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NEWS AND PERSPECTIVES

Tie one on: 'nest tying' by wild chimpanzees at Bulindi—a variant of a universal great ape behavior?

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Abstract

With data accumulating from a growing pool of chimpanzee field studies, new behaviors as well as novel variants on common behaviors continue to be described. Nest construction is a universal behavior in wild great apes. Among chimpanzee populations, reported variation in nest building behavior mostly reflects environmental constraints. Despite the ubiquity of nest making by chimpanzees, only ground nesting has been recognized as a behavioral variant, potentially determined by both environmental and social factors. In a study of nests made by chimpanzees (*Pan troglodytes schweinfurthii*) in Bulindi, Uganda, I identified a hitherto undescribed nest construction technique, termed 'nest tying'. Five observed nests lacked strong weight-bearing structures beneath them, such as large branches or a supporting trunk. Instead, the nests appeared 'tied' (or 'tethered') to an adjacent trunk by looping leafy stems or palm fronds around it and interweaving these into the nest mattress, securing the nest against the trunk; thus, nest tying presumably functions to provide added stability and support. This preliminary report presents a description of the observed nests. Irrespective of whether nest tying constitutes true knot making—commonly considered absent in wild great apes—this nest construction technique would seem to require advanced dexterity and a sophisticated understanding of the mechanical properties of the plants used. Forest fragments in Bulindi are highly degraded. Thus, nest tying—and construction of integrated nests (i.e., utilizing multiple plants, often small trees and shrubs) generally—may be promoted by a relative paucity of suitable nesting trees at this site. Still, insofar as nest building is learned in chimpanzees, different construction techniques including nest tying are potentially acquired through social learning. Further investigation is required to ascertain the prevalence and acquisition of this nest construction technique at Bulindi, and to verify its presence or absence in other habitats.

Keywords Behavioral diversity · Nest construction · Integrated nests · Knot tying · Palm nesting · Sleeping platform

Introduction

Nest construction is a universal behavior of great apes (Fruth and Hohmann 1996). In the wild, weaned individuals build a nest daily for sleeping at night and sometimes for resting during the day. A fundamental property of a nest (more accurately a 'bed' or 'sleeping platform') is that it is stable and capable of supporting the occupant's weight (van Casteren et al. 2012; Samson and Hunt 2014). The techniques employed by great apes to construct nests have been described previously (e.g., Bolwig 1959; Goodall 1962; Fruth and Hohmann 1993; Stewart et al. 2007; Prasetyo et al. 2009; van Casteren et al. 2012; Samson 2012). In arboreal nests, a sturdy branch, or branches, normally serves as the foundation or primary weight-bearing support, over which smaller branches and other foliage are bent, broken, and interwoven to form a springy leafy mattress. In some habitats, apes nest frequently in the crowns of palm trees (Leciak et al. 2005; Sousa et al. 2011; Ancrenaz et al. 2015), which lack lateral branches; for such nests, the palm's trunk provides the primary weight-bearing structure (Samson and Hunt 2014). Occasionally, nests are constructed from multiple trees. Such 'integrated' (Fruth and Hohmann 1993) or

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'composite' (Roffman et al. 2016; McCarthy et al. 2017) nests often use material from small trees and shrubs, which individually may be incapable of supporting an adult ape's weight. The use of multiple plants for nesting may be promoted in highly disturbed habitats with fewer large trees (Prasetyo et al. 2009; McCarthy et al. 2017). Even so, integrated nests are also common in some primary forest habitats (Fruth and Hohmann 1993; Koops 2011), suggesting that a scarcity of suitable nesting trees is not a prerequisite for this sophisticated nest construction technique.

While variation in nest building behavior across ape populations is apparent (Baldwin et al. 1981; Fruth and Hohmann 1994; Hernandez-Aguilar et al. 2013), differences can mostly be attributed to local habitat variables (e.g., the composition and characteristics of tree species available). However, some observed populational differences, such as ground nesting by chimpanzees, may also have a social or 'cultural' element (Koops et al. 2007; Hicks 2010; Tagg et al. 2013).

In a study of chimpanzee nests at Bulindi, Uganda, I identified a hitherto undescribed technique of nest construction termed 'nest tying'. Tied nests lacked a strong weight-bearing structure beneath them (i.e., a large sturdy branch or, in the case of palm nests, a supporting trunk) but were tied (or 'tethered') to an adjacent trunk, apparently for increased stability and/or additional support. This preliminary report presents a description of the observed nests and discusses potential factors influencing the occurrence of this technique of nest construction.

Methods

Bulindi is situated at 1°28′N and 31°28′E in Hoima District, western Uganda. Throughout Hoima, resident groups ('communities') of wild chimpanzees (*Pan troglodytes schweinfurthii*), including the Bulindi community, inhabit small, unprotected fragments of riverine forest amid farmland, villages, roads, schools and trading centers (McLennan 2008; McLennan et al. 2012; McLennan and Asiimwe 2016; McCarthy et al. 2015, 2017). From the 1990s until 2014, forest at Bulindi was heavily logged, resulting in the removal of many large trees (McLennan and Plumptre 2012). Additionally, between 2007 and 2014, ca. 80% of the forest area within the chimpanzees' home range in Bulindi was converted to agricultural land (Lorenti 2014). Common trees in forest fragments include the wild date palm *Phoenix reclinata*, *Pseudospondias microcarpa*, *Funtumia africana*, and members of the Moraceae family including *Trilepisium madagascariensis* and *Antiaris toxicaria* (McLennan and Plumptre 2012). Rainfall in the region is bimodal: March–May and August–November are usually wet months (> 100 mm rainfall per month). For further information on the ecology of Bulindi including climate and seasonality, see McLennan (2013, 2015) and McLennan et al. (2017).

Chimpanzees in Bulindi were first studied during 2006–2008 (McLennan and Hill 2010) and subsequently from 2012 to the present. I recorded cases of nest tying opportunistically during a study of chimpanzee nests at Bulindi between September 2012 and December 2015. Here, a 'tied nest' is defined as a nest in which one or more flexible stems (including slender branches, twigs or palm fronds) are looped around an adjacent trunk (or large branch) and reincorporated into the nest mattress, thereby tying or tethering the nest to the trunk.

I collected data on fresh nests built the previous evening (determined by presence of chimpanzees in nests in the early morning, or fresh dung and urine below nests), or 'recent' nests judged to be up to 1 week old. Recent nests contained leaves that were still green but starting to wilt. The following nest data were collected: tree/plant species used; whether a nest was integrated, i.e., constructed from ≥ 2 trees/plants [excluding nests with minor integration of climbing plants, and nests supported by multiple stems of a tree or shrub branching below diameter at breast height (DBH 1.3 m)]; and nest group size (number of same-age nests found within 30 m of the nearest nest; Mulavwa et al. 2010). For a subset of nests, I also recorded tree DBH and nest height [measured to the basal aspect of the nest with a rangefinder and clinometer (McLennan and Plumptre 2012); height of very low nests was sometimes estimated].

The Bulindi chimpanzee community numbered 18–21 individuals during the period considered here. The chimpanzees were habituated to researchers by late 2014 and were sometimes observed constructing day nests, which are considered structurally simpler than night nests (Fruth and Hohmann 1993; Brownlow et al. 2001). However, evening nest building was not observed and no direct behavioral observations of nest tying were made.

Results

Five cases of 'nest tying' were documented (Table 1; cases 1–5). These account for only 0.5% of the total nests recorded during the study ($N = 1064$). All five nests were presumed to be night nests, i.e., they were structurally complex, had dung or urine below, and/or were associated with other presumed night nests. Only in case 4 was the identity of the chimpanzee nest builder inferred (the alpha male). With the exception of case 3 (a medium-sized nest), the nests were large, suggesting that nest builders were adult chimpanzees. In each case, the nest lacked a strong weight-bearing structure beneath it such as a large branch (Fig. 1). Two nests were constructed in slender lateral branches of small trees (cases 1 and 2), one was

Table 1 Cases of 'tied nests' recorded during this study

Case # (date)	Nest age	Nest height (m)	Plant species used	Nest group size	Description of nest
1 (15 Oct 2012)	Fresh	2.5	*Ochna* sp. (including material from 2 trees and ≥ 2 saplings)	7	Low nest in *Ochna* tree. Horizontal support under nest provided by thin branch (ca. 6 cm diameter) protruding laterally from trunk. Nest incorporates leafy branches of ≥ 2 *Ochna* saplings and leafy branch from adjacent *Ochna* tree (broken and protruding from nest). Leafy stems from nest looped tightly around *Ochna* trunk (leaning at 45° angle) and reincorporated into nest mattress (Fig. 1a, b)
2 (19 Nov 2012)	Fresh	16.7	*Macaranga schweinfurthii*, *Pseudospondias microcarpa*, Unidentified liana, *Pycnanthus angolensis*	2	Nest in thin lateral branches of *Macaranga* tree. Nest incorporates terminal branches of adjacent *Pseudospondias* tree and leafy stems of unidentified liana. Liana stems looped around adjacent *Pycnanthus* tree trunk and integrated into basal structure of nest (Fig. 1c)
3 (11 Apr 2013)	Fresh	10	*Uvaria welwitschii*, *Funtumia africana*	8	Nest in *Uvaria* liana entangled around trunk of *Funtumia* tree. Nest not supported by any lateral *Funtumia* branch; ≥ 1 *Uvaria* stems from nest looped around trunk and reincorporated into nest structure (no image available)
4 (1 Oct 2014)	Fresh	2.8	*Phoenix reclinata* (including material from multiple young palms with support from adjacent mature palm)	1	Large, low nest in young, trunkless *Phoenix* palms leaning against adjacent palm trunk. Multiple fronds bent over forming a thick mattress; ≥ 2 fronds looped tightly around trunk and interwoven into nest (Fig. 1d, e). The alpha male (SL) and largest chimpanzee at Bulindi was seated in nest at 09:14 a.m. and was presumably the nest builder
5 (4 Oct 2014)	Recent	2	*Phoenix reclinata* (including material from multiple young palms with support from adjacent mature palm)	Unknown[a]	Large, low nest in young, trunkless *Phoenix* palms, leaning against adjacent palm trunk; ≥ 1 fronds looped around trunk and reincorporated into nest mattress (Fig. 1f). The 'knot' was loose but had presumably been tighter at time of construction

[a]Nest group size was undetermined for case 5. The nest was ≤ 1 week old. Other recent nests were nearby but it was not possible to determine if they were built on the same evening

constructed in shrubby stems of a liana (case 3), while two were built from fronds of young *Phoenix reclinata* palms without trunks (cases 4 and 5). In each case, leafy stems or palm fronds had been looped or wrapped around an adjacent trunk and interwoven into the nest mattress, 'tying' the nest to the trunk. In cases 2–5, the nest was tied to the vertical trunk of an adjacent tree, while in case 1 the nest was tied to the leaning trunk of the same tree. Physical examination of one nest (case 1) attested to how securely the nest was tethered to the adjacent trunk (Supplementary material).

Integrated (or composite) nests accounted for 14.8% ($n = 158$) of recorded nests. All tied nests qualified as integrated since each utilized more than one plant for nesting material or support. Nest height was measured for 586 nests. Mean height was 11.8 m (± 7.0 SD; range, 0.5–46.2 m). Four of the five tied nests were below this average height, and three (cases 1, 4, and 5)

Fig. 1 Examples of 'tied nests' constructed by chimpanzees in Bulindi. *Clockwise from top left*: **a** nest constructed in an *Ochna* sp. tree (case 1). Horizontal support beneath the nest is provided by a small lateral branch; the branch protruding from the top left of the nest is detached and does not provide support. On the right side of the nest, leafy stems have been looped tightly around the trunk and back into the nest mattress, securing the nest firmly to the adjacent trunk; **b** detail of the same nest showing leafy stems 'tying' the nest to the *Ochna* trunk (see also Supplementary material); **c** nest constructed in terminal branches of a *Macaranga schweinfurthii* tree (case 2); the *arrow* indicates stems of an unidentified liana that are wrapped around an adjacent tree trunk and incorporated into the nest mattress; **d** nest in young, trunkless *Phoenix reclinata* palms; several fronds used in the nest mattress are 'tied' to the trunk of an adjacent palm (case 4); **e** detail of the same nest showing overlapping fronds wrapped tightly around the adjacent trunk; **f** week-old nest in trunkless *Phoenix* palm fronds, leaning against an adjacent palm trunk (case 5); at least one frond is looped around the trunk and reincorporated into the nest mattress (indicated by *arrow*)

were constructed at markedly low heights (2–3 m). Integrated nests were generally constructed at lower heights than non-integrated nests (median height of integrated nests = 4.9 m, $n = 91$; non-integrated nests = 11.6 m, $n = 495$; Mann–Whitney test: $U = 7977.5$, $Z = -9.79$, $p < 0.0001$).

The five tied nests were recorded over a 2-year period (Table 1), and thus were not clustered temporally, although cases 4 and 5 were observed during 1 week in October 2014. All five nests were recorded during wet months (in April, October, and November).

Discussion

The five cases of 'tied nests' reported here represent a small proportion (0.5%) of nests recorded during the study period. Thus, nest tying is not a common nest construction technique at Bulindi. However, nests were not examined systematically for evidence of tying; cases were noted opportunistically only when nests were relatively low and easily visible. Thus, additional cases were probably missed in higher nests or nests obscured by foliage.

Nest tying apparently functions to gain increased stability and added support from an adjacent trunk for nests constructed without strong foundation branch(es) below. Notably, two tied nests (cases 4 and 5) were built in young *Phoenix reclinata* palms (Fig. 1d, f). Aggregations of *Phoenix* palms are a common structural feature of riverine and swamp forest in Bulindi (McLennan and Plumptre 2012) and large, low nests constructed from the fronds of young palms are not uncommon (28 nests recorded in this study were of this type; 2.6%). Since young palms lack trunks, such nests typically lean against an adjacent vertical trunk for added support and stability (i.e., to prevent them tilting), but do not normally show evidence of 'tying' (Fig. 2). Still, tying presumably makes leaning nests more stable than otherwise. While I found no similar descriptions of tying or tethering in previous studies of nest construction in great apes, this technique might be present in other studied populations but undescribed. Roffman et al. (2016) described a sophisticated integrated chimpanzee nest in Mali, in which bamboo stalks were "tied" and bent into the nest; however, bamboo is unlikely to have been tied in the manner described here for highly pliant palm fronds and leafy stems (i.e., looped around a trunk to secure the nest against it).

Fig. 2 Typical large, low nest constructed in fronds of young, trunkless *Phoenix reclinata* palms at Bulindi, without a strong supporting branch below. Unidentified lianas are also incorporated into the nest mattress. The nest leans against an adjacent *Phoenix* palm trunk for added support and stability. Such low palm nests do not ordinarily show evidence of tying (cf. Fig. 1d–f)

Knot tying is rare in captive great apes and possibly absent in the wild (McGrew and Marchant 1998; Herzfeld and Lestel 2005). In the present context, it would require a stem or frond being looped around a trunk and the two ends overlapped and pulled tight; however, I did not examine nests sufficiently to determine this (but see Fig. 1d, e). Furthermore, without behavioral observations, it remains possible that 'tying' is an incidental outcome of interweaving nest materials in proximity to an adjacent trunk. In future cases, detailed examination of nest architecture would help determine whether nest tying is indeed intentional. Assuming intentionality, however, and irrespective of whether nest tying constitutes true knot making, this technique would seem to demonstrate an advanced level of dexterity and—like other integrated nests that utilize tension and rely on the nest builder's weight to keep the nest together—a sophisticated understanding of the mechanical properties of materials used in construction ('engineering know-how': van Casteren et al. 2012; see also Samson and Hunt 2014).

Forest fragments in Bulindi are highly degraded. The canopy is broken and irregular with an abundance of trees in small diameter classes and a relatively low density of large trees (McLennan and Plumptre 2012). Thus, construction of integrated nests at Bulindi (15% of nests), including tied nests, may be promoted by a paucity of suitable nesting trees, as was proposed to explain the relative abundance of integrated chimpanzee nests observed elsewhere regionally (McCarthy et al. 2017). Even so, all tied nests were located near larger trees of species commonly used for nesting in Bulindi (e.g., *Pseudospondias microcarpa*). Adult male chimpanzees tend to nest at lower heights than females (Brownlow et al. 2001). Given the overall low height and large size of tied nests, nest tying (and construction of integrated nests generally) could be a male-biased behavior, similar to ground nesting (Koops et al. 2007). However, it is possible that nest tying is idiosyncratic at Bulindi, perhaps performed by the alpha male, the probable nest builder in case 4 (Table 1), and who was known to be present in at least two other nest groups that included a tied nest.

Nevertheless, insofar as nest building is a learned behavior in chimpanzees (Videan 2006; Fultz et al. 2013), different construction techniques such as nest tying are potentially acquired through social learning. In their list of candidate 'cultural' behavioral patterns in wild chimpanzees, Whiten et al. (1999, 2001) did not consider ordinary nest building. However, a variant of nest building behavior—ground nesting—was included, though its absence at some sites was attributed to environmental rather than social factors (cf. Koops et al. 2007). Similarly, nest tying may be considered a candidate variant of this universal great ape behavior.

Further investigation is required to ascertain the prevalence and acquisition of this nest construction technique at Bulindi, and to verify its presence or absence in other habitats.

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