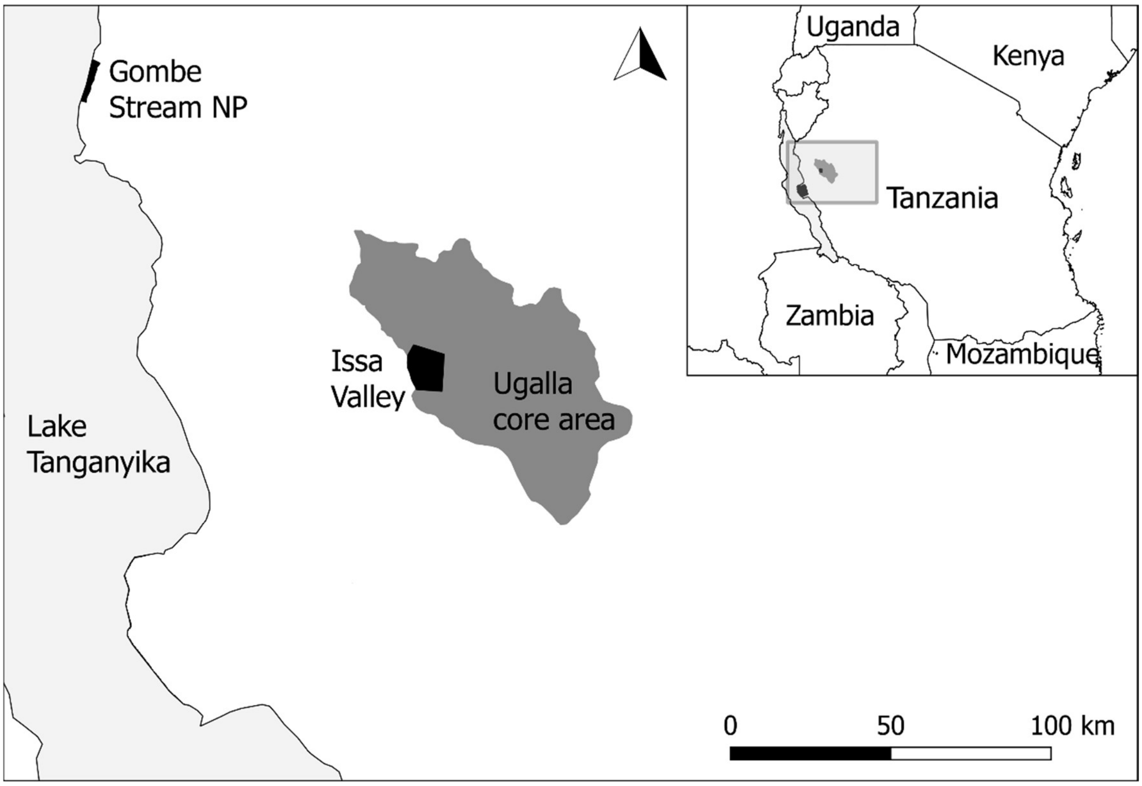

Figure 3 - Map of western Tanzania, indicating the locations of the study sites of Issa and Gombe. Map credit: Katarina Almeida-Warren.

The Gombe Stream National Park is on the eastern shore of Lake Tanganyika in western Tanzania. The 35-km^2 park is divided by stream valleys that run from the rift escarpment to the lake, separated from each other by steep ridges (Clutton-Brock & Gillett, 1979). The climate is characterized by a single rainy season and a marked dry season, the latter extending from May to October. Average rainfall per annum is 1495 mm (McGrew & Collins, 1985). The lower slopes are dominated by evergreen and semi-deciduous forest and the upper slopes consist of a mosaic of thicket, woodland, and grassland (Pusey, Pintea, Wilson, Kamenya, & Goodall, 2007). The Kasekela community of chimpanzees at Gombe has been the subject of research since the 1960s and comprises 55 individuals as of 2017 (McGrew et al., 1979; Pascual-Garrido, 2019). Chimpanzees termite fish year-round but their efforts concentrate at the start of the rainy season from October to December (Lonsdorf, 2005). The apes use various materials to make their tools, including bark, twigs, vine, grass, which they select from different plant species located at a relatively close distance from the center of the mound (McGrew et al. 1979; Pascual-Garrido 2018) (Fig. 4).

Figure 4 - Chimpanzees termite-fishing at Gombe: a) Inserting fishing-probe into a termite mound; b) Feeding on harvested termites. Photo credit: Alejandra Pascual-Garrido.

Issa chimpanzees reside in the Issa valley located in the Ugalla region in western Tanzania. It is one of the driest, most open habitats where chimpanzees reside. The habitat is characterized by broad valleys separated by deep mountains and flat plateaus. The vegetation is dominated by miombo woodland (*Brachystegia* and *Julbernardia*) but includes patches of swamp, grassland, and also evergreen gallery and thicket riverine forests (Stewart & Piel, 2014). Rainfall averages <1000 mm per annum, and as at Gombe, a wet season from October to April is followed by a dry period from May to September (Stewart & Piel, 2014). The Issa community, now partially habituated, comprises approximately 67 individuals with a minimum home range of 85 km^2 (Rudicell et al., 2011). As at Gombe, termite fishing is highly seasonal, occurring mainly during the wettest months of the year (Nov-Feb) (Stewart & Piel, 2014). Unlike at Gombe, where various types of materials are used, at Issa apes exclusively use bark to manufacture their tools which they select from plant species located tens of meters away from the mound. This exclusive use of bark cannot be explained by ecological constraints or genetics. In addition, Issa chimpanzees are known to use other plant parts, like sticks, when foraging other resources, and thus bark use seems to indicate a cultural preference of this population (Almeida-Warren et al., 2017).

2.2. Data Collection

Data was collected by APG and Katarina Almeida-Warren (KAW), Primate Models for Behavioural Evolution Lab, Institute of Cognitive & Evolutionary Anthropology, University of Oxford, during two consecutive termite fishing seasons (Gombe: 12Oct-12Nov2014, 14Nov-14Dec2015; Issa: 9Jan-9Feb2015, 2Nov-15Dec2015). At Gombe, an additional period outside of the termite fishing season was included in the study (16Apr-12May2015). Data on the spatial distribution of termite-fishing tools and raw material availability was collected in 21 termite mounds (*Macrotermes spp.*): 7 at Gombe and 14 at Issa.

i) Termite Mounds

Mounds that showed evidence of termite-fishing activities were identified and recorded (Fig. 5). A mound was considered to be targeted if at least one of the three following criteria applied: (a) chimpanzees were seen fishing; (b) presence of tools, fragments, or raw materials modified as a result of tool manufacture; presence of tool sources within the mound's periphery (cf., Pascual-Garrido, 2018). At every mound, records included GPS location, nest dimensions (cross-sections widths and heights), and habitat type (open/closed forest, woodland, miombo woodland, savanna). Mounds were monitored every 2-3 days to record frequency of use by chimpanzees (Almeida-Warren et al., 2017; Almeida-Warren, 2015). For each mound, a unique identification number was given (GTMXXX) and a site datum located close to or at the center of the mound was marked by a hammer nailed to a tree adjacent to the mound, to allow measurements within a standardized coordinate system. For this, a measuring tape was extended from the datum to the tool or tool source (a water level and plumb bob were used to ensure the correct positioning of the tape), and the deviation from the magnetic north was obtained by compass readings. The datum and the magnetic north thus served as the two fixed points that allowed the application of topographic triangulation to obtain data points with three coordinates: x (distance from datum), y (deviation from magnetic north), and z (height in relation to the datum) (cf., Carvalho et al., 2008; Almeida-Warren, 2015)

Figure 5 - Monitored termite-mounds: a) Mound GTM009 at Gombe; b) Mound ITM008 at Issa. Photo credit: Alejandra Pascual-Garrido.

During each monitoring visit artefact presence and sourced plants nearby were recorded, including the following parameters:

a) Discarded tools (Fig. 6): Distance measurements were taken for each tool in relation to the position of the site datum point. Once a tool was recorded, it was marked with a white paint marker to avoid recording it twice during following visits. Tools recorded were left at the tool use site to track movement and disappearance of tools over time.

b) Tool sources: Plants that showed evidence of sourcing for tool material by chimpanzees were identified by walking back and forth from the mound in a clockwise fashion (cf. Pascual-Garrido et al., 2012). To distinguish signs of broken or removed plant parts caused by chimpanzees procuring tool materials from breakage from other causes, the identification of tool sources in this study followed the criteria established by Pascual-Garrido (2018), based on Almeida-Warren et al. (2017): (1) source plant is within tens of meters from a fished termite mound's periphery; (2) source plant presents one or more scars on its stem or branches where chimpanzees removed one or multiple parts to use as tool material; (3) scars are characterized by outer bark that has been peeled off from one end in one long, narrow strip, usually between 60 and 80 cm long and not wider than 0.5 cm; (4) scars are in specific, indicative parts of the source plant; (5) few species of plants present scars. In addition to these 5 necessary criteria, there were other 6 optional conditions to identify a plant as a tool source (Pascual-Garrido, 2018). Each identified source was given a unique number and marked with a white paint marker to avoid recording it twice during consequent visits (Almeida-Warren et al., 2017; Pascual-Garrido, 2018).

Figure 6 - Discarded artefacts and fragments at mound ITM006 at Issa. Photo credit: Alejandra Pascual-Garrido.

ii) Raw material availability

The availability of raw material was estimated for living plants growing within 5 m from the center of each targeted mound (Koops et al., 2013; Warren, 2015). Using cardinal orientations (N-S-E-W), the vicinity of the mound was divided into four quadrants numbered clockwise from the north. The northwest quadrant, IV, was arbitrarily selected for scrutiny. Recorded parameters included: number and plant species suitable to provide raw materials for tools and raw material types. Suitable plant species were defined as those from where long flexible pieces of tool material from which to manufacture termite-fishing probes could be detached by the researcher with hands or fingernails (Almeida-Warren et al., 2017).

2.3. Data analysis

I processed all data in QGIS (v. 3.10) – a free open source Geographic Information System software (Open Source Geospatial Foundation, 2019). For each studied mound, field measurements were converted to the UTM coordinate system and site maps of discarded tools and location of source plants were generated. Maps were analysed to compare the cumulative deposition of discarded artefacts and understand the site formation process. Artefacts were mapped by sessions, that correspond to monitoring visits in which tools were identified by the researchers, and serve as a proxy for Gombe’s chimpanzees' termite-fishing events. Density of tools accumulated over time was calculated by dividing the number of identified tools by mound surface area and used to estimate the intensity of site-use and reuse. To compare tool accumulation between mounds and between seasons, tools were scaled by week: for each mound, the total number of tools was divided by the length of its monitoring period in weeks.

Data in this study was determined to have a non-parametric distribution, after conducting normality tests and visual inspection. As a result, only non-parametric tests were used, with the level of significance set at $\rho < 0.05$. Chi-squared tests were done to compare proportions between groups; Wilcoxon signed-rank test (WT) was used as an alternative to paired t-test to compare means; Pairwise Wilcoxon tests with Bonferroni correction were used to compare paired groups; linear regression analysis was used to compare tool accumulation with raw material availability and tool-site size. I did all statistical analysis in R (v. 3.6.3), a free software environment for statistical computing (R Core Team, 2020).

3. Results

Mound monitoring at Gombe resulted in the identification of 346 termite-fishing tools and 136 tool source plants. Additionally, 50 termite-fishing tools were identified outside the termite-fishing season (Table 1). At Issa, 163 termite-fishing tools and 113 tool source plants were identified (Table 2). Data on the spatial distribution of tools at tool-use sites (termite mounds) were recorded, and analysis on the cumulative deposition of discarded artefacts was done, with the support of maps. Statistical analysis was conducted to test: (i) differences in tool density and accumulation of tools on time between mounds, between years, and between study sites; (ii) correlation between raw material available and accumulation of tools; and (iii) correlation between termite mound size and accumulation of tools.

Table 1 - Summary of data recorded at the seven studied mounds in Gombe.

Mound	Season 1 Tools	Season 2 Tools	Total tools FS	Tools NFS	Tool Sources
GTM008	57	12	69	18	38
GTM009	44	16	60	2	35
GTM010	24	0	24	0	0
GTM011	39	43	82	5	42
GTM012	30	39	69	0	11
GTM013	16	3	19	25	2
GTM014	20	3	23	0	8
Total	**230**	**116**	**346**	**50**	**136**

FS – Termite-fishing season totals for the two seasons; NFS – outside of termite-fishing season.

Table 2 - Summary of data recorded at the thirteen studied mounds in Issa.

Mound	Season 1 Tools	Season 2 Tools	Total Tools FS	Tool Sources
ITM003	1	0	1	0
ITM004	7	13	20	15
ITM005	13	1	14	0
ITM006	4	43	47	26
ITM007	6	16	22	1
ITM008	3	8	11	7
ITM009	0	3	3	22
ITM011	1	0	1	0
ITM012	3	1	4	0
ITM013	3	16	19	25
ITM015	0	7	7	12
ITM016	2	3	5	5
ITM017	3	6	9	0
Total	**46**	**117**	**163**	**113**

3.1. Cumulative deposition of fishing tools

3.1.1. Gombe

A total of 230 tools were recovered during the first field season (S1), with a mean number of 32.9 tools counted per mound. Comparison between mounds revealed that chimpanzees exploited some tool-use sites more often than others (Test of equal proportions (TEP): $\chi 2$ = 17.945; df = 6; p = 0.00637). Pairwise breakdown of mounds indicates that GTM013 was significantly less visited than GTM008 (p = 0.028). GTM008 was the most intensively and frequently targeted mound, with a total of 57 fishing implements (24.8%) recovered across 17 sessions, while GTM013 was the least visited tool-use site, with only 16 artefacts (7%) recovered in the 3 identified sessions (Table 3; Fig. 7).

Overall, there were no significant differences in the average number of tools per session ($\bar{x}$ = 4.2) (TEP: $\chi 2$ = 1.1418; df = 6; p = 0.9797). Though GTM008 was the mound most repeatedly used by chimpanzees, it shows the lowest number of tools recovered per session (Table 3).

Table 3 – Tools recovered per session, Gombe - S1.

Mound	Tools	% Total Tools	Sessions	% Total Sessions	Mean tools/session
GTM008	57	24.8%	17	30.9%	3.4
GTM009	44	19.1%	9	16.4%	4.9
GTM010	24	10.4%	6	10.9%	4.0
GTM011	39	17.0%	7	12.7%	5.6
GTM012	30	13.0%	8	14.5%	3.8
GTM013	16	7.0%	3	5.5%	5.3
GTM014	20	8.7%	5	9.1%	4.0
$\bar{x}$	**32.9**	**-**	**7.9**	**-**	**4.2**

At most mounds, fishing probes accumulated around the centre of its surface (Figs. 8-11, 13), except mounds GTM010 and GTM013. In the former, almost all fishing implements were found grouped on its southwest quadrant (Fig. 12). GTM010 is located in steep terrain, with one of its sides near an edge, possibly constraining the position of the tool users. At GTM013, most artifacts were also found outside the surface of the mound, to its north side (Fig. 12).

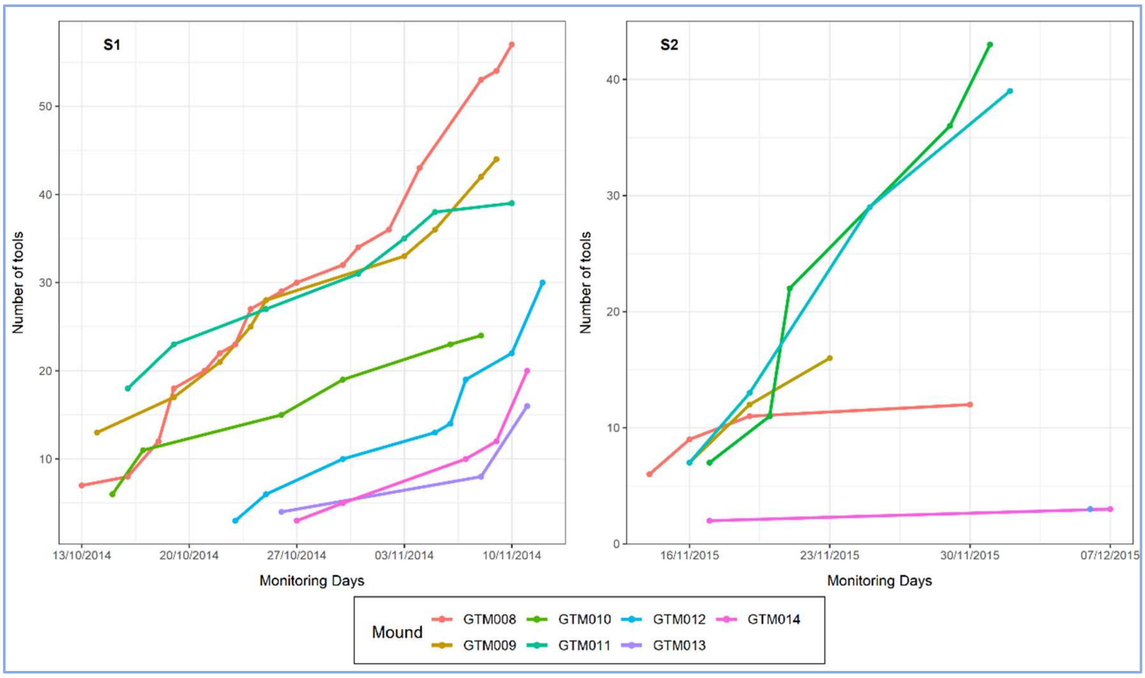

Figure 7 - Cumulative deposition of fishing tools by mound, Gombe.

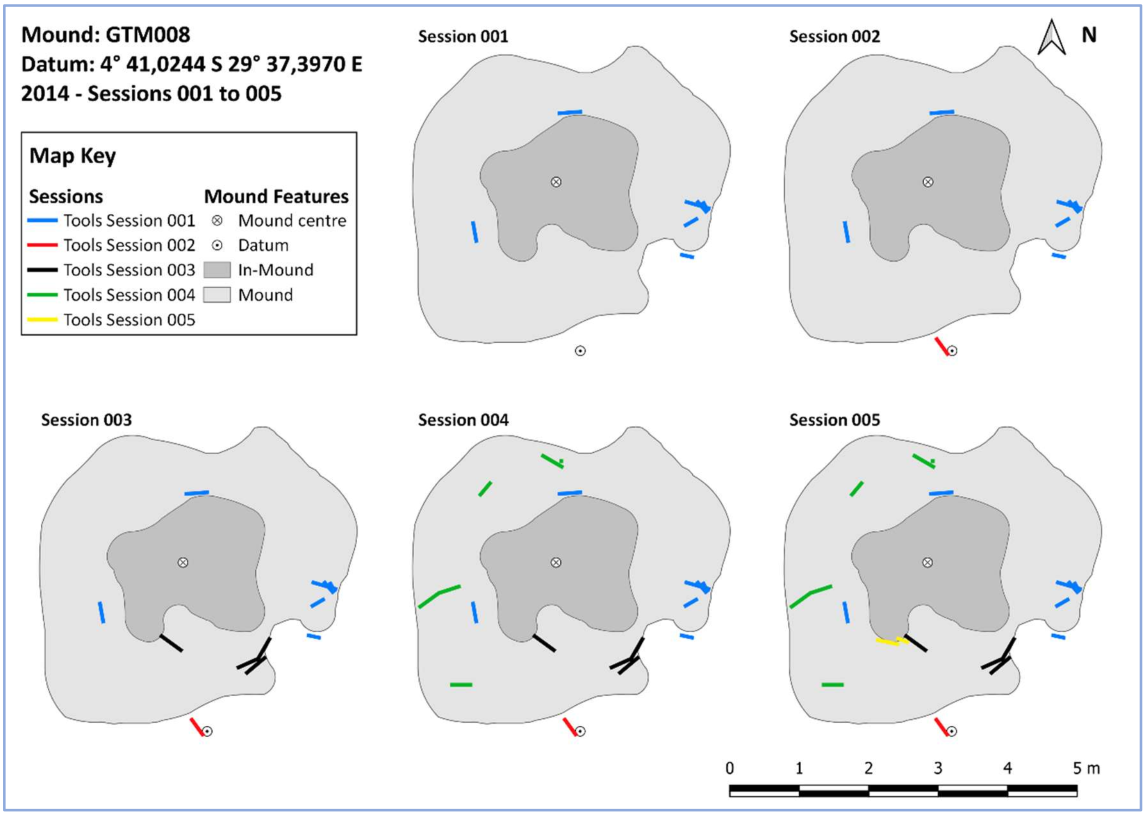

Figure 8 - Cumulative deposition of fishing tools at GTM008, sessions 001 to 005.

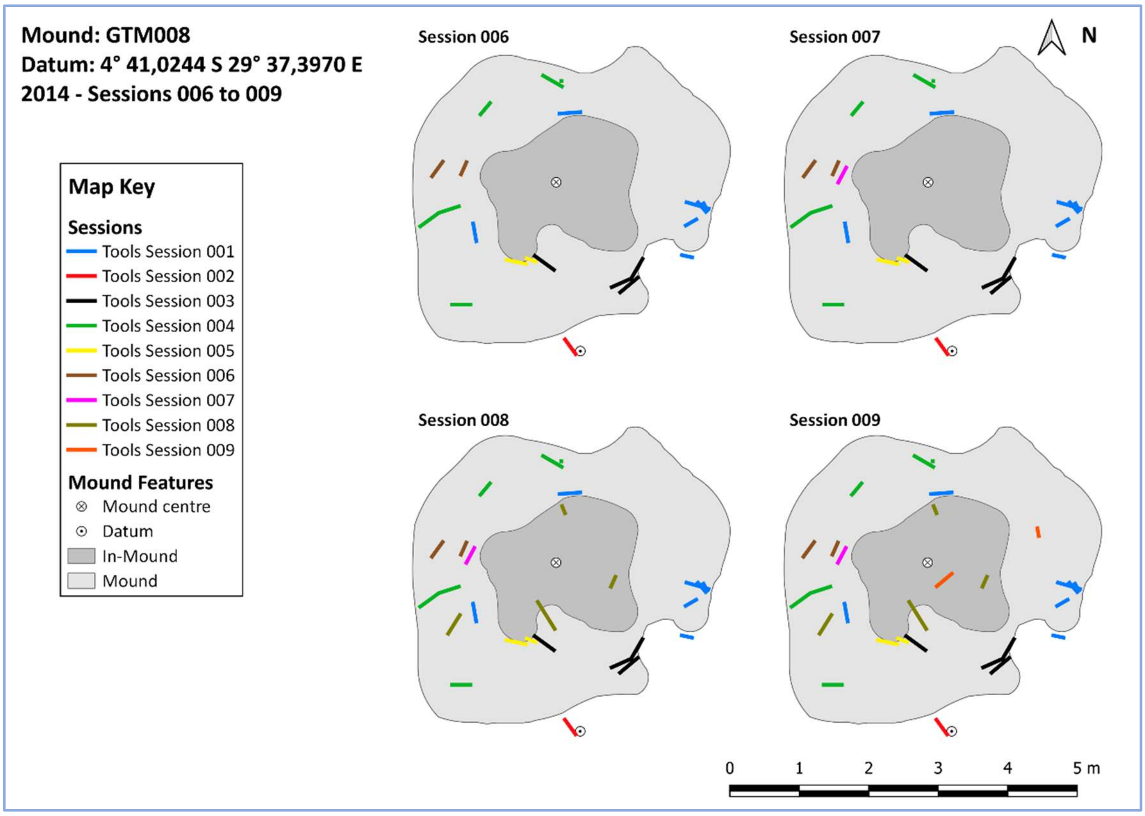

Figure 9 - Cumulative deposition of fishing tools at GTM008, sessions 006 to 009.

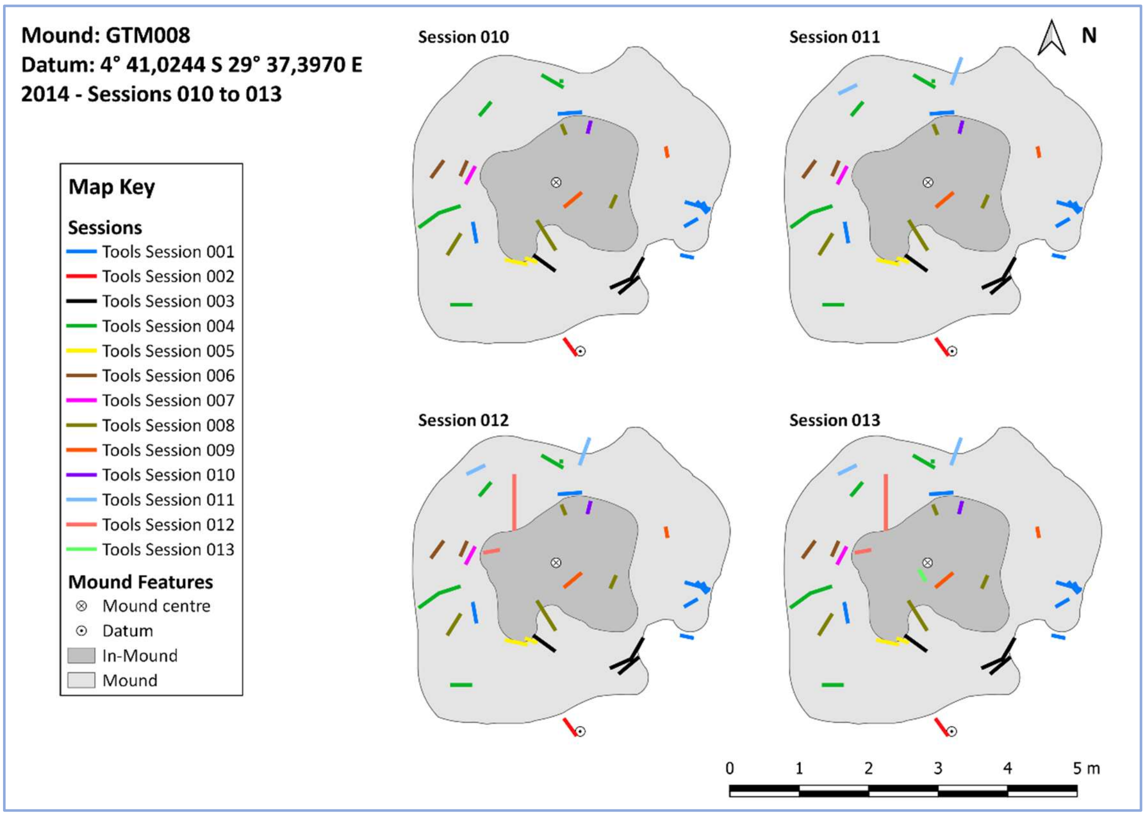

Figure 10 - Cumulative deposition of fishing tools at GTM008, sessions 010 to 013.

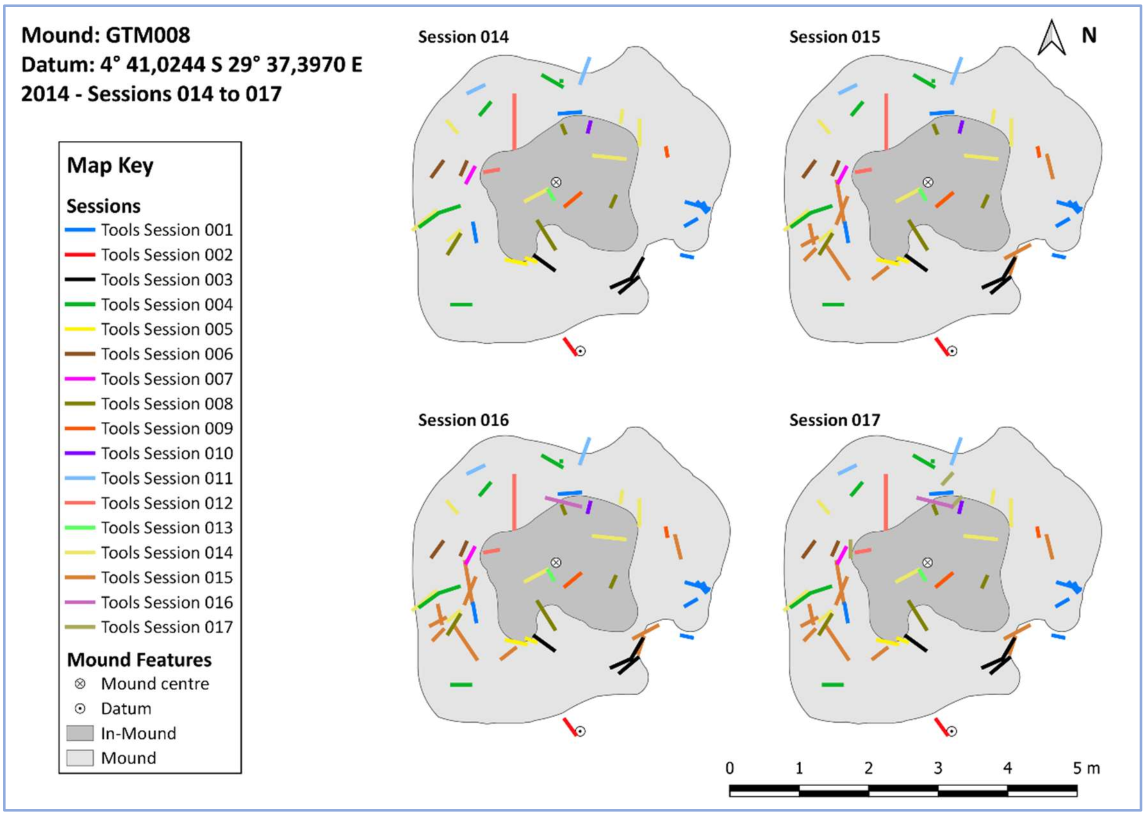

Figure 11 - Cumulative deposition of fishing tools at GTM008, sessions 014 to 017.

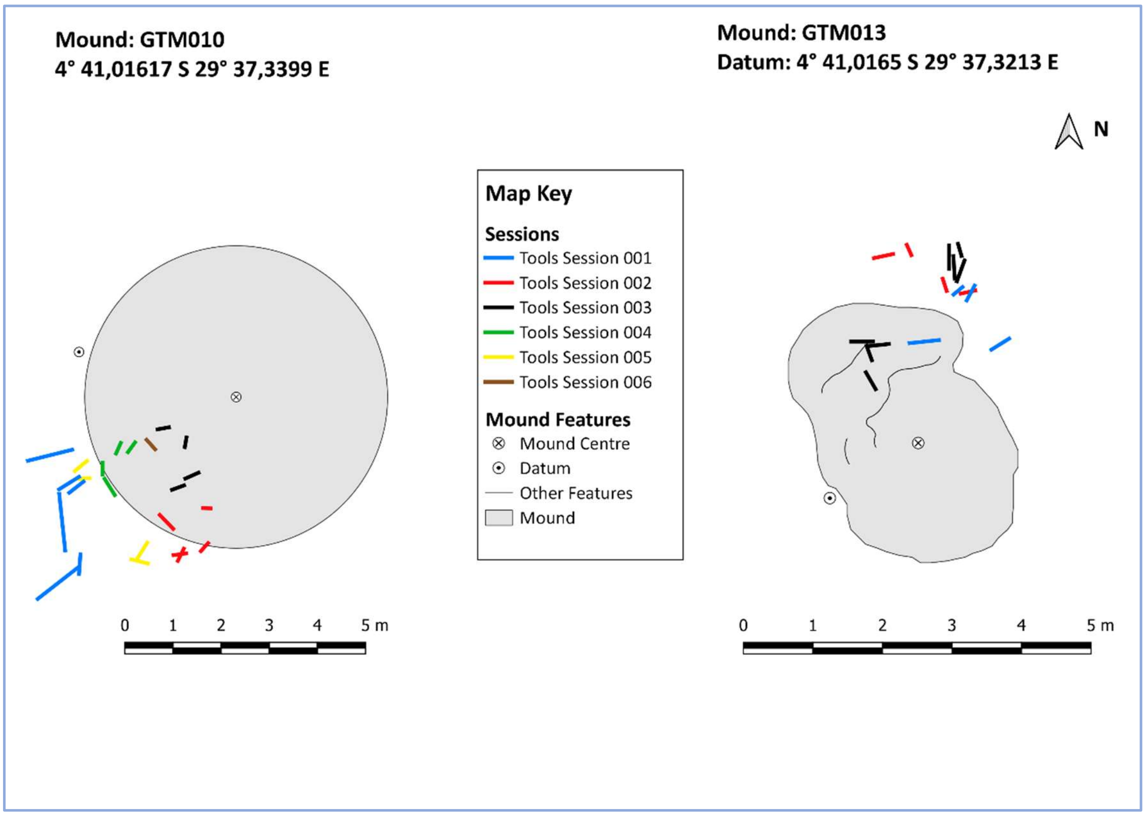

Figure 12 - Cumulative deposition of fishing tools at GTM010 and GTM013 at the end of Season 1.

During the second field season (S2), half of the total artefacts identified during the previous season (50.4%) were found, with a total of 116 artefacts identified, with a mean number of 16.6 tools per mound (Table 1, Table 4). Mounds were targeted differently: GTM011, with 43 artifacts recovered, and GTM012, with 39, were the most intensely used mounds, whereas GTM013 and GTM014, were the least targeted mounds, with a total of three fishing implements identified (Table 4; Figs. 7, 14-15).

Maps weren't produced for GTM010 and GTM013 where either no artefacts or a few artefacts were recovered. For the remaining mounds, there were no significant differences in the number of termite-fishing sessions (TEP: $\chi2$ = 1.8056; df = 4; p = 0.7715), contrary to the first season. The average number of tools discharged per session had a mean value of 6.3 (Table 4), 50% higher than in 2014, likely because monitoring visits were more evenly spaced in time. GTM012, with 9.8 tools per session was the most intensely exploited mound, while in GTM014 only 1.5 tools were identified, on average, per session (Table 4). Proportions comparison reveal significant differences in tools discharged per session (TEP: $\chi2$ = 11.056; df = 4; p = 0.02594).

Table 4 – Tools recovered per session, Gombe – S2.

Mound	Tools	% Total Tools	Sessions	% Total Sessions	Mean tools/session
GTM008	12	10.3%	4	22.2%	3.0
GTM009	16	13.8%	3	16.7%	5.3
GTM010	0	0.0%	NA	-	-
GTM011	43	37.1%	5	27.8%	8.6
GTM012	39	33.6%	4	22.2%	9.8
GTM013	3	2.6%	NA	-	-
GTM014	3	2.6%	2	11.1%	1.5
$\bar{x}$	**16.6**	**-**	**3.6**	**-**	**6.3**

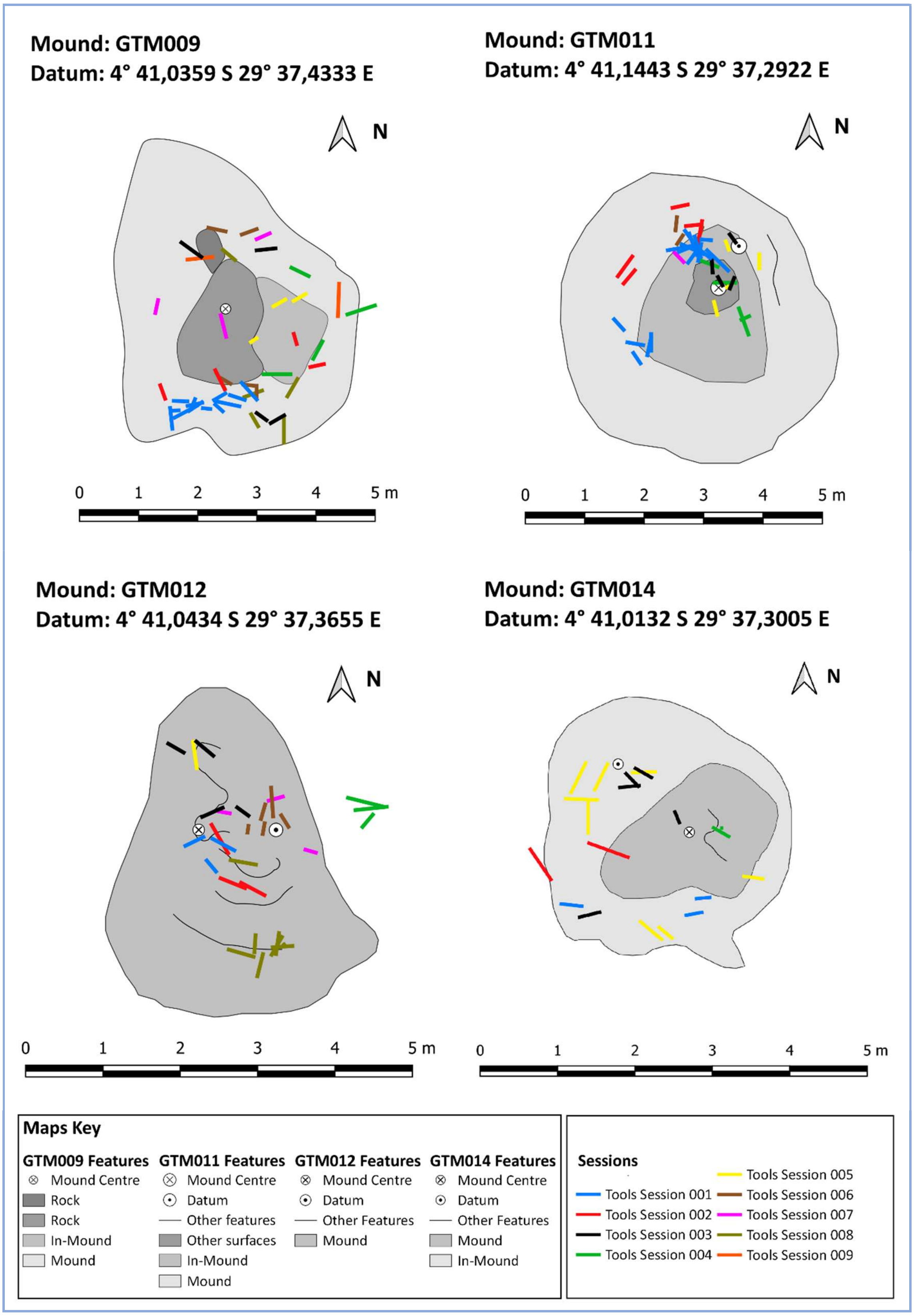

Figure 13 - Cumulative deposition of fishing tools at GTM009, GTM011, GTM012, and GTM014, at the end of Season 1.

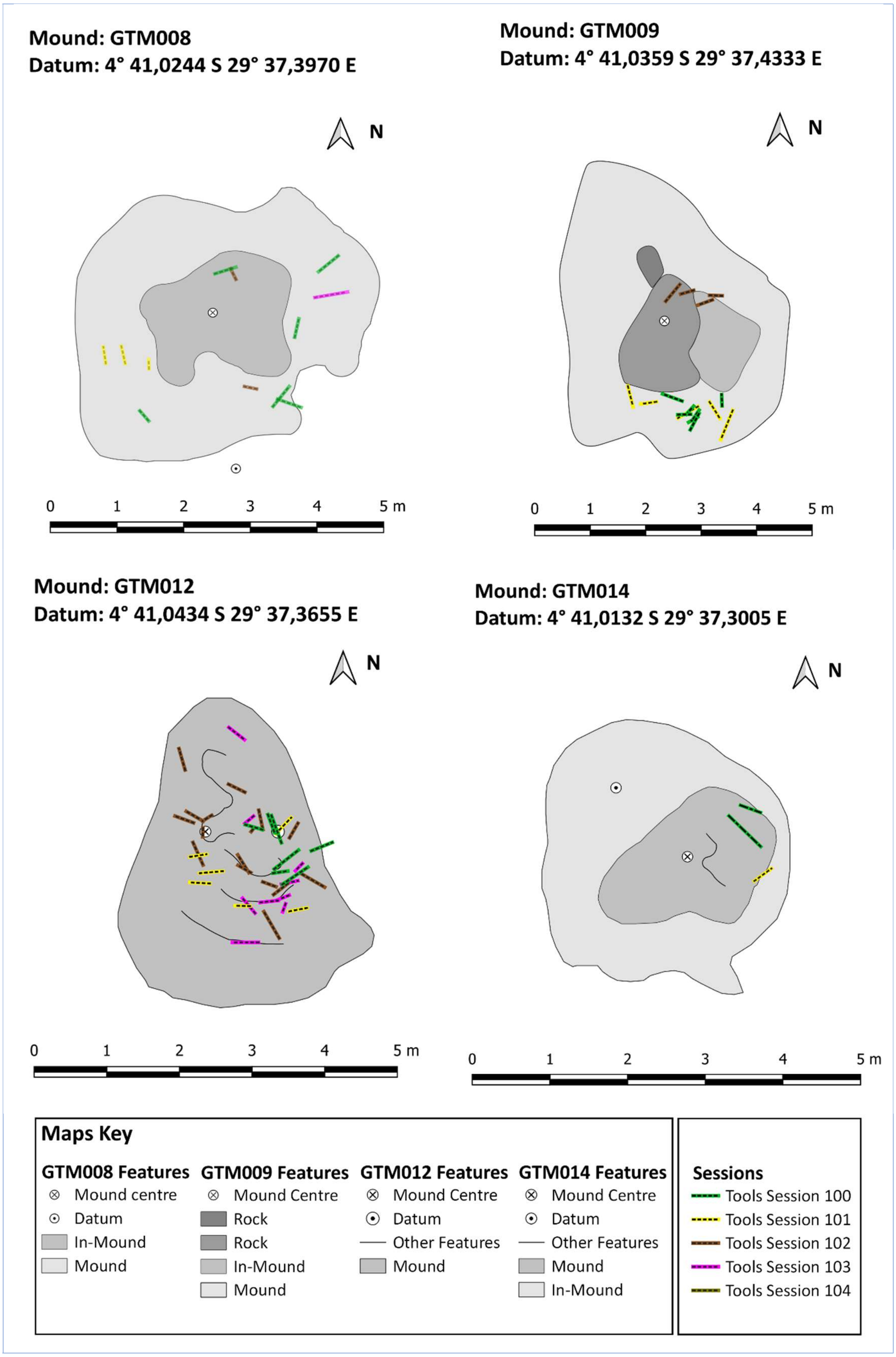

Figure 14 - Cumulative deposition of fishing tools: GTM008, GTM009, GTM012, and GTM014 at the end of Season 2.

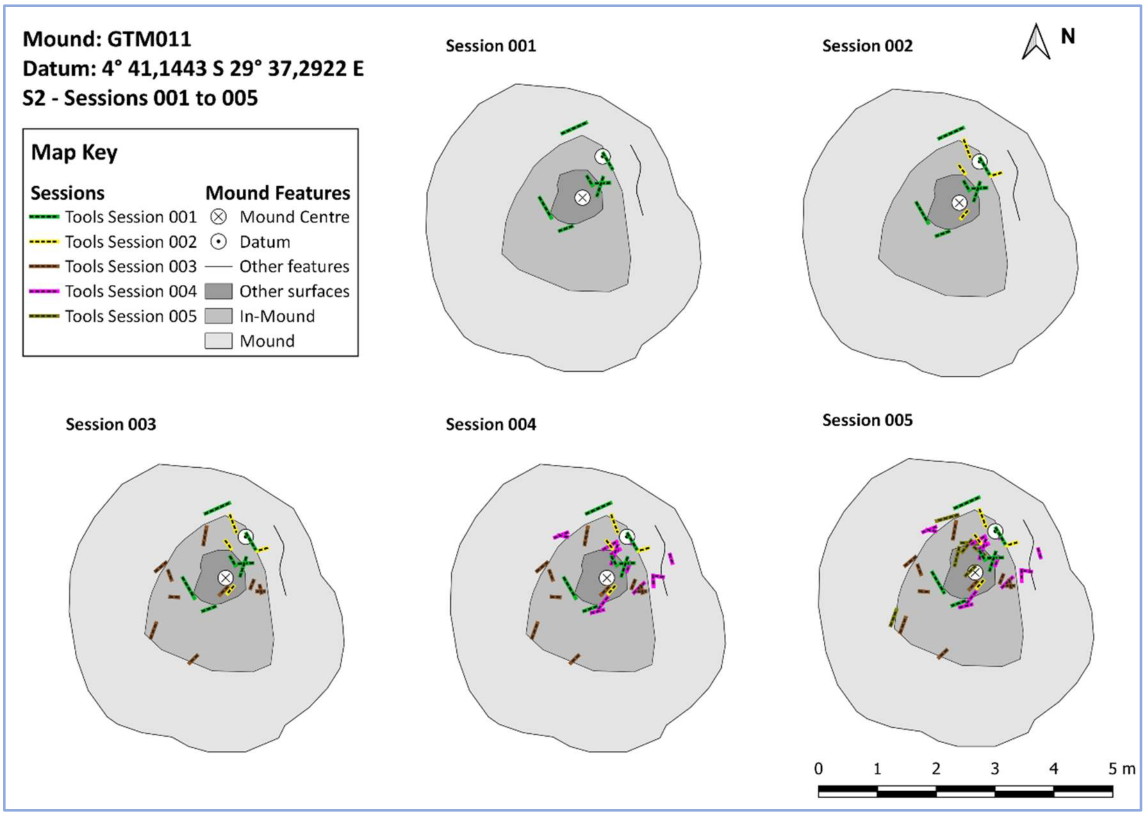

Figure 15 - Cumulative deposition of fishing tools at GTM011, sessions 001 to 005, second field season.

The monitoring that took place outside the first termite-fishing season resulted in the identification of 50 utensils (Table 1), much less than the average for the fishing seasons studied (28.9%). Gombe apes exploited only four mounds out of the eight included in this study during this period, with GTM013 accounting for 50% of the artefacts recovered. Only one session was recorded for each mound (Table 5).

Table 5 – Tools recovered per session, outside the termite-fishing season at Gombe.

Mound	Tools	% Total Tools	Sessions	% Total Sessions	Mean tools/session
GTM008	18	36.0%	1	25.0%	18
GTM009	2	4.0%	1	25.0%	2
GTM011	5	10.0%	1	25.0%	5
GTM013	25	50.0%	1	25.0%	25
$\bar{x}$	**7.1**	**-**	**1**	**-**	**7.1**

3.1.2. Issa

A total of 46 tools were identified during the first field season (Table 2), with a mean number of 3.5 tools per mound. ITM005 yielded the largest number of tools, with a total of 13 artefacts recovered, almost a third of the total number of tools recorded for this season (Table 6). It was also the most frequented mound by Issa's apes, with tools being recovered in five different monitoring visits, five times more than the other mounds in which tools were found (Figs. 16, 17). Although ITM005 was more frequently exploited, comparison between mounds yielded no significant difference in proportions (TEP: $\chi 2$ = 11.733; df = 10; p = 0.3033).

On average, 3.1 artefacts were recovered per session, with the highest number corresponding to ITM004, in which seven tools were recovered in the only identified session (Table 6). Overall, there were no significant differences in the number of tools recovered across mounds (TEP: $\chi 2$ = 11.742; df = 10; p = 0.3027).

Table 6 - Tools per session, S1 - Issa.

Mound	Tools	% Total Tools	Sessions	% Total Sessions	Mean Tools/Session
ITM003	1	2.2%	1	6.7%	1
ITM004	7	15.2%	1	6.7%	7
ITM005	13	28.3%	5	33.3%	2.6
ITM006	4	8.7%	1	6.7%	4
ITM007	6	13.0%	1	6.7%	6
ITM008	3	6.5%	1	6.7%	3
ITM009	0	0.0%	0	0.0%	NA
ITM011	1	2.2%	1	6.7%	1
ITM012	3	6.5%	1	6.7%	3
ITM013	3	6.5%	1	6.7%	3
ITM015	0	0.0%	0	0.0%	NA
ITM016	2	4.3%	1	6.7%	2
ITM017	3	6.5%	1	6.7%	3
$\bar{x}$	**3.5**	**-**	**1.2**	**-**	**3.1**

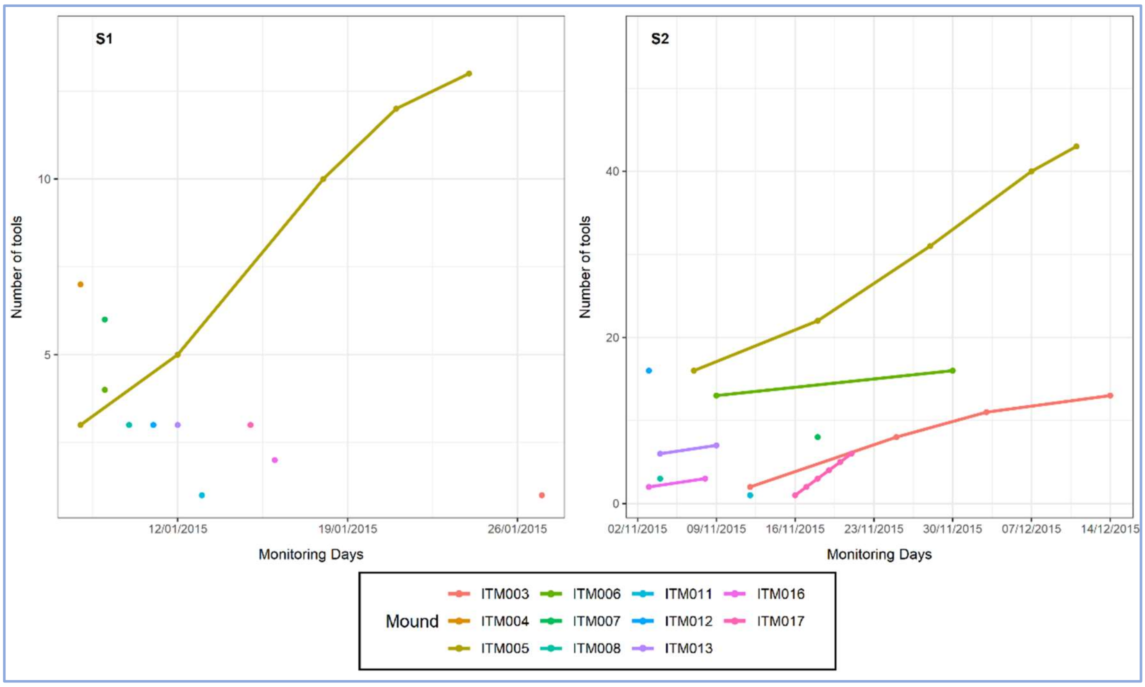

Figure 16 - Cumulative deposition of fishing tools by mound - Issa.

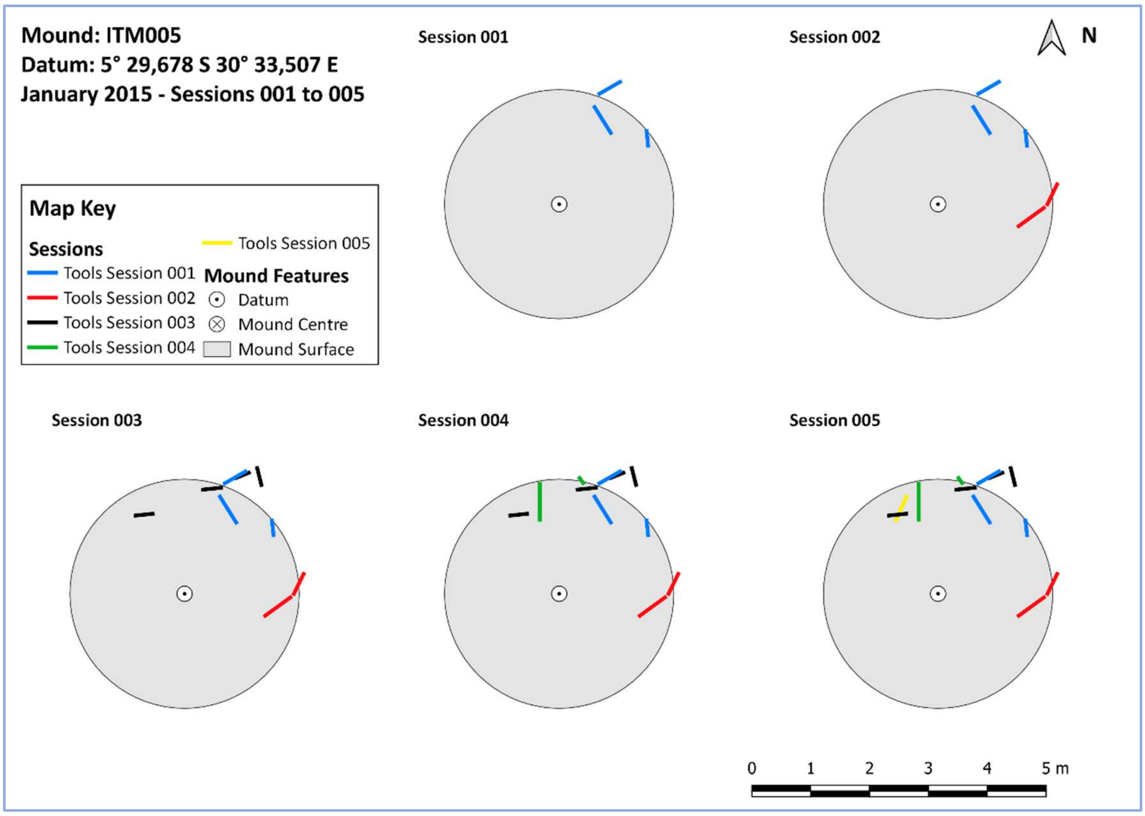

Figure 17 - Cumulative deposition of fishing tools at ITM005, sessions 001 to 005, first field season.

During the second field season, a total of 117 artefacts were identified (Table 2), more than double the number identified in the previous season. ITM006 was the most targeted mound, with a total of 43 artefacts (39%) recovered during five sessions (Fig. 18), a tenfold increase when compared to the previous season. Mounds ITM005 and ITM012, with only one tool (0.9%) recovered, were the least intensively used (no fishing probes were identified in mounds ITM003 and ITM011). The mean number of tools per mound was 9.0, 2.5 times higher than in the first field season (Table 7).

There were no significant differences in the number of termite fishing sessions in this season, as had happened in the previous one (TEP: $\chi 2 = 15.146$; $df = 10$; $p = 0.1268$). The average number of tools discharged per session had a mean value of 4.5 (Table 7), 47% higher than in the first season. Comparing the proportion across tool-use sites reveals significant differences for this season (TEP: $\chi 2 = 48.868$; $df = 10$; $p = 4.307e\text{-}07$). Looking at mounds individually, the number of tools per session was significantly higher in ITM013 (16 tools in one session) than in ITM005 (1/1), ITM012 (1/1), ITM016 (3/2) and ITM017 (6/6) ($p = 0.12$, $p = 0.12$, $p = 0.22$, $p = 0.12$). Figure 16 shows the accumulation of tools over this field season.

Table 7 - Tools per session, season 2 at Issa.

Mound	Tools	% Total Tools	Sessions	% Total Sessions	Mean Tools/Session
ITM003	0	0.0%	0	0.0%	-
ITM004	13	11.1%	4	15.4%	3.3
ITM005	1	0.9%	1	3.8%	1
ITM006	43	36.8%	5	19.2%	8.6
ITM007	16	13.7%	2	7.7%	8
ITM008	8	6.8%	1	3.8%	8
ITM009	3	2.6%	1	3.8%	3
ITM011	0	0.0%	0	0.0%	-
ITM012	1	0.9%	1	3.8%	1
ITM013	16	13.7%	1	3.8%	16
ITM015	7	6.0%	2	7.7%	3.5
ITM016	3	2.6%	2	7.7%	1.5
ITM017	6	5.1%	6	23.1%	1
$\bar{x}$	**9.0**	**-**	**2.0**	**-**	**4.5**

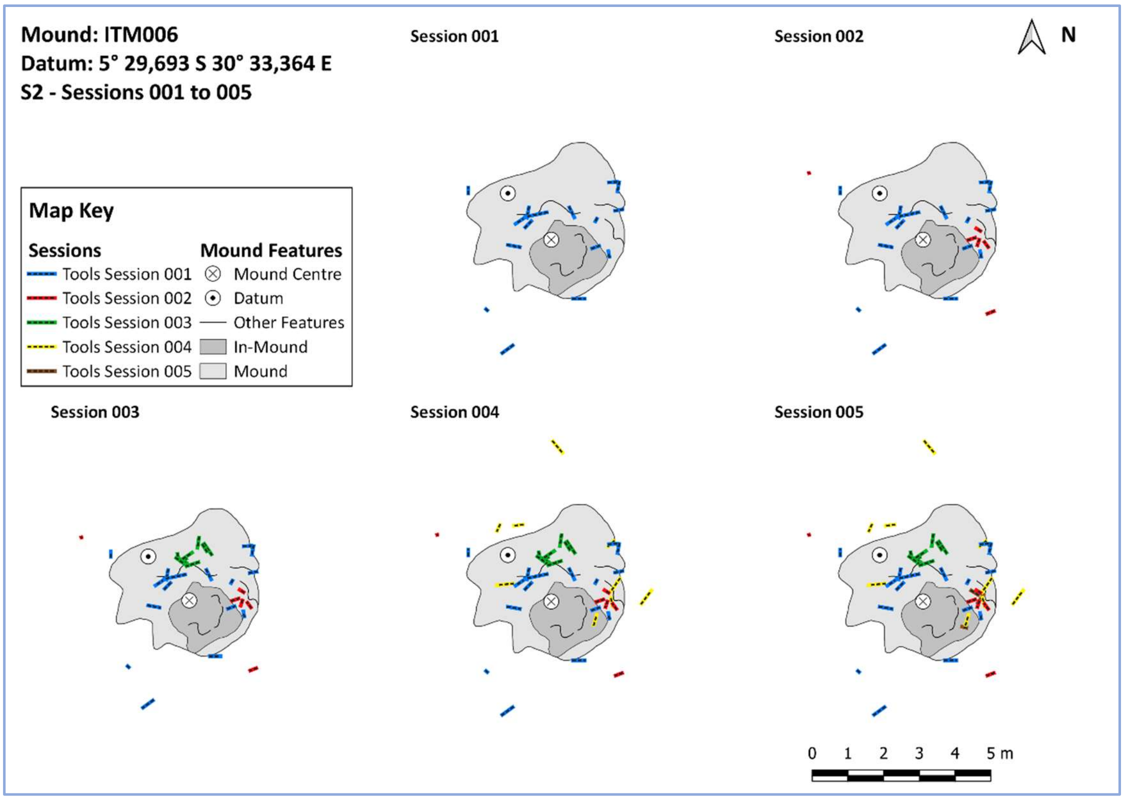

Figure 18 - Cumulative deposition of fishing tools at ITM006, sessions 001 to 005, second field season.

3.2. Tool density at chimpanzee tool use sites

To estimate the density of tools discharged at tool-use sites, the number of tools was scaled by the mound surface area. This allows for direct comparisons between mounds, as well as comparisons with tool densities reported for other primates that engage regularly in stone tool-use, including humans.

3.2.1. Gombe

The estimated density of tools per square meter ranged from 1.07 tools/m^2 (GTM013) to 3.52 tools/m^2 (GTM012), with a mean density of 2.11 tools/m^2 (Table 8). While the total number of fishing implements was generally higher in larger mounds, when areas were taken into account, comparison between mounds didn't yield significant differences (TEP: $\chi 2$ = 2.2539; df = 5; p = 0.813). As the surface of mound GTM010 was not mapped, it was excluded from this analysis.

Table 8 - Surface areas and tool density values, by mound and by season - Gombe.

Mound	Surface (m2)	Tools/m2 S1	Tools/m2 S2	Mean Tools/m2
GTM008	14.82	3.85	0.81	2.33
GTM009	16.48	2.67	0.97	1.82
GTM011	17.65	2.21	2.44	2.32
GTM012	9.79	3.06	3.98	3.52
GTM013	8.91	1.80	0.34	1.07
GTM014	8.80	2.27	0.34	1.31
$\bar{x}$	**12.74**	**2.69**	**1.52**	**2.11**

When comparing the two field seasons, tool density was higher for S1 (2.69) than for S2 (1.52) (Table 8). Although a non-significant difference was found (WPT: W = 2.2539; p = 0.07813), it may still indicate that there might be variation in the use of sites across years. Looking at mounds individually (Fig. 19), there is a decline in tool density for every mound except for mounds GTM011 and GTM012, where intensity of tool-use increased slightly (2.21 to 2.44; 3.06 to 3.98).

Figure 19 - Comparison between tool densities of the two field seasons, by mound - Gombe.

3.2.2. Issa

For those mounds in which surfaces were mapped, the density of artefacts per square meter was estimated, ranging from 0.04 tools/m^2 (ITM015) to 1.85 tools/m^2 (ITM006), and a mean density of 0.64 tools/m^2 (Table 9). Contrary to Gombe, the total number of tools recovered at Issa was generally lower in larger mounds, with no significant differences in the number of tools found between mounds (TEP: $\chi 2$ = 4.3991; df = 4; p = 0.3547).

Table 9 - Surface areas and tool density values, by mound and by season - Issa.

Mound	Surface (m2)	Tools/m2 Season 1	Tools/m2 Season 2	Mean Tools/m2
ITM004	11.62	0.60	1.12	0.86
ITM006	13.25	0.30	3.25	1.85
ITM009	12.84	0.00	0.23	0.12
ITM013	29.66	0.10	0.54	0.32
ITM015	80.36	0.00	0.09	0.04
$\bar{x}$	29.55	0.20	1.04	0.64

When comparing between seasons, tool density was higher for S2, although no significant difference was found (WPT: W = 0; p = 0.0625; Table 4). When analysing mounds individually (Fig. 20), there was an increase in tool density from season 1 to season 2 in every single mound.

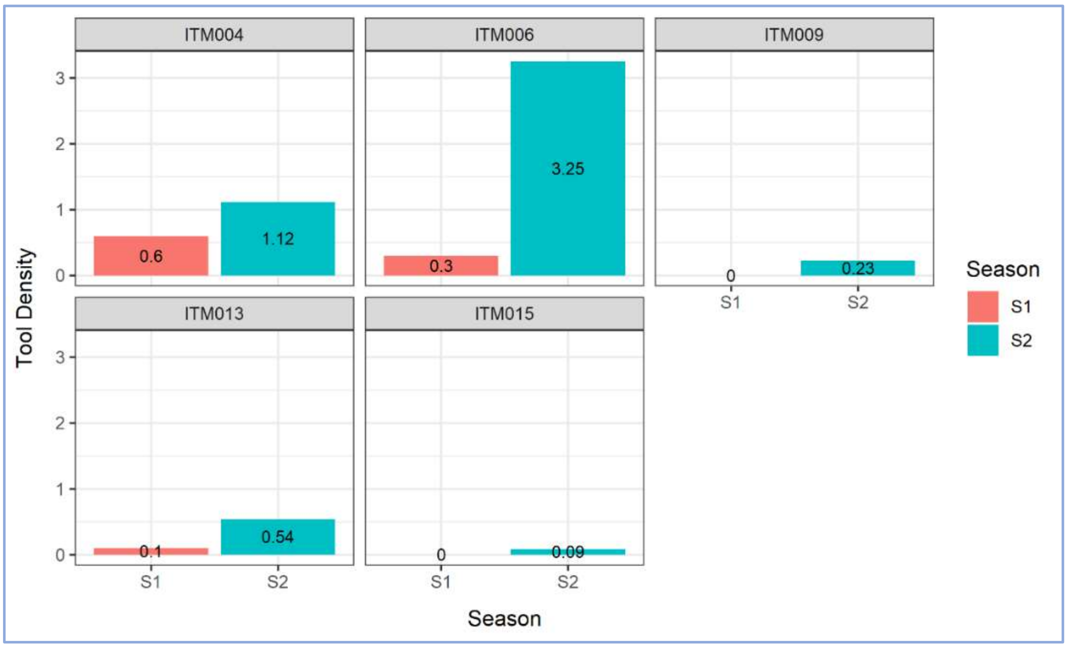

Figure 20 - Comparison between tool densities of the two field seasons, by mound – Issa.

3.2.3 Comparison between study sites

Over the two field seasons, the mean density of tools at Gombe was 2.11 tools/ m^2, whereas at Issa this was lower, with 0.64 tools/m^2 (Fig. 21), revealing significant differences between the two (Mann-Whitney U Test (MWT): $W = 27$; $p = 0.0303$). This could indicate that termite mounds at Gombe are more intensely exploited by chimpanzees than at Issa.

As the first field season at Issa took place at the end of the termite-fishing season, a comparison was made between the second season densities of the two sites (Gombe = 1.52 tools/m^2; Issa = 1.04 tools/m^2). Issa mounds still seem to be used less intensively (Fig. 22), though no significant differences were found (MWT: $W = 19$; $p = 0.5219$).

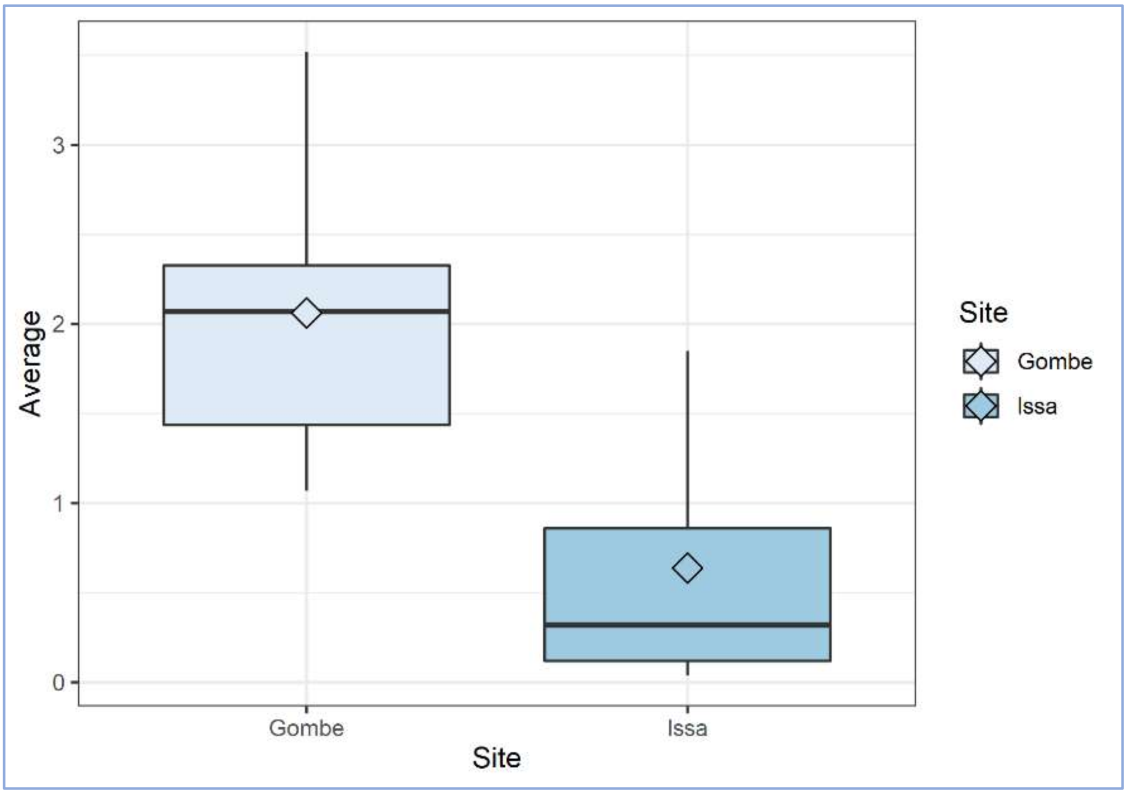

Figure 21 - Tool densities at Gombe and Issa, two-season mean. Boxplots indicate upper and lower quartile with median as thicker horizontal line, and arithmetic mean as diamonds. Whiskers indicate maximum and minimum data range (excluding outliers). Dots show individual outliers.

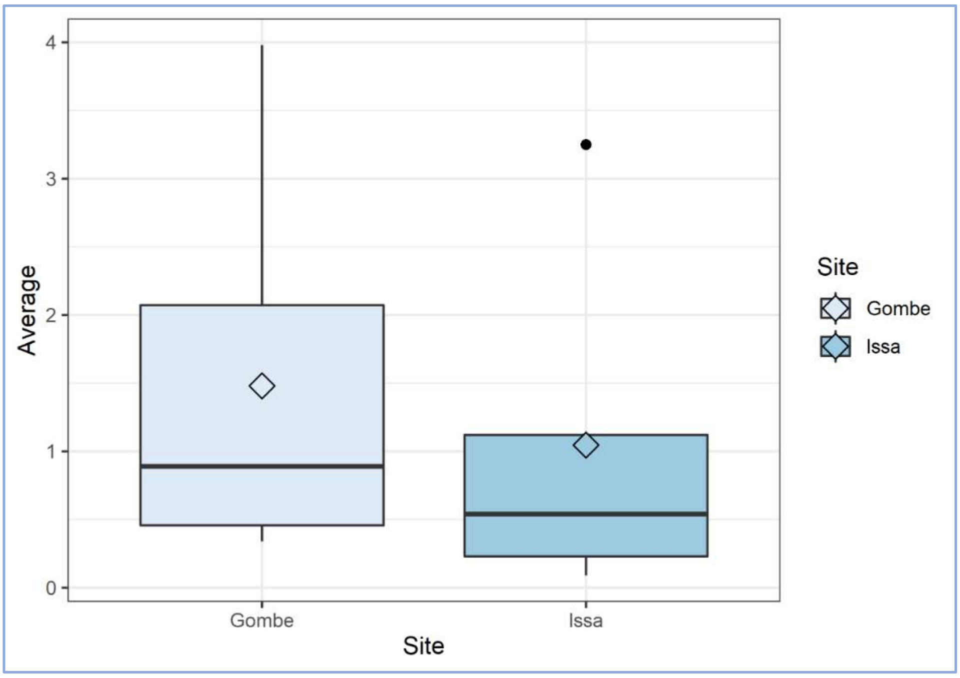

Figure 22 - Tool densities at Gombe and Issa, Season 2 means. Boxplots indicate upper and lower quartile with median as thicker horizontal line, and arithmetic mean as diamonds. Whiskers indicate maximum and minimum data range (excluding outliers). Dots show individual outliers.

3.3. Differences in tool accumulation between mounds

3.3.1. Gombe

As the monitoring periods differed between mounds and seasons, the number of recovered tools per mound was scaled by week. Due to the small number of artefacts recovered at mounds GTM010 and GTM013 during 2015, these mounds were only included in the analysis for the 2014 season and the non-fishing season periods.

Mound GTM011 had the highest rate of utensils accumulated of all studied mounds, with a mean of 11.2 tools per week and a total of 82 tools identified during both seasons. The same number of fishing implements were recovered during the two field seasons in GTM008 and GTM012 (n = 69), but when adjusted to the monitoring period, the weekly accumulation rate at GTM012 was higher than at GTM008 ($\bar{x}$ = 10.3 vs $\bar{x}$ = 7.8). The least targeted mound was GTM014 ($\bar{x}$ = 3.8) (Fig. 23). The overall mean of tools recovered for the two seasons was 8.13 tools/week. The number of artefacts recovered per mound shows that there were no significant differences between tool-use sites (TEP: $\chi 2$ = 5.1291; df = 4 p = 0.2743).

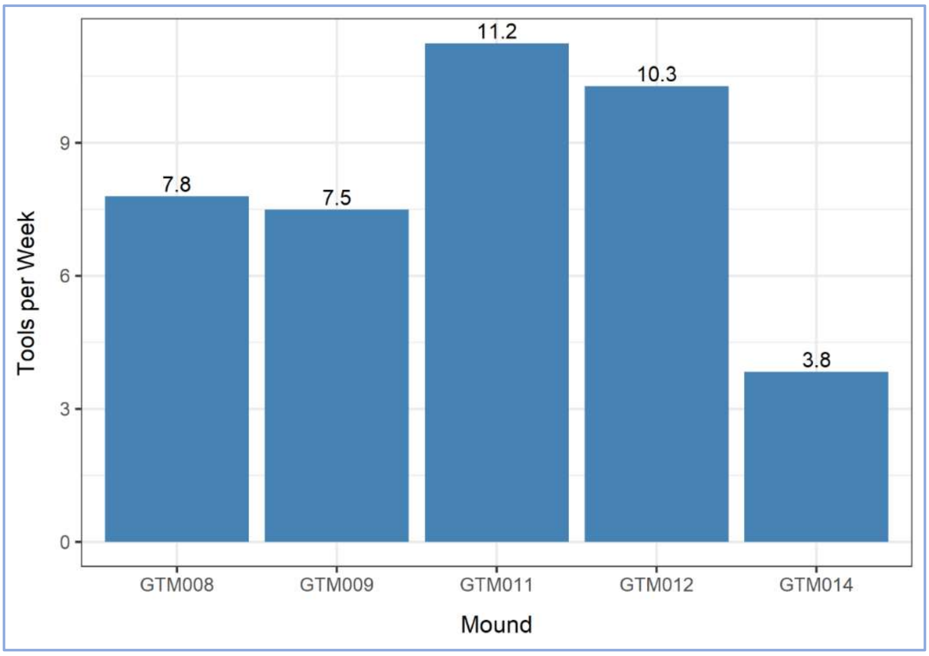

Figure 23 - Mean tools per week of the two field seasons, by mound – Gombe.

Tools identified in the 2014 season, when scaled by week, ranged from 6.22 (GTM014) to 12.87 (GTM008) (Fig. 24), with a mean accumulation across mounds of 9.31 tools per week. However, proportion comparisons revealed that these differences in accumulation were non-significant (TEP: $\chi 2$ = 4.1018; df = 6; p = 0.6629), as was the case when looking to the means of the two seasons.

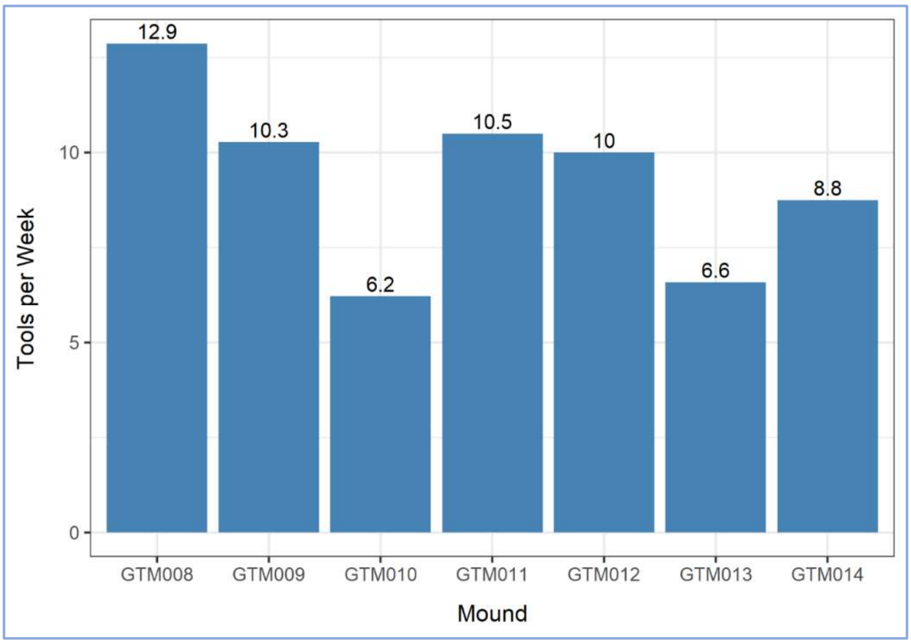

Figure 24 - Tools per week, first field season, by mound - Gombe.

Differences in accumulation between mounds were higher for the 2015 field season with only three fishing probes identified in mound GTM014 (0.81 tools per week), as opposed to 43 and 39 in GTM011 and GTM012, respectively (12.04 and 10.5 tools/week) (Fig. 25), with mean accumulation across mounds of 6.07 tools/week. Proportion analysis revealed that there were significant differences in tool accumulation between mounds in 2015 (TEP: $\chi 2$ = 20.028; df = 4; p = 0.004931). Comparing between individual mounds, the analysis revealed that the accumulation of tools in mound GTM014 was significantly lower than in mound GTM011 (p = 0.013) and mound GTM012 (p = 0.042), which suggests that there might have been specific factors influencing the intensity of some tool-use sites in the 2015 season. If GTM010 and GTM013 were included in this comparison, differences between mounds would likely be even more significant, as tools identified in these mounds in 2015 amounted to, respectively, 0 and 3.

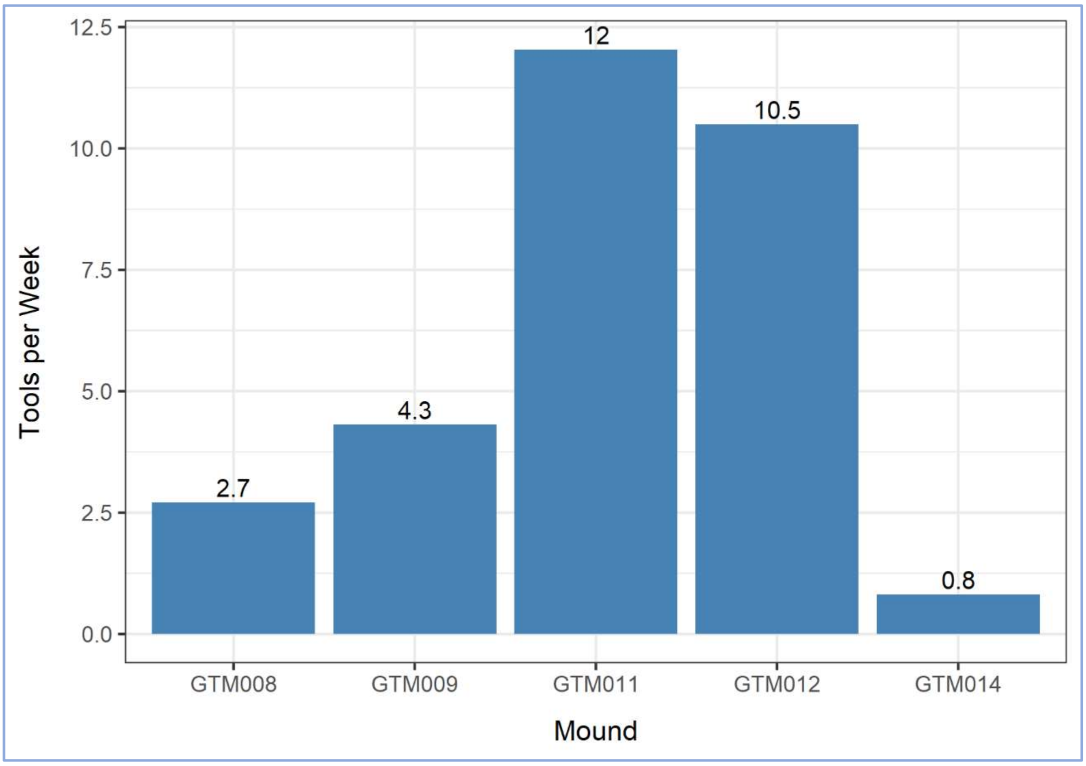

Figure 25 - Tools per week, second field season, by mound – Gombe.

Outside of the termite-fishing season, the mean rate of tool accumulation across the seven studied mounds was 2.39 tools/week (Table 10). No tools were identified in GTM010, GTM012, and GTM014; in mounds GTM009 and GTM011, artefacts were identified at a low rate of 0.6

and 1.4 tools/week, respectively. On the other hand, mounds GTM008 and GTM013 showed rates of 7.3 and 7.4 tools/week (Fig. 26). In the latter, this value is higher than the rate of accumulation for the 2014 rainy season. As expected, when proportions are compared, the differences are significant (TEP: χ2 = 34.34; df = 6; p < 0.0001), reflecting the sporadic nature of chimpanzee's termite-fishing events outside of the rainy season at Gombe.

Table 10 - Comparison of mean Tools/week between non-fishing season and fishing season - Gombe.

Mound	Tools/Week S1	Tools/Week S2	Mean Tools/Week FS	Tools/Week NFS
GTM008	12.87	2.71	7.79	7.41
GTM009	10.27	4.31	7.50	0.64
GTM010	6.22	NA	6.22	0.00
GTM011	10.50	12.04	11.25	1.40
GTM012	10.00	10.50	10.28	0.00
GTM013	6.59	NA	6.59	7.29
GTM014	8.75	0.81	3.83	0.00
$\bar{x}$	9.31	6.07	7.64	2.39
$\bar{x}$ (excluding GTM010/13)	10.48	-	-	-

FS – field seasons during the termite-fishing season
NFS – field season of April/May 2015, outside of the termite-fishing season

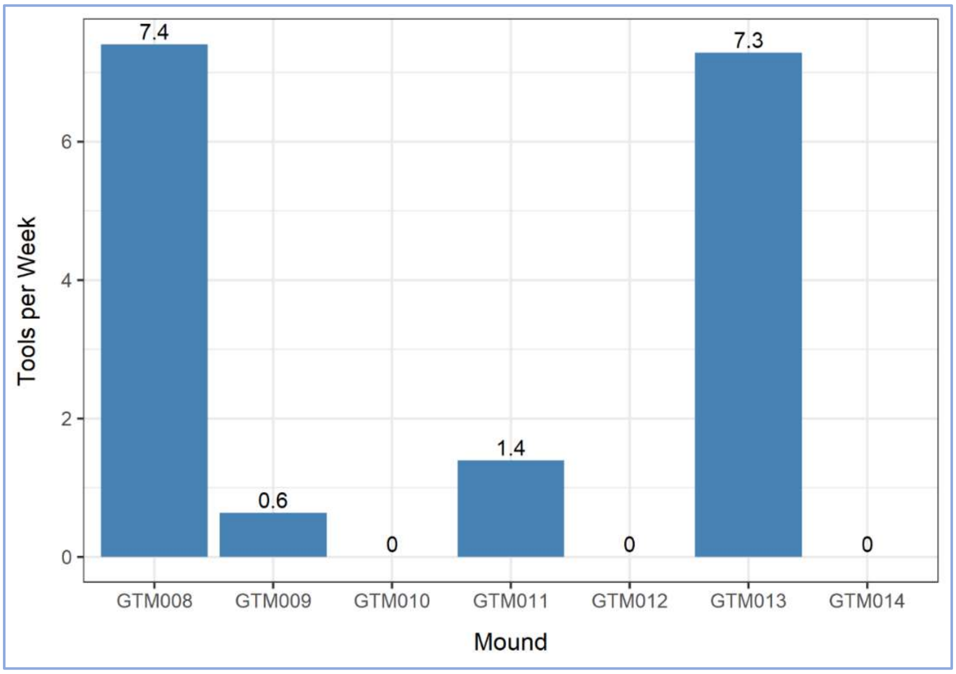

Figure 26 - Tools per week, field season April/May 2015, by mound – Gombe.

3.3.2. Issa

Mounds ITM003, ITM011, and ITM012 were only included in the analysis of the first season, as there was only one monitoring visit during the second field season. Likewise, ITM017 was only included in the analysis of the first season, as the monitoring period for the second season is unknown.

Mound ITM006, with 47 artefacts identified during the two field seasons, shows the highest rate of accumulation of all studied mounds, with a mean of 4.8 tools per week over the two seasons. The least targeted mound was ITM009 ($\bar{x}$ = 0.4) (Fig. 27). The overall mean of the two seasons was 1.57 tools/week (Table 11). When proportions between mounds are compared, there aren't significant differences in the rate of tool accumulation (TEP: $\chi 2$ = 9.0311; df = 8 p = 0.3397).

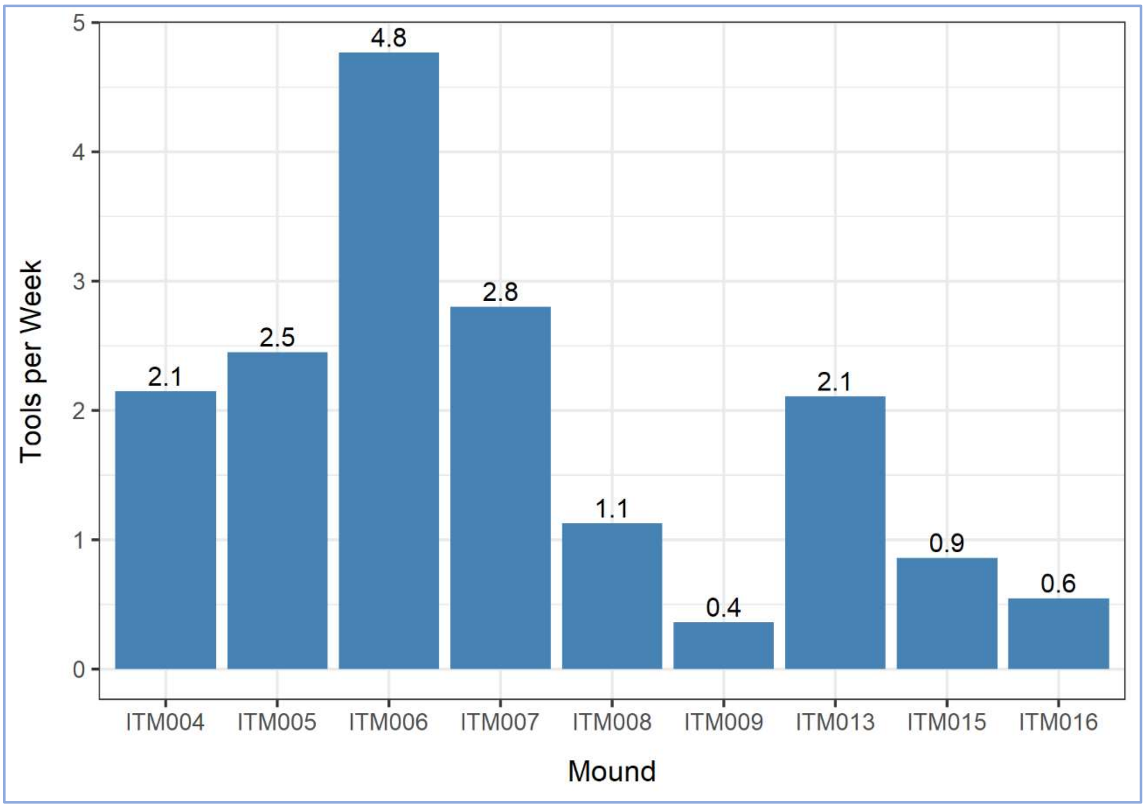

Figure 27 - Mean tools per week of the two field seasons, by mound – Issa.

In the first field season, no tools were recorded in mounds ITM009 and ITM015. For the other mounds, tools identified, when scaled by week, ranged from 0.26 (ITM003) to 3.14 (ITM015) (Fig. 28), with a mean rate of accumulation across mounds of 0.96 tools per week (Table 11). However, proportion comparisons revealed that these differences in tool accumulation were non-significant (TEP: $\chi 2$ = 10.004; df = 12; p = 0.6156), as was the case when looking to the means of the two seasons.

The number of artefacts identified in the second field season, when scaled by week, ranged from 0.50 (ITM016) to 7.53 (ITM006) (Fig. 29), with mean accumulation across mounds of 2.35 tools per week (Table 11). Proportion analysis revealed that there were significant differences in tool accumulation between mounds in this season (TEP: $\chi 2$ = 19.207; df = 8; p = 0.01379), which suggests that there might have been specific factors influencing the intensity of some tool use sites in the second field season.

Table 11 - Comparison of mean Tools/week between seasons – Issa.

Mound	Tools/Week S1	Tools/Week S2	Mean Tools/Week
ITM003	0.26	0.00	0.25
ITM004	1.69	2.53	2.15
ITM005	3.14	0.64	2.45
ITM006	0.97	7.53	4.77
ITM007	1.75	3.61	2.80
ITM008	0.78	1.37	1.13
ITM009	0.00	0.60	0.36
ITM011	0.32	0.00	0.30
ITM012	0.88	7.00	1.12
ITM013	0.84	2.95	2.11
ITM015	0.00	1.40	0.86
ITM016	0.64	0.50	0.55
ITM017	1.24	NA	NA
$\bar{x}$	0.96	2.34	1.57
$\bar{x}$ (excluding ITM003/011/012/017)	-	2.35	1.91

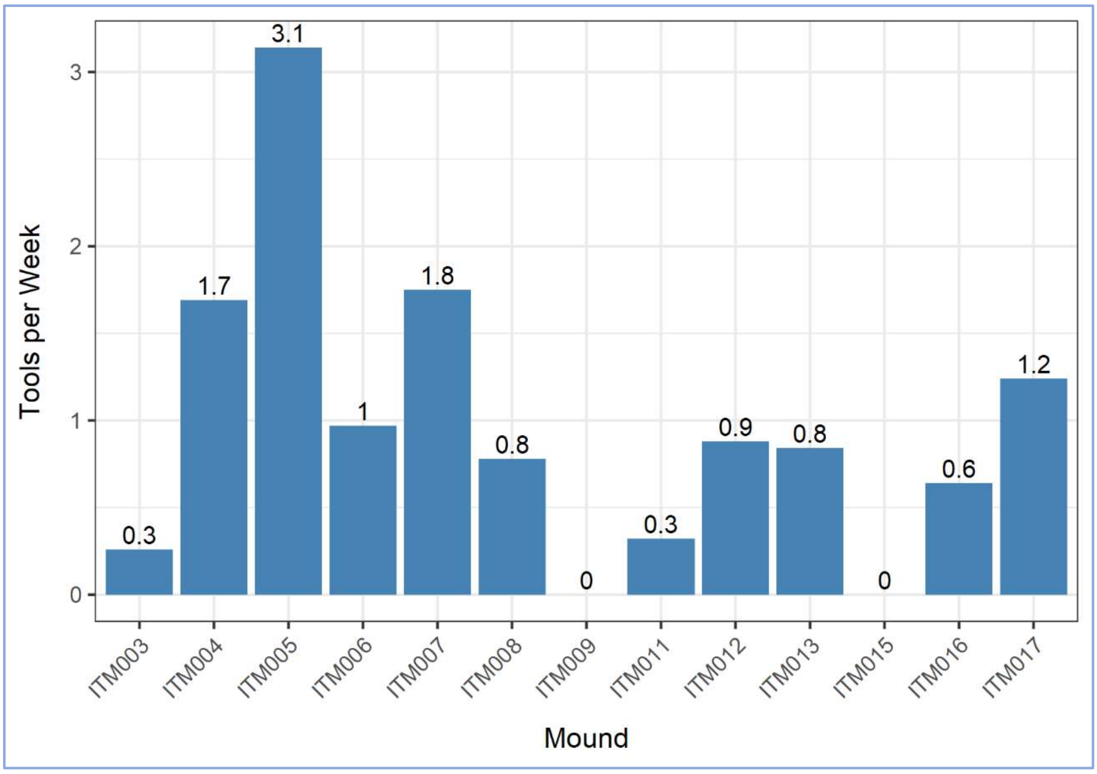

Figure 28 – Tools per week, first field season, by mound - Issa.

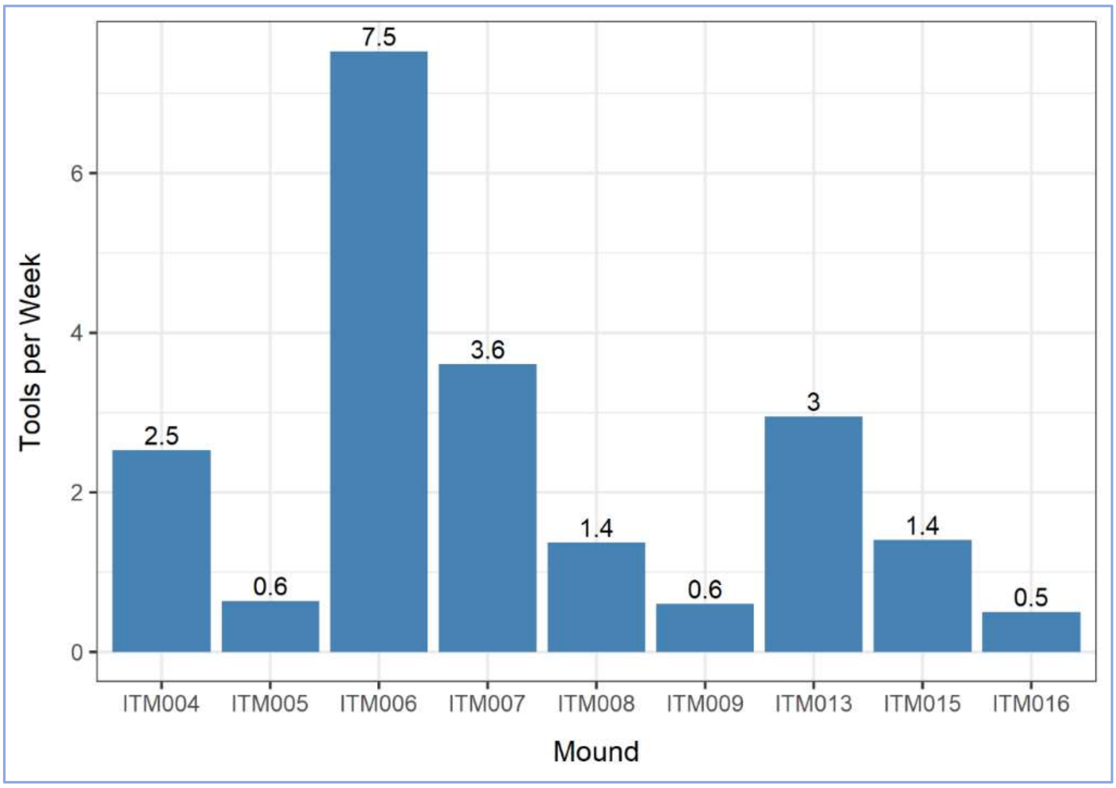

Figure 29 - Tools per week, second field season, by mound – Issa.

3.4. Differences in tool accumulation between seasons

3.4.1. Gombe

To allow for direct comparisons between seasons, identified tools were scaled by week, as described in the previous section. Mounds GTM010 and GTM013 were excluded from this analysis, as the length of the monitoring period is not available for the second season.

a) Differences in tool accumulation between field seasons

The first field season shows a mean tool accumulation rate per mound of 10.48 tools per week, compared with 6.07 tools per week for the second season (Table 10; Fig. 30), a non-significant difference (Wilcoxon signed-rank test (WT): W = 12, p = 0.1562).

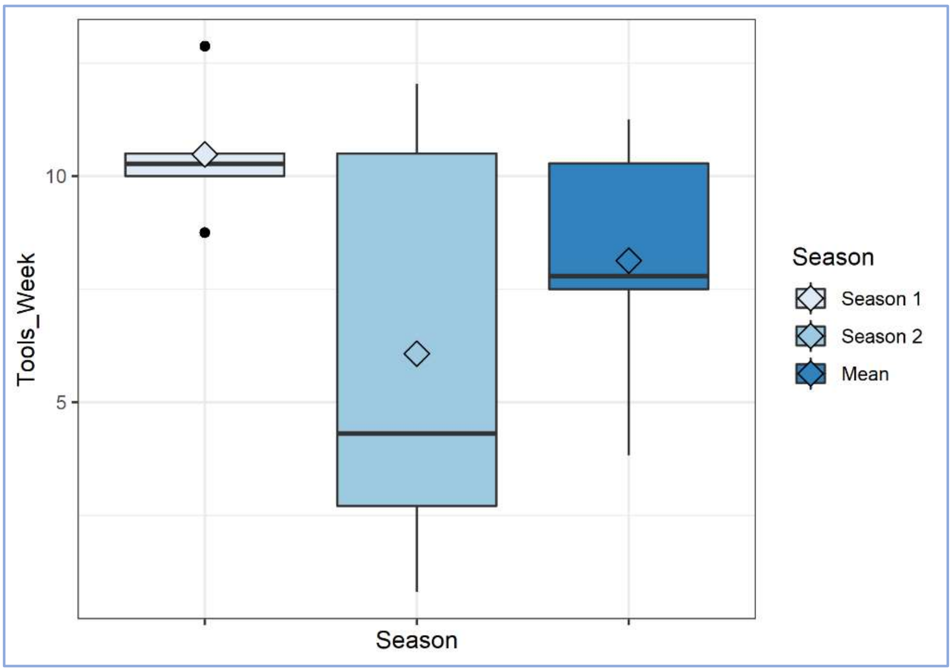

Figure 30 - Comparison of tool accumulation by season - Gombe. Boxplots indicate upper and lower quartile with median as thicker horizontal line, and arithmetic mean as diamonds. Whiskers indicate maximum and minimum data range (excluding outliers). Dots show individual outliers.

However, when looking at mounds individually (Fig. 31), there are significant differences in tool accumulation between years for mounds GTM008 (CS: $\chi 2$ = 6.6255; df = 1; p = 0.01005) and GTM014 (CS: $\chi 2$ = 6.5945; df = 1; p = 0.01023), in which the rate of accumulation declined sharply from 2014 to 2015. GTM009 also showed a decline in 2015, with the number of tools per week decreasing from 10.30 to 4.31, although this difference is not significant (CS: $\chi 2$ = 2.4363; df = 1; p = 0.1186). For mounds GTM011 and GTM012, the number of tools accumulated remained virtually constant (GTM011 - CS: $\chi 2$ = 0.10522; df = 1; p = 0.7457; GTM012 CS: $\chi 2$ = 0.012195; df = 1; p = 0.9121).

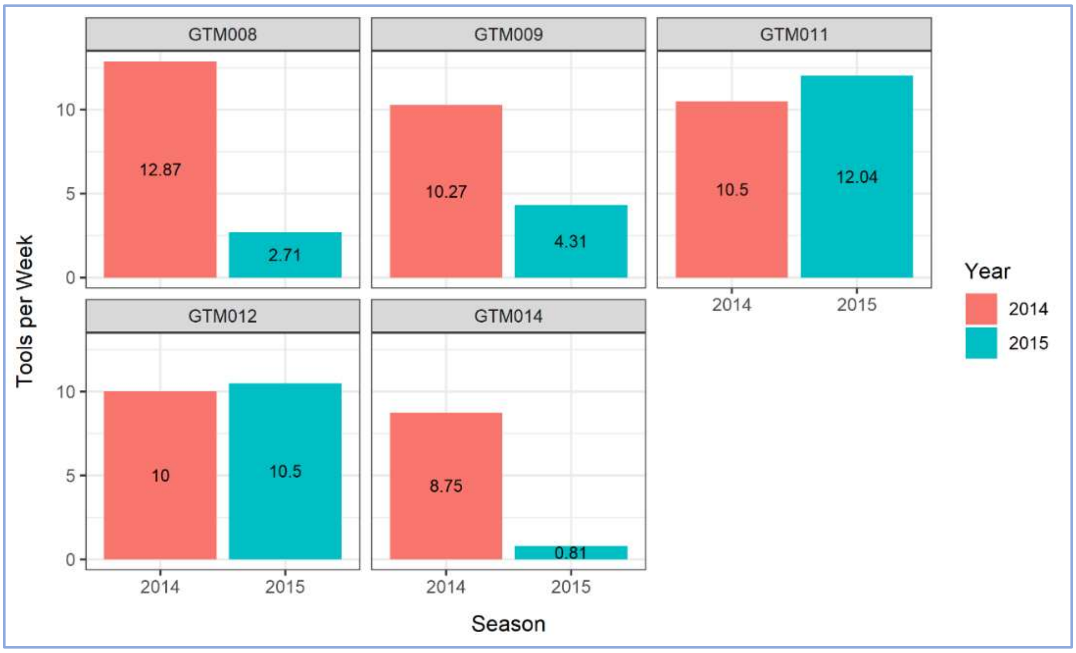

Figure 31 - Comparison of tool accumulation between 2014 and 2015, by mound – Gombe.

b) Fishing season vs non-fishing season

Chimpanzees exploited mounds less intensively outside the termite-fishing season, resulting in a mean tool accumulation rate of 2.39 tools per week overall, compared with an average of 7.64 tools per week for the combined field seasons of 2014/2015 (Table 10; Fig. 32), indicating, as expected, that intensity of tool site use is significantly higher during the rainy season (Wilcoxon signed-rank test ((WT): W = 26, p = 0.02344).

When looking at mounds individually (Fig. 33), tool-use is significantly higher during the termite-fishing seasons for GTM009 (CS: $\chi 2$ = 5.7813; df = 1; p = 0.0162), GTM010 (CS: $\chi 2$ = 6.22; df = 1; p = 0.01263), GTM011 (CS: $\chi 2$ = 7.6698; df = 1; p = 0.005615), GTM012 ($\chi 2$ = 10.28; df = 1; p = 0.001345), and GTM014 (CS: $\chi 2$ = 3.83; df = 1; p = 0.05034). GTM008 and GTM013 show similar means for the considered season; for the latter, it is worth noting that more tools were identified in April/May of 2015 than in the two termite fishing seasons combined.

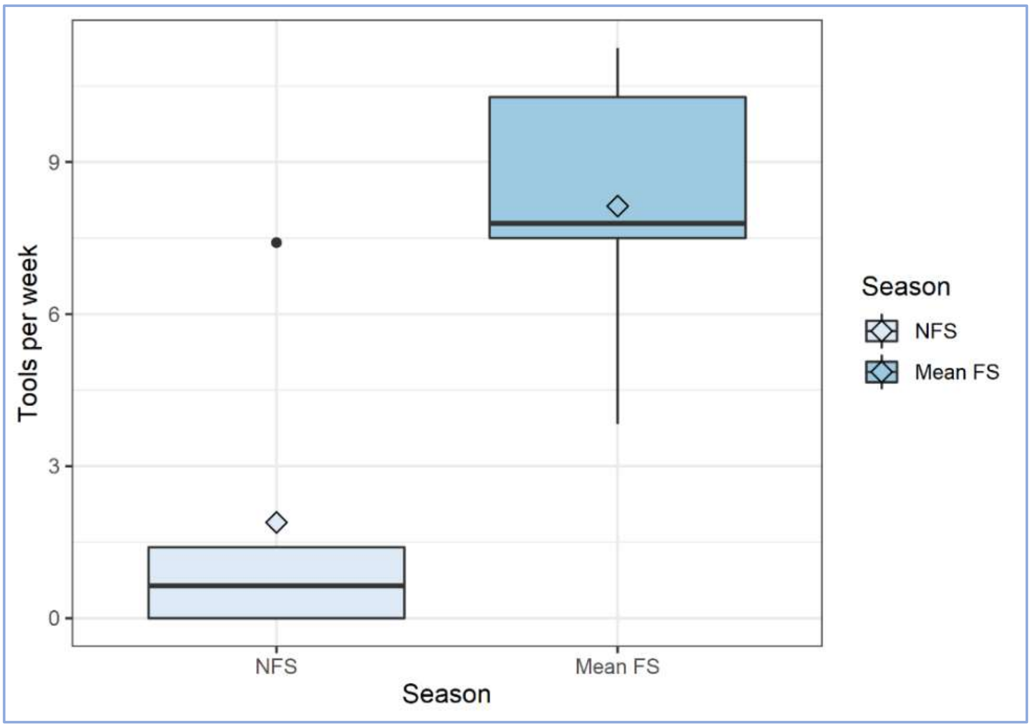

Figure 32 - Comparison of tool accumulation between fishing and non-fishing seasons - Gombe. Boxplots indicate upper and lower quartile with median as thicker horizontal line, and arithmetic mean as diamonds. Whiskers indicate maximum and minimum data range (excluding outliers). Dots show individual outliers.

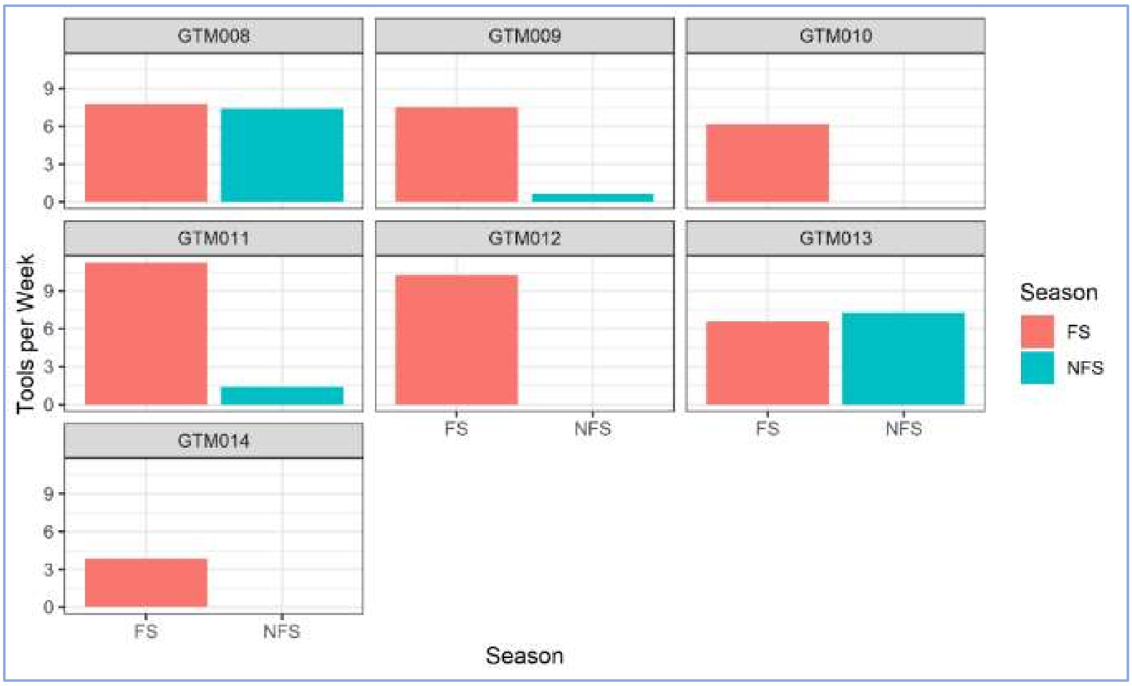

Figure 33 - Comparison of tool accumulation between fishing and non-fishing seasons, by mound - Gombe.

3.4.2. Issa

The first field season shows a mean tool accumulation rate of 0.96 tools per week, compared with 2.35 tools per week for the second field season (Table 11, Fig. 34), a difference that is, contrary to what was expected, non-significant (Wilcoxon signed-rank test (WT): W = 9, p = 0.9512). Looking at mounds individually (Fig. 35), there is a significant difference in tool accumulation between years only for mound ITM006 (CS: $\chi 2$ = 5.0628; df = 1; p = 0.02445) in which tool accumulation increased sharply from the first to the second field season (0.97 to 7.53 tools per week) (Table 11).

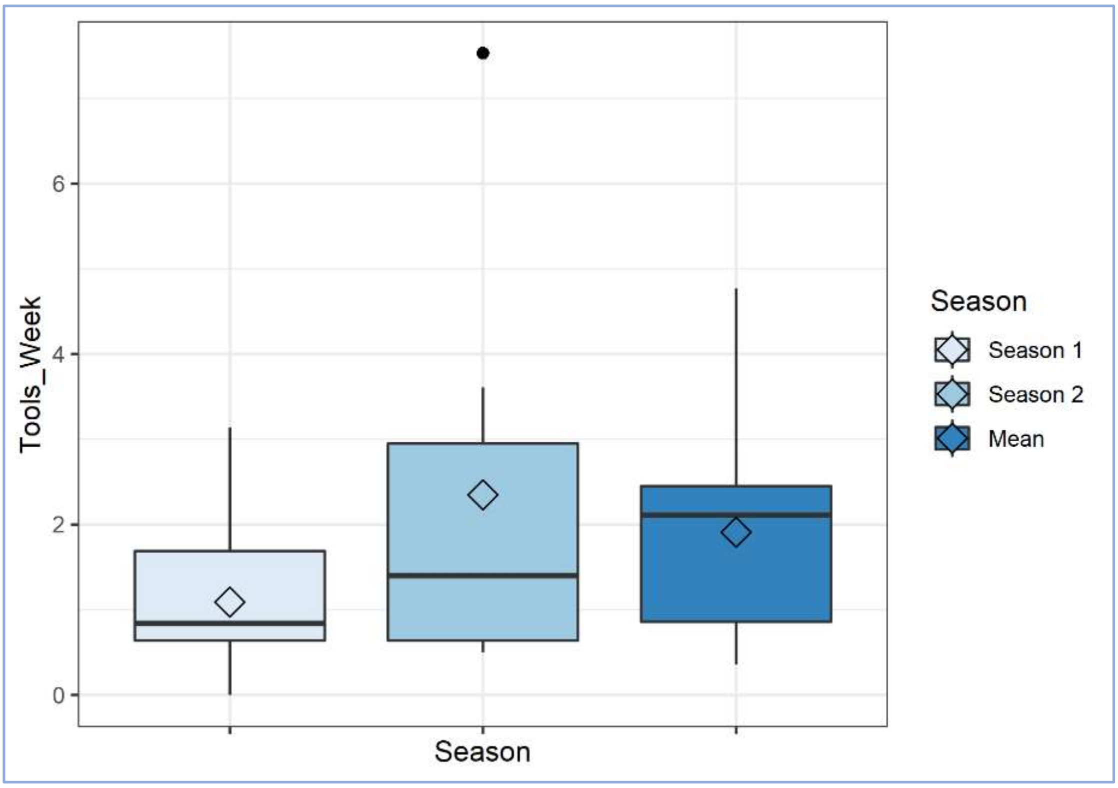

Figure 34 - Comparison of tool accumulation by season - Issa. Boxplots indicate upper and lower quartile with median as thicker horizontal line, and arithmetic mean as diamonds. Whiskers indicate maximum and minimum data range (excluding outliers). Dots show individual outliers.

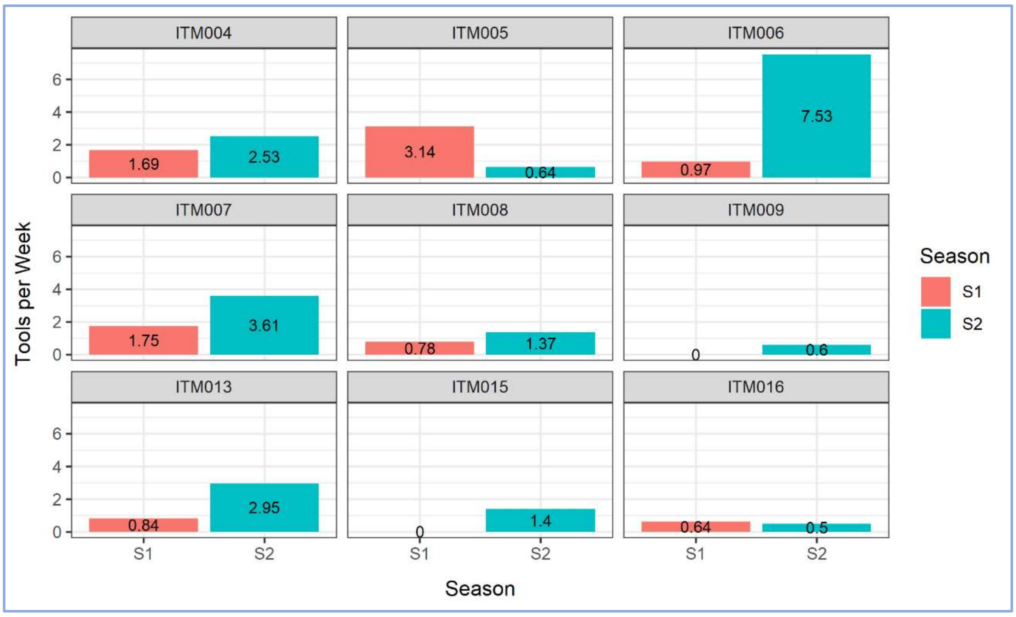

Figure 35 - Comparison of tool accumulation between first and second field seasons, by mound – Issa.

3.5. Differences in tool accumulation between study sites

Based on the number of artefacts recovered at termite mounds, Gombe chimpanzees exploited termite mounds more intensively than Issa chimpanzees. For the two seasons studied, discharged tools accumulate at a rate of 7.64 tools/week at Gombe, versus a rate of 1.91 at Issa (Fig. 36) (MWT: W = 44; p = 0.001998).

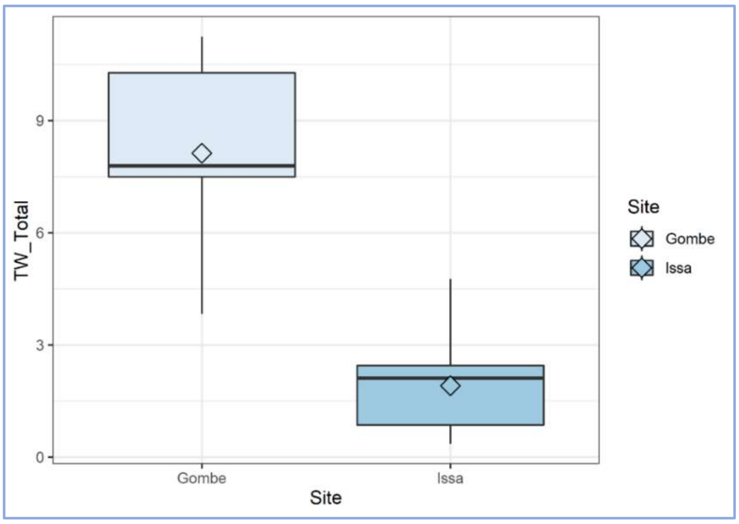

Figure 36 - Comparison of tool accumulation by study site, two-season average. Boxplots indicate upper and lower quartile with median as thicker horizontal line, and arithmetic mean as diamonds. Whiskers indicate maximum and minimum data range (excluding outliers). Dots show individual outliers.

That the first field season at Issa took place at the end of the rainy season, could have influenced these results. Comparing only the data of Issa's second season ($\bar{x}$ = 2.35 tools/week) against the two-season average at Gombe, the difference is still significant (MWT: W = 43; p = 0.003996), confirming that termite mounds are exploited with more intensity at Gombe (Fig. 37).

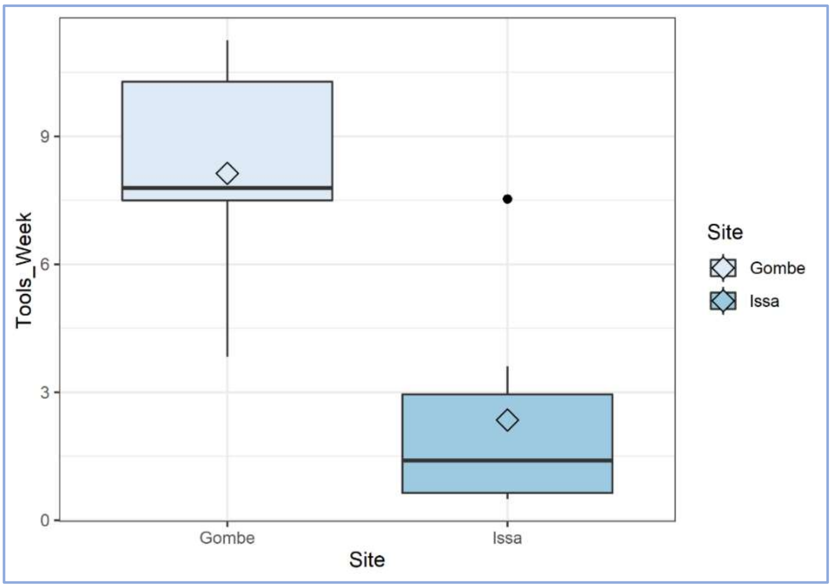

Figure 37 - Comparison of tool accumulation of Issa second field season with Gombe two-season average. Boxplots indicate upper and lower quartile with median as thicker horizontal line, and arithmetic mean as diamonds. Whiskers indicate maximum and minimum data range (excluding outliers). Dots show individual outliers.

3.6. Raw material availability

In order to analyse the effect that the availability of raw material may have on the intensity of use of tool-use sites, the density of raw material was calculated for each targeted mound. Raw material availability, although moderately correlated to the number of fishing utensils accumulated at tool use sites (0.711168), was not a good predictor for the intensity of tool-site use at Gombe (p = 0.1131; R^2 = 0.5058) (Fig. 38). At Gombe, raw material seems to be abundant and not a limiting factor (Table 12) on chimpanzee termite-fishing activity.

Table 12 - Raw material availability - Gombe.

Mound	Suitable plants	Plants of known sourced species	Raw material availability	Tools
GTM008	44	38	0.86	69
GTM009	33	26	0.79	60
GTM011	61	58	0.95	82
GTM012	59	54	0.92	69
GTM013	62	58	0.94	19
GTM014	139	107	0.77	23
$\bar{x}$	66.3	56.8	0.86	53.7

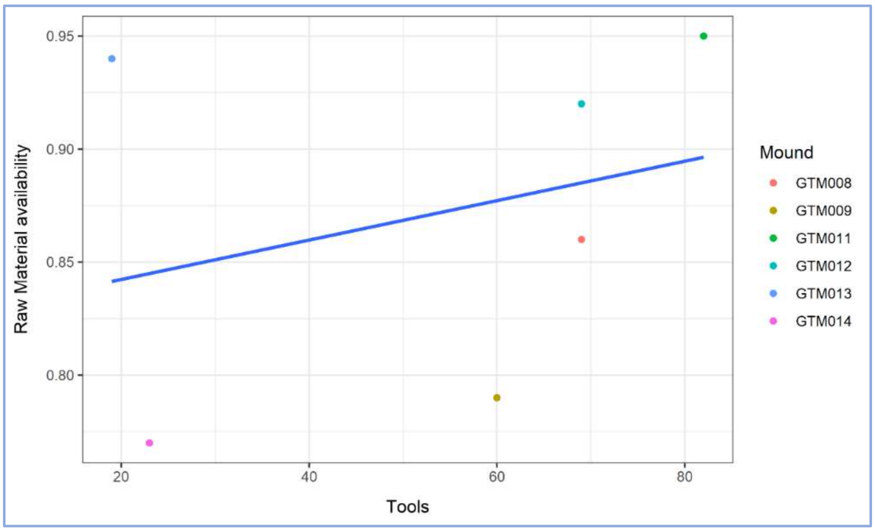

Figure 38 - Total number of tools relative to raw material abundance, by mound - Gombe.

At Issa, raw material available is less abundant, compared to Gombe (Table 13). Though this could likely influence the frequency of tool-site use in general, differences in tool accumulation between mounds, as in Gombe, do not seem to respond to the availability of raw material (p = 0.9339; R^2 = 0.002) (Fig. 39).

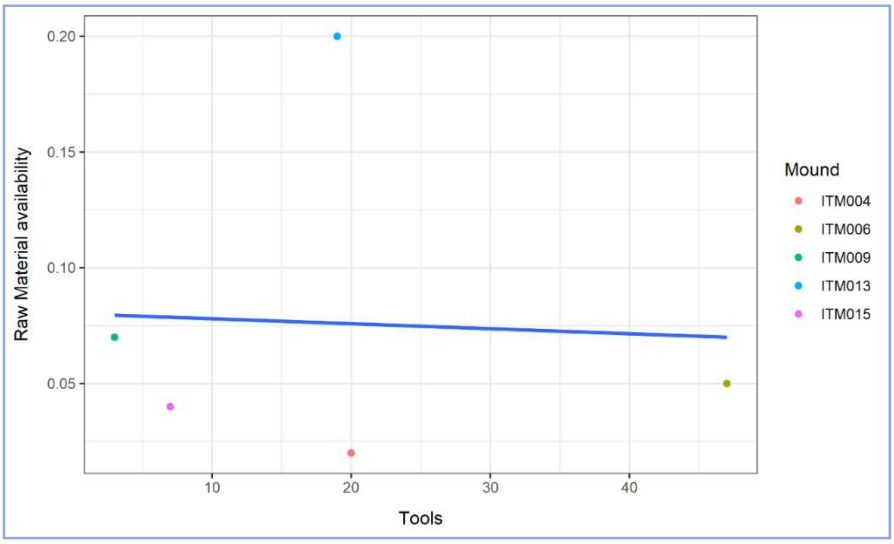

Figure 39 - Total number of tools relative to raw material abundance, by mound - Issa.

Table 13 – Raw material availability - Issa. Adapted from Almeida-Warren, 2015.

Mound	Suitable plants	Plants of known sourced species	Raw material availability	Tools
ITM004	50	1	0.02	20
ITM006	42	2	0.05	47
ITM009	67	5	0.07	3
ITM013	99	20	0.20	19
ITM015	25	1	0.04	7
$\bar{x}$	56.6	5.8	0.10	23

3.7. Mound Size

To test if mound size is a good predictor of intensity of tool site use at Gombe, a regression analysis was done (Fig. 40). Though not statistically significant, surface area seems to be a better predictor for intensity of site use than raw material availability (p = 0.07924; R^2 = 0.5782). Mound size can act as a constraint to chimpanzee's termite-fishing activity, with bigger mounds allowing for more chimpanzees to fish simultaneously. Contrary to Gombe, mound surface area does not seem to be related to the differences in frequency of termite-fishing activity by chimpanzees at Issa (p = 0.911; R^2 = 0.007).

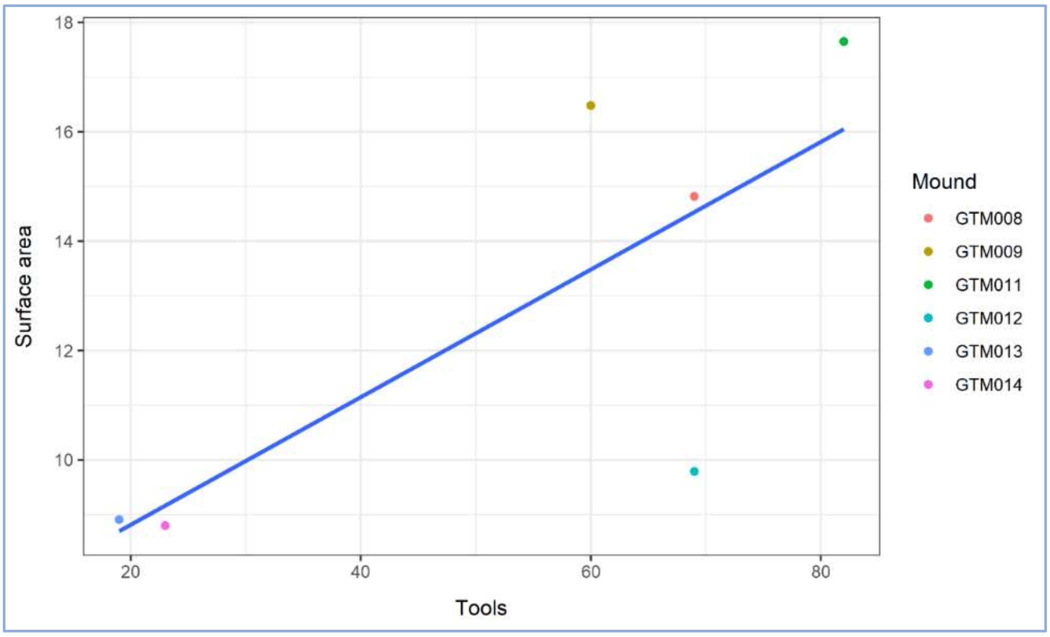

Figure 40 - Total number of tools relative to mound size, by mound - Gombe.

4. Discussion

For the monitoring period considered in this study, the Kasekela community of chimpanzees at Gombe exploited *Macrotermes* mounds more intensively and frequently than their counterparts at Issa. The cumulative discharge of fishing probes during the wet season resulted in higher tool densities at Gombe than at Issa, in both cases higher than known densities at non-human primate stone tool-use sites. Within each site, tool-site use remained fairly constant throughout tool-sites and throughout seasons, although chimpanzees reuse some mounds more than others during the same season, and do not exploit the same mounds with the same frequency in different years. These variations in site use do not seem to be explained by raw-material availability for any of the studied sites. For Gombe, intensity of site use could be related to mound size, but the same was not true for Issa, where it seems to be related to the community's strategies to exploit a vast and dry habitat. This study also confirmed that Gombe chimpanzees, although they engage in termite fishing also during the dry season, do so in a sporadic way, much less intensively than during the rainy months.

Why were termite mounds more intensively exploited at Gombe than at Issa? Differences in habitat could account for this difference – Issa is a dry and open habitat, with considerably less raw material available relatively to Gombe. Raw material type, availability, and distance to the source are known to influence stone technology in chimpanzees (Carvalho et al., 2008; Luncz et al., 2016) and early humans (Andrefsky, 1994; Braun et al., 2008, 2009; Kimura, 1999). At Gombe, raw material is abundant, with around 90% of plants available being from species normally sourced by chimpanzees (Almeida-Warren, 2015). Gombe chimpanzees are also known to use diverse types of plant materials (McGrew & Collins, 1985; Almeida-Warren, 2015), and this is especially true for the Kasekela community (Pascual-Garrido, 2019). At Issa raw material is less abundant, with only 10% of the plants available being of species sourced by the local community (Almeida-Warren, 2015), but this apparent scarcity could be an artefact of this specific population raw-material preferences: Issa chimpanzees seemingly ignore suitable plant materials for termite-fishing tools, sourcing their utensils exclusively from bark, likely indicating a cultural preference (Almeida-Warren, 2015; Almeida-Warren et al., 2017). Thus, raw-material availability doesn't seem to explain the differences between the two sites. Other ecological variables could explain this variation. Issa is one of the driest, more open habitats where chimpanzees dwell (Stewart & Piel, 2014) and it would be interesting to compare mound productivity with other habitats in which chimpanzees fish for termites, as we know that even the same species of termites can construct different types of nests under different environments, and this could, in turn, possibly influence chimpanzees' exploitation strategies (Pomeroy, 1977; Sanz et al., 2014).

Other factors could be influencing this differential exploitation of termite resources in these two sites. Chimpanzee density in the Ugalla valley is one of the lowest of known chimpanzee populations, because of the marginal quality of its habitat (Hernandez-Aguilar et al., 2007; Stewart & Piel, 2014). Even though the Issa community is estimated to be a little higher in numbers than the Kasekela group (Pascual-Garrido, 2019; Rudicell et al., 2011), its members form smaller parties than chimpanzees in both open and forested habitats, especially in the rainy season, to exploit their huge territory (Yoshikawa & Ogawa, 2019). Issa chimpanzees seem to be more sparsely distributed throughout its range, exploiting resources in a more patchy pattern, resulting in lower artefact densities at the tool-sites. Habitat differences thus could explain variation in resource exploitation strategies, but we need to know more about group sizes and its ranging patterns, and also look at the individual use of mounds by chimpanzees. This study's archaeological approach needs to be complemented with behavioral data to give us a better picture of the revealed variations, either between sites or within sites.

Looking at tool accumulation within sites, there are some differences in the intensity of site use and reuse between particular mounds – at both Gombe and Issa, chimpanzees seemingly ignore some mounds in specific years. This is unlikely to be explained by ecological or seasonal factors, like differences in rainfall, as, for each of the sites, all the studied mounds are located close together, subject to the same ecological constraints. However, there could be finer-scale differences that could be tested. Sanz et al. (2014) found that tool-using behaviours can vary according not only to the characteristics of termite prey species and the structure of its nests, but also to its behaviour. Investigating further the characteristics of the termite-mounds, including the behaviour of the termite prey, could help in understanding the impact of subtler ecological variables in termite-fishing strategies by wild chimpanzees.

Although mound structure and productivity could account for differences in the exploitation of resources and should be looked into, it is also possible that different choices can reflect different preferences. Studies on the nesting behaviour of chimpanzees show that the geographical distribution of nests, and their repeated use, could indicate preferential use of favourite sites

(Hernandez-Aguilar, 2009; Stewart et al., 2011) and this strategy of territory exploitation could, by analogy, explain why some mounds are more targeted than others. At Gombe, mound size seems to also act as a constraint to chimpanzee termite-fishing activity. Bigger mounds show, in general, a higher intensity of use, perhaps because they allow for the possibility of more chimpanzees fishing simultaneously. Carvalho et al. (2008) showed that nut-cracking chimpanzees at Bossou sometimes transport tools and nuts to a more isolated area to avoid being disrupted in their activity. This strategy, that would otherwise not be optimal, may reflect social constraints on many individuals feeding at the same time in a limited area (Carvalho et al., 2008). A similar strategy could be at play here: as termite harvesting constricts the individuals to exploit the resources in the nest itself, a bigger nest surface would allow for more chimpanzees to feed simultaneously. When we look at densities, resources are exploited similarly by the Kasekela group in different sized termite mounds, and this seems to confirm that site-use is related to size. Contrary to Gombe, mound size does not act as a constraint to tool-site use at Issa. As said above, likely because the population density of chimpanzees is lower and foraging parties may be smaller (Hernandez-Aguilar et al., 2007; Yoshikawa & Ogawa 2019). As a consequence, termite mounds seem to be exploited less intensively. It would be important to consider group sizes of tool-users, as it is likely to influence tool-site use (Carvalho & McGrew, 2012); it would also be relevant to consider individual fishing behaviors, as social pressures can influence strategies of site use (Carvalho et al., 2008).

Gombe chimpanzees, though they concentrate their termite-fishing efforts in the rainy season, are known to fish throughout the year (Goodall, 1986). Expectedly, this study confirms that tool accumulation is higher during the rainy season, when mounds are more porous and termites are closer to the surface (McGrew et al., 1979). Outside of the termite-fishing season, there is also much more variability in the intensity of site-use, with some mounds being targeted more specifically, which may reflect a more opportunistic approach to termite fishing by the Kasekela community during this period.

This study is limited by its lack of behavioural data, instead relying exclusively on archaeological methods to analyse the material record produced by tool-using behaviours. However, the detailed and methodological data collection allows to draw comparisons with excavated tool-use sites of early hominins, and especially non-human primates, by looking at density of artefacts. The discharge of termite-fishing implements at tool-use sites by the Kasekela community of Gombe chimpanzees led to the formation of sites where tool accumulation results in an overall density of 2.11 tools/m^2, ranging from 0.34 tools/m^2 to 3.98 tools/m^2. At Issa sites, estimated tool densities were lower, ranging from 0.04 tools/m^2 to 1.85 tools/m^2, with a mean value of 0.64 tools/m^2. Previous studies have analysed the density of artefacts at excavated chimpanzee nut-cracking sites in Côte d'Ivoire (Mercader et al., 2007, 2002), but tool densities reported (1.27 and 1.46, respectively) did not differentiate horizons (Carvalho & McGrew, 2012), making it difficult to compare with this study. A study of present-day nut-cracking sites at Bossou, Guinea, reported low tool densities, from 0.002 to 0.05 (Carvalho & McGrew, 2012), much lower than the ones reported here. A higher value, 0.45, was reported for bearded capuchin monkeys nut-cracking surface sites at SCNP (Haslam et al., 2016). Although it is still lower than the tool density values of this study, it is closer to the values reported for the Issa community.

These results suggest that, at least for the studied communities, the exploitation of termite mounds with the use of perishable implements results in a higher accumulation of tools than reported for sites exploited with lithic tools. Contrary to plant utensils, stone tools can be reused over long periods of time, and raw-material availability can constraint the number of stone tools that accumulate at a site (Carvalho & McGrew, 2012), leading to lower densities than those presented here. However, at Bossou nut-cracking sites, low densities cannot be explained by the lack of raw materials, as potential tools are readily available throughout the site (Carvalho, 2011; Carvalho & McGrew, 2012). Chimpanzees seem to have preferences for particular tools, reusing them for long periods, and this could mean that densities are better explained by group size (Carvalho & McGrew, 2012), and also probably by individual preferences (Carvalho et al., 2008). Furthermore, the activity areas considered to estimate tool densities at Bossou study are much bigger (707 m^2) (Carvalho & McGrew, 2012) than the ones in this study - the maps show that termite fishing concentrates around the mound centres, in a relatively small area, leading to higher tool densities (at ITM015, the largest mound considered in this study (80 m^2), estimated tool density was 0.04, similar to Bossou values). This suggests that there are other factors beyond raw-material availability influencing site use and reuse. Wild capuchin monkeys at SCNP use stone tools to process cashew nuts at different stages, creating recognizable accumulation sites (Haslam et al., 2016). Unlike capuchin monkeys living at FBV, they have abundant access to potential hammer stones, indicating that raw material availability is not a constraint to their nut-cracking activities (Ottoni & Izar, 2008). Tool densities calculated at SCNP are much higher than the ones at Bossou (Haslam et al. 2016), and closer to the values reported in this study, especially at Issa. Capuchins discharge tools around the base of cashew trees after use, in a specific area (Haslam et al., 2016) in a similar pattern to the discharge of termite-fishing implements by chimpanzees. It thus seems that the physical characteristics of resources constraint the way they are exploited and that their distribution has a significant impact in the formation of tool sites – smaller activity areas lead to denser, and likely more easily recognizable, tool-use sites. It would be useful to confirm this pattern by comparing with other tool-using primate sites, taking other factors into account, like group size, raw material availability, resource characteristics, and proximity to resources. Burmese long-tailed macaques exploit a wide range of marine resources in intertidal habitats with stone tools (Haslam et al., 2017; Malaivijitnond et al., 2007; Musgrave & Sanz, 2018), and these resources exhibit different characteristics: for example, they exploit sessile molluscs and swimming crustaceans (Malaivijitnond et al., 2007). This makes the study of this species tool-use especially relevant to understand how resource characteristics influence tool-site formation, and also to understand the importance of marine resources in the evolution of our technological path (Haslam et al., 2017). Haslam et al (2016b) excavated wild macaque stone artefacts and found that most of the tools were likely used close very close to where they were found, but did not report on tool densities.

Many studies on chimpanzee tool-assisted termite-fishing have reported on tool accumulations at insect nests, but it is difficult to draw comparisons with this study, as in many cases tools were collected opportunistically, monitoring periods are not known or are not comparable, and tool finds are not discriminated by the nest where they were found, as these studies were not specifically focused on site-use intensity (Bermejo & Illera, 1999; Fay & Carroll, 1994; McGrew et al., 2005; McGrew & Rogers, 1983; McGrew et al., 1979; Sanz et al., 2014; Sanz et al., 2004; Stewart & Piel, 2014; Sugiyama, 1985; Suzuki et al., 2005). One particular study, focusing on the Bilenge community of chimpanzees living at Mahale Mountains National Park used a similar methodology to this one, reporting a value of tools per find (9.5) slightly higher than this study (McGrew & Collins 1985). Overall, these studies suggest that the exploitation of termites produces a high amount of discarded artefacts at tool sites, and the same seems to be true also of other chimpanzees perishable technologies, like ant dipping, and honey and bee harvesting (Humle & Matsuzawa, 2002; Pascual-Garrido et al., 2012). Though it is out of the scope of this study, compiling the huge amount of tool accumulation data that the former studies have reported would be very useful to expand our knowledge about tool-site use.

Comparisons with Oldowan sites are difficult to make, as few studies have published density of artifacts (Carvalho & McGrew, 2012). Looking at the density values calculated by Carvalho and McGrew (2012) for twenty-three Oldowan sites, based on Plummer's review (2004), the values obtained seem to overlap with the low-range of these sites. However, it should be noticed that these densities likely do not represent discrete tool-use sites, as they are not separated by horizon (Carvalho & McGrew, 2012). At the same time, there is high variability in these values, possibly reflecting great differences in the behaviours that lead to the formation of the sites, and also variables like group size and proximity to resources, amongst others (Schick & Toth, 2006), and thus comparisons should be made carefully.

In conclusion, this study is the first of its kind, adding to the knowledge of processes of site formation and tool accumulation, and providing clues to the timescales and behaviours represented at known hominin sites (Haslam et al., 2009). The continued and repetitive use of tool-sites by living primates results in the accumulation of artefacts that can be directly compared to the progressive build-up that underlies early human tool-sites, providing the unique opportunity of studying the formation of sites as they happen in real-time (Haslam et al., 2017). It can also help in identifying the diversity of behaviours behind tool-site formation, including the social and ecological contexts. Plant technology is particularly important, as not only it represents the majority of tools employed by early humans (Hurcombe, 2008) but it probably played a significant role in their daily lives and development (Hardy, 2018). Furthermore, our ancestors were probably consuming insects, including termites, with the use of perishable tools as those used by chimpanzees today (Lesnik, 2014; Sanz et al., 2014). By extending Primate archaeology from lithics to the perishable, we can gain a broader perspective of our technological past and a better interpretation of archaeological sites. Testing how the exploitation of resources, including sleeping sites (Sept, 1992, 1998), is related to chimpanzee ranging patterns can also help model ranging behaviours of early humans (Sept, 1992). Although the perishable has its limitations, as perishable materials rarely fossilize, it can nonetheless help us identify the archaeological signatures of resource exploitation by plant tools in early hominin sites.

Future efforts should continue to gather more detailed data from perishable sites in different habitats, for comparative analysis of the factors behind tool-site use and site formation, considering not only ecological variables like habitat, raw material availability, and characteristic of resources, but also social and cultural variables like group size and individual use of tool-sites. Pairing archaeological methods with observations of behaviours is fundamental to a better understanding of how behaviours translate into the material record.

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Appendix: Pairwise Wilcoxon results tables

Table 14 – Monitoring visits during which tools were identified (Sessions) at Gombe during the first season. Comparison between mounds. Pairwise Wilcoxon p-value results.

Mound	GTM008	GTM009	GTM010	GTM011	GTM012	GTM013
GTM009	1.000	-	-	-	-	-
GTM010	0.362	1.000	-	-	-	-
GTM011	0.679	1.000	1.000	-	-	-
GTM012	1.000	1.000	1.000	1.000	-	-
GTM013	0.028	1.000	1.000	1.000	1.000	-
GTM014	0.175	1.000	1.000	1.000	1.000	1.000

Table 15 – Discarded tools per session at Issa during the second season. Comparison between mounds. Pairwise Wilcoxon p-value results.

Mound	ITM 004	ITM 005	ITM 006	ITM 007	ITM 008	ITM 009	ITM 012	ITM 013	ITM 015	ITM 016
ITM005	1.000	-	-	-	-	-	-	-	-	-
ITM006	1.000	1.000	-	-	-	-	-	-	-	-
ITM007	1.000	1.000	1.000	-	-	-	-	-	-	-
ITM008	1.000	1.000	1.000	1.000	-	-	-	-	-	-
ITM009	1.000	1.000	1.000	1.000	1.000	-	-	-	-	-
ITM012	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-	-
ITM013	0.159	0.012	1.000	1.000	1.000	0.126	0.012	-	-	-
ITM015	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.200	-	-
ITM016	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.022	1.000	-
ITM017	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.012	1.000	1.000

Table 16 – Discarded tools per week at Gombe, during the second season. Comparison between mounds. Pairwise Wilcoxon p-value results.

Mound	GTM008	GTM009	GTM011	GTM012
GTM009	1.000	-	-	-
GTM011	0.127	0.515	-	-
GTM012	0.347	1.000	1.000	-
GTM014	1.000	1.000	0.013	0.042