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Living archaeology: Artefacts of specific nest site fidelity in wild chimpanzees

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ABSTRACT

Savanna chimpanzees are known to re-use areas of the landscape for sleep, and patterns of chimpanzee sleeping site re-use are proposed as a referential model for early hominin archaeological site formation. We recorded the prevalence of deformed but healed branches and remnants of dead branches found around fresh nests at the savanna site of Issa in Ugalla, Tanzania. These old nest scars were found in 79% of 112 beds. We also randomly selected potential nesting locations for a subset of 32 beds within the same trees, and found nest scars in only 19% of these “control” locations. We then monitored 275 nests for up to 19 months for decay, regeneration of new branches, and re-use. Of these 275 nest locations, 24% were re-used within the first nine months of monitoring, and most re-use occurred when the nest had already decayed and was not easily visible from the ground. After 18 months, the proportion of specific nest positions re-used increased to 48%. This fidelity is likely a result of the creation of ideally-shaped support structures and supple new growth for mattress material with successive use of nest locations. We propose that specific nest site re-use may not be a direct product of environmental determination, but a result of “niche construction” through formation of good building sites within trees. Environmental modification through construction behaviour may have influenced both chimpanzee and early hominin ranging, and thus leaves behind recognisable patterns of artefact deposition across the landscape.

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Introduction

All great apes build at least one nest daily for their entire (post-weaning) lives, as sleeping platforms serve for both day-time rest and overnight sleep. In a lifetime, an individual may build more than 19,000 nests (Fruth and Hohmann, 1994a), making this behaviour the most pervasive form of technology in the great apes. Both across and within species, construction behaviour is more frequent than tool manufacture and use, and the study of nest building may reveal insights into the evolution of cognition (Hansell and Ruxton, 2008). Nest building is a learnt behaviour (Videan, 2006), which requires sequential combination of branches into a secure platform over highly variable arboreal substrates. As an example of problem-solving ability, nest building may demand similar or greater cognitive complexity to some tool-use behaviours (Hansell and Ruxton, 2008) Fruth and Hohmann (1994b, 1996) proposed nest building to have facilitated the evolution of cognition and technological skill in hominoids. Coolidge and Wynn (2009) suggested that a major jump

in cognitive evolution may have occurred during the transition from tree to ground sleeping in *Homo erectus*. Determining factors involved in nest site selection, construction, and nest function in existing hominoids is thus important in modelling the behaviour of pre-*erectus* hominins. Nests, plus other remnants of chimpanzee material culture, are evidence of chimpanzee habitat use and site selection and can therefore be used to interpret evidence of early hominin ranging behaviour and archaeological sites (McGrew, 1992, 2004; Sept, 1992, 1998; Moore, 1996; McGrew et al., 2003; Hernandez-Aguilar, 2009).

Although chimpanzees produce an archaeological record (Mercader et al., 2002, 2007), and a new field of (non-hominin) primate archaeology has begun to study these phenomena (Carvalho et al., 2008, 2009; Haslam et al., 2009), most ape material culture is ephemeral (McGrew, 1992). Because of this, studies of nests as “artefacts” on the landscape (*sensu* Sept, 1992; Hernandez-Aguilar, 2009) have considered their decay rate. However, Fruth and Hohmann (1994a) found that traces from bonobo nest building last much longer than the time taken for the nest to decay. They observed deformed but healed branches growing at nest height in the canopy, sometimes even beneath fresh nests, which they interpreted as evidence of past nest construction events.

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Theoretically, the lifetime of such scars could be as long as the lifetime of the trees containing the nests, thus increasing the time-depth of nests as “living artefacts” and suggesting them as identifiable archaeological signs. Fruth and Hohmann observed re-use of nest sites, nest trees, and sometimes even nest-spots within a tree, which led them to hypothesise that great apes may “inadvertently alter their favourite trees in such a way as to create branch structures prefabricated for future nest construction” (1994a: 311). Such a feedback system of environmental modification occurs in a range of species, forming a part of evolutionary theory termed “niche construction” (Odling-Smee et al., 2003). Using an archaeological framework, Biro et al. (2010) highlighted the importance of “use-wear” and “functional analysis” in studying the effectiveness of technologies, and the same will be applied here to nests. The remnants of nest building described by Fruth and Hohmann (1994a) can be defined as macro-scale use-wear of nest construction, and can be used to study these nests from an archaeological perspective, as functional artefacts in specific locations within trees to reveal information about chimpanzee nest site re-use and formation through niche construction.

During our study of nest architecture in Issa, Tanzania, we aimed to test Fruth and Hohmann’s (1994a) hypothesis that nests are built in locations that have been prefabricated by previous building events for future nest construction through investigation of: (a) the greater prevalence of scars in nest vs. non-nest locations; (b) the proportion of old nest locations re-growing new nesting material; and (c) the frequency of specific nest location re-use within trees over time. If specific nesting locations are re-used artefacts, then we predict that more scars or “use-wear traces” (these terms are used inter-changeably in this paper) will occur around the nest than around random non-nest locations within the same trees. Prefabrication of nest sites could occur through moulding of branch structures or increased growth at sites of damage, which we use as a qualitative measure of nest site improvement, or prefabrication. Finally, monitoring of specific nesting locations in trees sought to measure and predict the rate of specific nest artefact re-use over time-scales beyond the lifetime of a nest.

Woody plant growth is a feedback system primarily under apical control and is influenced by water, nutrients, hormones, and branch biomass (Wilson, 2000). Apical control means that the main stem of the plant controls the growth of side stems or branches. These side branches then control growth of further side branches, and so on. Thus, when an apex at any level within the tree breaks, apical control ceases and new branch growth occurs. Re-growth varies due to a range of influences, including tree species, climate, light level, and natural growth rate. Humans have exploited natural regenerative abilities of woody plants for millennia, exemplified by such practices as pruning, pleaching, training, moulding, coppicing, and pollarding (Harris, 1983). Pruning, pollarding, and coppicing produce denser re-growth around sites of damage, whilst pleaching, training, and moulding rely on branches continuing to grow in a new, desired direction. Other primate species, such as *Cebus capucinus*, benefit from the natural regenerative properties of plants by removing the terminal buds of branches when feeding, thus increasing branching and food availability (Oppenheimer and Lang, 1969). Such a feedback system of woody plant re-growth may improve or shape nest sites resulting from damage caused by manipulation of branches during chimpanzee nest building.

Fruth and Hohmann (1994a: 310) described three types of scars, likely resulting from damage during nest building with associated re-growth of branches: “(1) broken but healed and continuing growth in a new direction, (2) dead at the site of fracture with a young shoot perpendicular to the branch, either vertical or horizontal in relation to the living part, and (3) a combination of the two.” Similar deformations of branches occur in trees often used for nest building by orang-

utans (Ancrenaz et al., 2004) and around nests built by chimpanzees in Kibale National Park, Uganda (Llorente Caño, 2004). During a study of chimpanzee nest building behaviour in Fongoli, Senegal, similar scars of what seemed to be previous nesting events were found within and around fresh nests. These scars near fresh nests were found in 77% of 104 nests (Stewart et al., 2010).

Re-use of recent nests occurs in all great apes, albeit at low and variable frequencies across seasons and study sites (Fruth and Hohmann, 1994a; Ancrenaz et al., 2004; Iwata and Ando, 2007). For example, male chimpanzees in Gombe National Park, Tanzania, were never seen to re-use nests during the wet season, yet during the dry season they re-used nests in 30% of direct observations (Wrangham, 1992); in Budongo Forest, Uganda, 16% of night nests were re-used (Plumptre and Reynolds, 1997), and in Kibale National Park, Uganda, 12% of recent nests were re-used (Llorente Caño, 2004). Re-use of nests usually occurs over short periods when nests are still cushioned with green leaves, prior to substantial nest decay (Wrangham, 1992; Llorente Caño, 2004; Stewart, pers. obs.). Re-use of a nest vs. re-use of a specific nest-spot differs, as the former occurs through modification of an intact structure by adding new material, whilst the latter has not been investigated before and could occur long after a nest has disappeared. Re-use of recent nests is hypothesised to occur at higher rates in drier habitats because nesting material is scarcer in areas with few semi-deciduous trees (Wrangham, 1992; Fruth and Hohmann, 1996). By studying nests and nest scars archaeologically, when use-wear of nests is classified and measured, one can determine re-use beyond the nest’s lifetime.

Chimpanzees differentially use areas of the landscape for feeding and nesting and prefer specific tree species and structures, vegetation types, proximity to food resources, and topography (Goodall, 1962, 1986; van Lawick-Goodall, 1968; Suzuki, 1969; Jones and Sabater Pi, 1971; Baldwin et al., 1981; Ghiglieri, 1984; Sept, 1992; Brownlow et al., 2001; Furuichi and Hashimoto, 2004; Hernandez-Aguilar, 2009). However, these factors alone cannot account for nest site selection at a landscape scale (Hernandez-Aguilar, 2006). Sept (1992) found nesting patterns of the chimpanzees in Ishasha, Democratic Republic of Congo, to be “spatially redundant” as the chimpanzees re-used some areas in the landscape but not others, which did not seem to be due only to resource distribution. Sept’s (1992) research using chimpanzee nests as a proxy to interpret debris or artefacts at early archaeological sites, was part of an innovative interdisciplinary approach seeking to understand archaeological site formation processes and functions. Hernandez-Aguilar (2009), expanding on the work of Sept (1992, 1998), found that re-use of nesting sites by chimpanzees in Ugalla occurs across seasons and even years. Sept (1992) and Hernandez-Aguilar (2009) challenged earlier interpretations of early archaeological sites as being temporary home-bases where division of labour, central place foraging, and food sharing were hypothesised to account for the spatial patterning of concentrations of stone tools (such as cores and flakes) and bones (Isaac, 1978). Hernandez-Aguilar (2009) elaborated that re-use of chimpanzee nesting sites may represent a precursor to full home-base use requiring significant changes in social structure. Such interpretation is part of a broader perspective using archaeological evidence from extant species to understand hominin behaviour (McGrew, 1992, 2004; Sept, 1992, 1998; McGrew et al., 2003; Carvalho et al., 2008, 2009; Hernandez-Aguilar, 2009; Haslam et al., 2009). This study investigates re-use of specific nest locations, which are long-lasting artefacts in the landscape, and whether or not these artefacts may be prefabricated for future use. Such environmental modification through construction behaviour may have played a role in both chimpanzee and early hominin ranging and patterns of artefact deposition across the landscape.

Methods

Study site

We studied nest architecture at Issa, in Ugalla, western Tanzania (S5.50429°, E30.56271°), one of the driest, most open habitats where chimpanzees occur (Moore, 1992, 1996; Hernandez-Aguilar, 2006, 2009). We collected data on nest scars from October 2008–2009, and on nest decay, re-use, and branch regeneration over an extended period from October 2008 to May 2010.

Issa lies in the west of the Ugalla region, 81 km inland and east of Lake Tanganyika. Ugalla is likely the easternmost distribution of chimpanzees in Africa (Massawe, 1992); it is a 3300 km² region of broad valleys broken up by steep mountains and flat hilltop plateaus of 900–1800 m in elevation. The vegetation of the Ugalla region is miombo woodland, named for the dominant tree genera of *Brachystegia* and *Julbernardia* (Fabaceae). Hernandez-Aguilar (2006, 2009) described the vegetation of the Issa study area as: swamp, dry grassland, wooded grassland, woodland, gallery forest, thicket forest, and hill forest. The first four vegetation types are “open” vegetation, which covers 98.5% of the study area, whilst the other three are broadly classified as “forest” and comprise only 1.5% (Hernandez-Aguilar, 2009). Of open habitats, only woodland was used for nesting, and so only woodland and forest are used here. There is a rainy (October–April) and a dry season (May–September), with dry months defined as having <100 mm of rainfall. Rainfall averages <1000 mm per annum (Hernandez-Aguilar, 2009) and temperatures range from 11°C to 35°C.

Data collection

We found and measured 80 fresh nest groups containing 517 fresh nests. Fresh nests usually had moist faeces or urine below the nest. We used a compass and clinometer to measure the location of each nest in relation to the nesting tree base and other nests in the group. We marked each nesting tree with a metal numbered tag, and the specific location of the nest within the tree with a numbered metal stake in the ground below the nest; for some trees with large crowns, a branch map recorded the location of the nest within the tree. Nest groups were added to the monitoring sample as they were found, from October 2008 to August 2009, so the duration of monitoring varies. We monitored nests for 9–19 months. Fifteen groups with 88 nests were too far away from camp for monthly visits. Thirteen other groups with 153 nests were excluded as we could not confirm reliable monitoring of the correct location. One nest was dropped as the tree died prior to nest decay. Thus, we report here on 275 nests monitored monthly.

As part of a concurrent study of nest characteristics, shape, and architecture, FS climbed trees to measure fresh nests using arborist tree-climbing equipment. Nests were deconstructed by taking them apart in reverse sequence of construction in order to study their architecture and reveal all scars. FS climbed to nests with safe accessibility, using a combination of single-rope technique (SRT) and double-rope technique (DRT). Some nests were therefore inaccessible, introducing a bias into the nest sample; however, comparative data collected from random locations within nesting trees is similarly biased, which controls for differences in scarring propensity due to location within trees. Houle et al. (2004) described SRT in full: it uses mechanical ascenders to climb a single line installed in the canopy, thus permitting rapid ascent and descent without damage to the tree. DRT, although slower, relies on friction knots rather than mechanical ascenders and permits a greater degree of horizontal movement in the canopy.

We recorded presence or absence of scars for 112 nests. We counted each type of scar within the specific nest site – a 1.5 m

radius area from a nest's centre (as most material used in nest building is from within this distance; Stewart, pers. obs.). We recorded four types of scars: (a) old breaks, with the branch more than 50% broken but still attached, and new growth sprouting at the point of fracture (while the branch has often died); (b) old bends, when the unbroken branch has healed and continues to grow in the new, aberrant direction; (c) dead ends, when characteristic tails of stripped bark show where a branch has been detached and new shoots sprout from the break; and (d) old frame branches, where dead, detached branches remain from a nest that has decayed (Fig. 1). Old frame branches are often invisible from the ground, as just one or two branches may remain, but this scar type can be classified as re-use of a stage 4 nest (as defined by Plumtre and Reynolds [1997], see categories described below), as sometimes several branches forming an intact frame remain. Signs of previous nests were rarely visible from the ground, as the frame and scars are usually hidden by fresh leaves used for nest building.

We randomly selected 10 fresh nest groups and re-visited nesting trees that we had climbed for fresh nests ($n = 32$ of 89 trees and 117 nests) and recorded scar frequency. We randomly selected a suitable potential nesting site within each tree and counted the scars within a 1.5 m radius around the site. We used a random number generator to select the potential site to access for control measures. We defined a suitable potential nesting site as having both available building material and a supporting branch structure resembling observed nest supports in Issa, as outlined below. Of 517 fresh nests, 6.2% were re-used and so were supported by recent nests, and only 1.7% had no discernable support (e.g., integrated nests using crowns of multiple saplings may not always have discernable supporting branch structures). The rest were supported by one or more branches in the following configurations: cup formed by several branches (30%), horizontal or inclined V-shape (22.2%), single horizontal or inclined branch (21.1%), one or more branches crossing (12.4%), or a vertical V-shape (6.2%).

We monitored nests weekly for the first four weeks, then monthly after that. Periodically, we confirmed age categories and nest locations within trees and groups. Each month we recorded the state of nest decay (following Plumtre and Reynolds, 1997) and the presence of twigs or branches re-growing from breaks and bends in the nests. State of decay was categorised as stages 1–4: (1) leaves green and nest structure intact; (2) some leaves brown, but nest structure intact; (3) nest rotting and structure disintegrating; and (4) only the frame and <5% of leaves remaining. Nests were considered decayed from stage 4, following Plumtre and Reynolds (1997), and recorded as gone when no nest frame remained. Time to complete disappearance is used in some studies to calculate decay rate (Tutin and Fernandez, 1984; Kouakou et al., 2009). With these broad definitions of decay stage, we recognised re-use if the nest “reverted” in age from an older to a younger state (amount of re-use may be underestimated, as re-use may occur before decay to stage 3, and a stage 3 nest could be re-used and return to stage 3 within the one month interval between checks). We recorded the numbers of new branches sprouting from the nest site on a scale of “few” (0–5), “some” (5–10), and “many” (>10). Of 275 nests monitored, FS had climbed into and fully deconstructed 57 for architectural study. Although FS re-built the nest as it had originally been made, this deconstruction process may affect rate of decay so we excluded these nests from calculations of decay rates. As the goal was to calculate decay rate, we excluded 17 nests that were re-used when fresh, and 10 nests that were re-used before stage 4. As not all nests decayed fully during the study period, decay rate was calculated to stage 4 for 191 nests using the exponential method (Plumtre and Reynolds, 1996), which uses the decay curve to calculate the time for 50% of nests to decay. No difference in proportion of nests, or specific nest locations re-used within the



Figure 1. Four types of scars, or macro-use-wear, described as follows: (A) an “old break” – note the new shoots sprouting around the break; (B) an “old bend” – normal growth continues (horizontally) in the direction of the main branch. Two side branches continue growing aberrantly perpendicular to the main branch; (C) a “dead end” – note the characteristic tail at the old detachment point and that two new shoots have sprouted. Above, one continues to grow vertically, and to the left, the other was freshly detached and used in nest building; (D) an “old frame” branch - several dead branches remain, some detached and others broken, forming an old frame.

first nine months of monitoring, was found between deconstructed vs. all other nests ($n_1 = 57$, $n_2 = 218$, d.f. = 1, $\chi^2 = 1.83$, $p > 0.05$), so we included all nest locations in analysis of re-use. We included all 275 nests in analysis of branch regeneration.

Results

Deconstruction of nests *in situ* revealed both scars and construction pattern. Nests were made from branches that were broken or bent radially into a central structure to form an interwoven, stable, and comfortable circular platform. Most (98.3%) nests had visible supports as outlined above, over which the first branches manipulated often formed a triangular shaped support, overlain by a mattress of overlapping branches. “Old bends” were usually found beneath the nest and formed triangular support structures. Manipulated support and mattress branches usually remained attached and pliable, whether broken (defined as >50% severed) or bent (<50% severed), and so later sprang out undamaged or retained their previous shape when healed. Fully detached branches and twigs were often added as a lining. Fresh use-wear traces around the nest were seen where branches or twigs had been freshly detached and were characterised by a tail of bark. As nests decayed, broken branches died and sprouted new growth, as opposed to bent branches, which continued growing. Whether the characteristic tails of “dead end” scars were the use-wear traces of detached lining material or the remnants of broken branches is unknown (Fig. 1).

Scars

Of 112 nests studied architecturally, 79% had scars (Fig. 1). The median number of scars found at a nest site was 5 ($n = 112$, range = 0–21). Of these, dead ends were most frequent (73% of

nests, median per nest = 3, range = 0–14), then frame branches (50% of nests, median per nest = 2, range = 0–7), old breaks (47% of nests, median per nest = 1, range = 0–5), and old bends (44% of nests, median per nest = 1, range = 0–6). The proportion of nests with scars did not differ by season ($\chi^2 = 3.1$, d.f. = 1, $p > 0.05$), nor did the most frequently used tree species (including species used on more than six occasions: *Brachystegia stipulata* [plus *Brachystegia pubulara* and *Brachystegi utilis*, which could not be discerned in the field and so are combined for analyses], *Brachystegi bussei*, *Brachystegi spiciformis*, *Combretum molle*, and *Julbernardia unijugata*; $\chi^2 = 2.7$, d.f. = 4, $p > 0.05$).

Fewer control locations had scars than nesting sites (19%, $n_1 = 112$, $n_2 = 32$, d.f. = 1, $\chi^2 = 38.2$, $p < 0.01$). The median number of scars per site was 0 (range = 0–11). Dead ends were most frequent (16% of sites, median per site = 0, range = 0–4), followed by old breaks (12% of sites, median per site = 0, range = 0–1), old bends (9% of sites, median per site = 0, range = 0–5), and potential old frame branches (6% of sites, median per site = 0, range = 0–1). In three cases, the randomly selected location appeared to be a previously used nest location. In order to control for possible effects of tree species on scarring propensity, a paired-comparison was made between the number of scars found in nesting vs. random locations within the same tree. More scars were found within a 1.5 m radius of a fresh nest than at a randomly selected location suitable for nesting within the same tree ($n = 32$, $z = 4.6$, $p < 0.001$, Wilcoxon’s matched pairs). Some natural dead ends were found at random locations, however, these did not meet the criteria of dead ends counted around nest sites, as they lacked characteristic “tails” of bark that occur whenever a branch is detached or broken by hand. If, however, these data are conservatively included as scars, the relationships remain significant (56% of random sites, $n_1 = 32$; 79.5% of nests, $n_2 = 112$; d.f. = 2, $\chi^2 = 5.9$, $p < 0.05$; $n = 32$, $z = 4.2$, $p < 0.001$, Wilcoxon’s matched pairs).

Branch re-growth

Of 275 nests monitored, 181 (or 66%) had re-growth of branches within the first nine months of monitoring. New twigs sprouted in a few nests as soon as one month after nest construction, although most re-growth began three (24% of nests) to four (44% of nests) months later (see Fig. 2). FS counted the number of branches re-grown per nest for some nests within four to eight months of monitoring. A mean maximum number of 7.5 branches or twigs re-grew per nest, ranging from 1–35 ($n = 70$). More nests built during the rainy season had new branch growth than nests built during the dry season in both forest (rainy: 62%, $n_1 = 33$, vs. dry: 16%, $n_2 = 38$; d.f. = 1, $\chi^2 = 14.28$, $p < 0.01$) and woodland (rainy: 83%, $n_1 = 135$, vs. dry: 59%, $n_2 = 69$; d.f. = 1, $\chi^2 = 12.05$, $p < 0.01$) vegetation. Also, more nests built in woodland (75%, $n_1 = 204$) regenerated during the study period than nests built in forest (38%, $n_2 = 71$; d.f. = 1, $\chi^2 = 29.3$, $p < 0.01$).

Nest decay

Time to decay of nests in Issa was highly variable, ranging from 7 to >427 days. Comparisons of the median time to decay for nests that decayed fully revealed differences between vegetation types and seasons (Kruskal–Wallis, $\chi^2 = 13.2$, $p = 0.004$). Thus, mean time to decay was calculated separately for nests built in each vegetation type and season. Mean time to decay of nests built in woodland was longer in the dry season (185.5 days, $n = 49$, range = 14 to >357) than nests built in the rainy season (139.2 days, $n = 91$, range = 7 to >427). Nests built in forest in the dry season decayed faster (83.3 days, $n = 26$, range = 14–224) than nests built in forest in the rainy season (118.9 days, $n = 25$, range = 14–350). Decay curves are shown in Fig. 3. Excluding nests that were re-used prior to complete disappearance, mean time for a nest to disappear completely is 243 days for nests built in forest ($n = 33$) and 432 days for nests built in woodland ($n = 101$).

Re-use

Of 517 fresh nests, 32 (6%) were seen from the ground to be episodes of re-use, with fresh material added to existing older nests. Only four of these cases were stage 3 nests (0.8%), whilst 28 (5%) were stage 1 or 2. Fresh nests not classed as re-use were targeted for architectural measurements. Despite this, of 112 fresh nests that were accessed, 7 (6%) were found to be re-used at stage 1 or 2. On these occasions, we found dried or wilted leaves beneath fresh new material on the surface of the nest. Thus, nests classed as

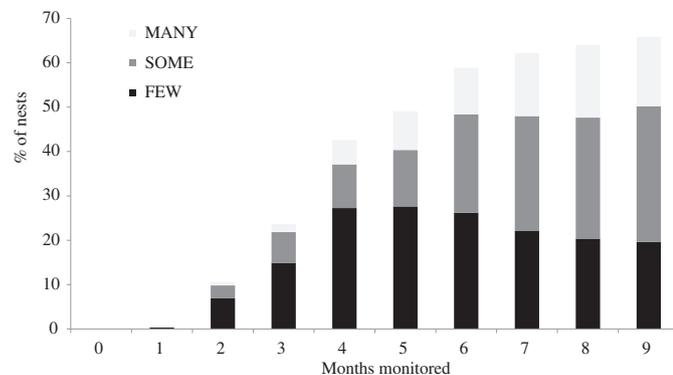


Figure 2. Percentage of nests with re-growth and amount of re-growth at each nest increases over time. Re-growth measured in categories of few (0–5), some (5–10), or many (>10) branches or twigs.

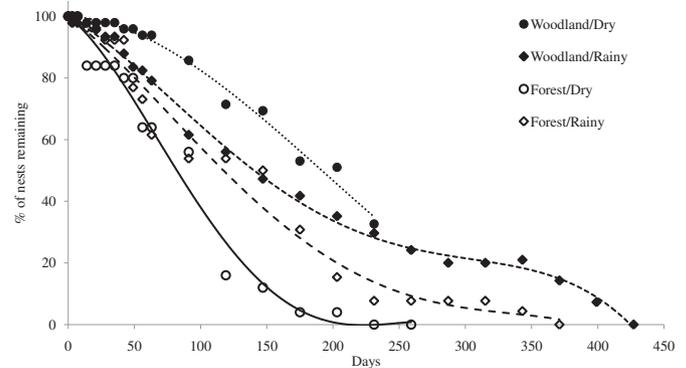


Figure 3. Nest survival over time. Nests built in forest during the dry season ($n = 26$) decay faster than nests built in the wet season ($n = 25$), whilst nests built in woodland during the dry season ($n = 49$) take longer to decay than nests built in the rainy season ($n = 91$). Nests built in woodland overall take longer to decay than those in forest.

“fresh” from the ground may show re-use that cannot be determined without close-up inspection.

We monitored 275 nests for nine months in order to investigate proportions of locations re-used in different vegetation types or seasons. During this time, 24% of locations were re-used: 4% of nests were re-used prior to decay (stage 2–3), 15% after the nest had decayed to stage 4, and 5% following complete disappearance of the nest. Thus, most re-use occurs at the same nesting position within the tree once the nest has decayed. Four specific nest locations were re-used more than once. More specific nest locations were re-used in forest (41%, $n_1 = 71$) than in woodland (19%, $n_2 = 204$, d.f. = 1, $\chi^2 = 12.81$, $p < 0.01$). There was no difference in re-use of locations built in the wet or dry season (forest: $\chi^2 = 0.01$, d.f. = 1, $p > 0.05$; woodland: $\chi^2 = 1.41$, d.f. = 1, $p > 0.05$), or between frequently used tree species ([*B. stipulata*, *B. pubulara*, *B. utilis*], *B. bussei*, *B. spiciformis*, *C. molle*, *J. unijugata*, *Pterocarpus tinctorius*, *Isoberlinia tomentosa*, *Brachystegia microphylla*, *Lannea schimperi*, and *Parinari capensis*; $\chi^2 = 11.9$, d.f. = 9, $p > 0.05$).

Over nine months of monitoring in forest, and 17 months of monitoring in woodland, the proportion of specific nest positions that had been re-used at least once increased exponentially (Fig. 4). Data beyond nine months of monitoring in forest were not included, as the sample size of nests monitored dropped too low,

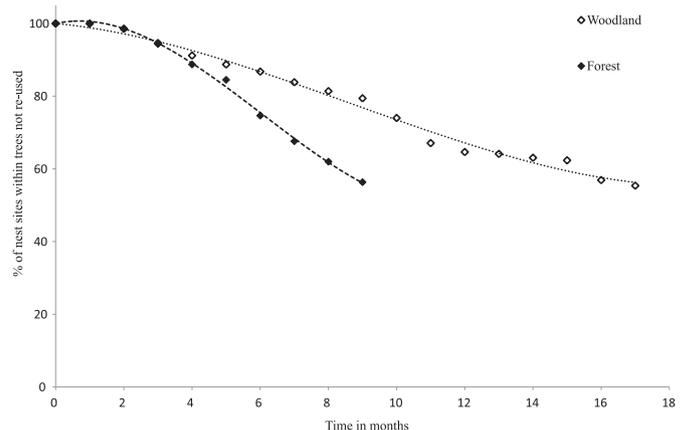


Figure 4. Percentage of specific nest locations not re-used over time in woodland and forest trees. Specific nest sites in forest were re-used at a faster rate than in woodland. Polynomial trend lines indicate possible continued re-use in forest ($y = -0.08x^3 - 1.51x + 100$, $r^2 = 0.998$) and woodland ($y = 0.011x^3 - 0.29x + 100$, $r^2 = 0.989$).

from 71 to 35. After nine months of monitoring in woodland, the sample size of nests dropped gradually, and data beyond 17 months of monitoring were excluded as the sample size dropped below 50. The proportion of nest positions re-used increased in both vegetation types over time. We hypothesise that all nest positions eventually may be re-used, but longer term monitoring is needed to test this. These data did not consider more than one re-use of specific nesting locations. Of 56 nests in woodland and 15 nests in forest, all monitored for 19 months, 12 specific nest locations were re-used twice and one site was re-used three times. Mean time between bouts of re-use of the same nest position was 6 months, including all nest positions re-used on multiple occasions ($n = 24$, range = 3–12).

Discussion

Since Fruth and Hohmann's (1994a) observations that nest building by bonobos leaves long-lasting living artefacts in the form of misshapen tree branches, there has been little further study of such artefacts. Given that such scars occur in the nesting trees of bonobos (Fruth and Hohmann, 1994a) and orang-utans (Ancrenaz et al., 2004), and are found in fresh chimpanzee nest sites in Fongoli, Senegal (77%; Stewart et al., 2010), in Kanyawara in Kibale (58%; Llorente Caño, 2004), and in Issa, Tanzania (79%), such identifiable types of use-wear traces in these ape artefacts are probably widespread. However, without corresponding data on type and abundance of traces or scars from control sites, as collected here, it is not possible to know if apes or other natural processes (e.g., feeding activities, plant disease, or climate) are responsible for their creation, or whether or not macro-use-wear is distributed evenly throughout trees frequently selected by chimpanzees for nesting. Our results show that use-wear traces of nest building are distributed unevenly throughout trees, and in greater numbers around nests. This provides the first evidence that nests are built preferentially at specific positions within trees where nests were previously built.

Following Fruth and Hohmann (1994a), we hypothesised that nest sites may be improved through branch re-growth at sites of damage. They tested the potential for bonobo nesting sites to regenerate new growth by monitoring cut and broken saplings and trees along transects at Lomako, Democratic Republic of Congo. They found that 97% of cuts or breaks regenerated and 39% healed, much higher rates than in the current study (although results presented here are from a shorter monitoring period). They also hypothesised that regeneration rate may be influenced by climate and vegetation type, where trees in forests may regenerate more often than those in woodlands. Issa nests more often regenerated if built during the rainy season, suggesting climatic influence, yet more nests built in woodland regenerated than nests in forests. This incongruity may be due to better visibility of re-growth in woodland, or may result from variation in growth rates of different tree species, e.g., those in forest may take longer to regenerate.

Nest sites may also become "prefabricated" through the healing of support branches. Fruth and Hohmann (1994a) noted that beneath some nests the typical triangular structure of a nest was formed by previously broken but healed branches growing in a new formation. These residual structures may be as important in specific nest site re-use as re-growth of supple new materials. We found similar triangular structures of healed branches at Issa and Fongoli.

Although most nests (66%) re-grew branches within nine months of monitoring, few new branches seemed to reach sufficient size and number to be the sole material used in construction of a fresh nest in that time. However, we often observed that around fresh nest sites less than half of the new growth sprouting from scars was incorporated into fresh nests (See Fig. 1A and B for

new growth used in building and left to grow). Therefore new branches may continue growing even whilst the nest is re-used, leading to more frequent opportunities for re-use than is reflected in the rate of re-growth of new branches. A specific nesting location may also have ample available material for multiple nesting events over a short period.

Re-use of specific nest positions within trees occurring after the nest has decayed should be distinguished from the re-use of nests that usually occurs while the nest is fresh or recent. Re-use of monitored nests supports this, as only 4% of nests were re-used before decaying to stage 4. However, this measure may underestimate nest re-use during the four weeks between successive monitoring checks or may not be discernable while nests are at stage 3. The proportion of all fresh nests found that were fresh cases of re-use (6%) also may be underestimated, as re-use cannot always be seen from the ground. This proportion is low and similar to that observed at other study sites (Wrangham, 1992; Plumtre and Reynolds, 1996, 1997). That only nests thought to be freshly built were accessed using climbing equipment, and that 6% of these nests were actually fresh episodes of re-use emphasises the importance of climbing in field studies of chimpanzee nest building. Houle et al. (2004) also emphasised the importance of tree-climbing in primate ecological study; here, we add its utility for non-hominin primate archaeology.

No other study of nest decay has reported continued monitoring of nests beyond the point of decay (Tutin and Fernandez, 1984; Marchesi et al., 1995; Tutin et al., 1995; Plumtre and Reynolds, 1996). By doing so, we found that re-use of specific locations occurs well beyond nest lifetime. Following habituated individuals at long-term research sites would allow a validity test, and would also help to determine whether or not the same individuals re-use locations over time. Chimpanzees at Fongoli often nested in what appeared to be virgin positions, but upon deconstruction of nests the following day, scars were found (Stewart, pers. obs.).

Hernandez-Aguilar (2009) found that, although 93% of 5354 nests were built in woodland, chimpanzees preferred building in forest, which represents only 1.5% of the present study area. However, Hernandez-Aguilar (2009) also found that forest trees are larger and occur at higher densities, so they may afford more specific nest sites than woodland. Our study reveals a preference for re-use of nests in forest (41% in forest vs. 19% in woodland), supporting the hypothesis that forest is a preferred nesting habitat, but specific locations may be more heavily re-used due to greater availability of good building sites and forest vegetation. Faster return to re-use nests in forest may reflect ranging patterns (forest foods are patchily distributed and may be visited frequently to monitor food patches), quicker nest site re-usability (because forest nests decay faster), or greater density of available branches within the specific building area. Lack of seasonal differences in scar prevalence suggests that re-use did not occur as a result of paucity of material; fresh nests continued to be built in woodland habitat throughout the year at Issa.

Chimpanzees living in dry, open habitats, such as Ugalla, are estimated from nest counts to have home ranges between 278 and 560 km² in size (Kano, 1972; Baldwin et al., 1982; Ogawa et al., 2007). At the only dry study site where chimpanzees are currently habituated, so that home range is known from direct observation, the community has an estimated minimum home range of 63 km² (Pruetz, 2006). A high proportion of nests in Issa (19%) were re-used before the nest completely disappeared, which could slightly underestimate chimpanzee density and overestimate home range size. Accurate rates of decay, re-use, and construction of nests in the landscape are known to be crucial parameters for censusing chimpanzees using nest counts in varied ecological conditions (Plumtre and Reynolds, 1996, 1997; Plumtre, 2003; Plumtre and Cox, 2006).

The repeated use of specific nesting locations may be a result of the benefits of building a nest atop a prefabricated support structure, using supple new growth from repeated “pruning” of building positions. Human niche construction is a defining characteristic driven by cultural transmission processes, which form a feedback system that likely influenced the rate and processes of hominin evolution (Laland et al., 2000). Kimura (1999) argued that patterns of tool production in Oldowan sites reveal a flexible strategy that adapts to the type of available raw material, keeping energy costs low to achieve desired goals. Similarly, chimpanzees may select tool composites for nut-cracking based on the quality, or efficacy, of specific combinations of tools (Carvalho et al., 2009). Biro et al. (2010: 150) proposed the utility of an archaeological definition of ‘tool’ (from Karlin and Pelegrin, 1988: 823) for integrating the study of human and nonhuman tools: “Intentionally (or purposefully) made objects, or any natural object or knapping debris which show use-wear at the macro or micro scale.” In this way, a “tool construction” has affinities to nest construction as “two or more objects (transformed or not) that need to be used in combination in order to function and achieve a specific goal” (Carvalho et al., 2008: 159). Thus, a nest can be seen as a tool construction formed from several branches used in combination to achieve a unique goal (to make one nest). Carvalho et al. (2009) suggested that such preferential and frequent re-use of tools may lead to augmentation of use-wear traces: this appears to occur in re-use of nests as “composite tools” of combined branches.

Hernandez-Aguilar (2009) found that although food abundance and distribution influenced the ranging of chimpanzees at Issa, it did not explain the patchy distribution of nests. Topographical features of the landscape and morphological features of trees influence site selection as well, but these environmental features alone do not explain why certain areas are selected over others for nesting (Hernandez-Aguilar, 2006, 2009). Density of high quality specific building sites within trees, and stages of re-growth and healing of support structures, may also influence landscape scale nest site selection. Such environmental modification is common among many species of animal builders and burrowers (e.g., nests and burrows may be millennia- or centuries-old [Hansell, 2005, 2007]).

To date, only at the dry study sites of Issa (Hernandez-Aguilar, 2009) and Ishasha (Sept, 1992) have chimpanzee nest distributions been systematically studied to determine if the patterning of debris (using nests as a proxy) produced through chimpanzee ranging behaviour is distinguishable from that of early hominins as seen in the archaeological record. Both Sept (1992) and Hernandez-Aguilar (2009) found redundant re-use of nesting sites resulting in a patchy, clumped distribution, similar to the distribution of archaeological materials in early hominin sites. Their results demonstrate that Isaac’s (1978) home-base model with associated social changes such as food-sharing and division of labour is not necessary to produce this spatial patterning of materials. Hernandez-Aguilar (2009) additionally proposed that preferential use of favourite sleeping sites by chimpanzees may be analogous to the transport of food to preferred and tree-shaded places offering refuge to early hominins. She thus hypothesised that ape nesting behaviour may have been a precursor to such hominin-specific behaviour as carcass processing sites. The number of nests within sites monitored by Hernandez-Aguilar (2009) may be underestimated, as specific nest locations were counted once (unless signs of nest re-use were observed). Our results indicate that these locations show multiple episodes of use. Hernandez-Aguilar (2009) and Sept (1992, 1998) showed that chimpanzees return repeatedly to use the same geographic areas for nesting. Combined with hominin discard and deposition of archaeological materials as proposed by Sept (1992), the result would be scatters and patches of debris over large areas, e.g., Hernandez-Aguilar (2009)

monitored nest sites up to 1.5 km long. Specific artefact (i.e., nest) re-use shown here, within this larger geographic scale, if combined with archaeological debris, could account for micro-structuring of archaeological sites. Blumenshine and Masao (1991) found through “landscape archaeology” that artefacts were scattered across wide areas “off-site,” but scatters were not homogenous and higher densities of artefacts correlated with densities of bones. Potts (1984) proposed that concentrations of artefacts could occur by deliberate caching of stone tools, whilst Schick (1987) proposed an inadvertent build-up through a feedback system of artefact re-use, transport, and discard. However, few archaeological sites provide densities of artefacts measured in a way directly comparable to analogous chimpanzee archaeological sites (Carvalho and McGrew, in press). Despite the longevity of chimpanzee artefacts (nests and use-wear traces) seen in this study, the specificity of sleeping site re-use is a behaviour that is absent in the archaeological record, but which provides clues to factors such as niche construction that may have influenced early hominin artefact use and discard in the landscape.

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