

The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve, Uganda

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Abstract The nightly construction of a sleeping platform (SP) or “nest” is widely regarded as a universal behavior among great apes, yet SP structural morphology has been incompletely quantified to date. This is in part due to the inherent difficulties of gathering empirical data on arboreally sited SPs. I gathered quantitative structural data on SPs ($n = 65$) at the Toro-Semliki Wildlife Reserve from May to June 2008 and from August 2010 to January 2011. I measured SP length (semi-major axis length), width (semi-minor axis length), radii (length from the surface center to the rim edge 45° from the axis), depth (width of the concavity from the surface center to the parallel rim), and thickness (ventral center to the dorsal underside of the SP). SP complexity was defined with a scored index. SP complexity was found to be correlated with SP circumference, surface area, mass, proportion of soft leafy material to hard woody material, number of frame support branches used in its construction, and other measures that are argued to index “comfort.” In addition, the height of the tree canopy above the SP was negatively correlated with SP complexity. Greater complexity (and therefore stability) is argued to maintain SP integrity, stability and restraint in the face of greater wind speeds, thereby reducing the probability of falls. Given the observation that males site SPs lower than females (Fruth and Hohmann, *Ethology* 94:113–126, 1994; Brownlow et al., *Am J Primatol* 55:49–55, 2001), and that SP diameters were greater for SPs sited low in the canopy at Semliki, it is inferred that more massive males benefit from lower climbing expenses and greater stability. These data support Baldwin and colleagues’ (Primates

22:474–486, 1981) hypothesis that the principal advantage of SPs over open-branch sleeping sites is the greater stability required by large-bodied great apes.

Keywords Chimpanzee · Nest · Sleep · Morphology · Evolution · Methodology · Structure

Introduction

Great apes spend half of their lives in a “night nest.” The construction of a new nest each day requires time and effort as individuals search for an appropriate site and maneuver into position to construct the platform by manipulating a large volume of foliage (Goodall 1962, 1968). The nest is a complex construction (Shumaker et al. 2011) that is manufactured to function as a stable, comfortable mattress (Stewart et al. 2007). This behavior has been observed in every chimpanzee, bonobo, gorilla, and orangutan population yet studied.

During the sixteenth and seventeenth centuries, Portuguese explorers in the Sierra Leone referred to the chimpanzee sleeping substrate as a “bed” (Sept and Brooks 1994). The term “nest” had been popularized during nineteenth-century African expeditions (Du Chaillu 1861). Attempts at objective, naturalist observation began in the early twentieth century, with a thorough review of all ape sleeping substrate literature by Yerkes and Yerkes (1929). Nissen (Nissen 1931) was the first to describe the wild chimpanzee sleeping substrate as a “nest” in a field study. The popularity of this term has since been lamented by several authors. Although these structures superficially appear analogous to large bird nests, they do not fit the definition of a nest, which is generally a fix-point for central foraging, breeding, rearing of young, or storage of

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resources (Hediger 1977; Baldwin et al. 1981; Hansell 1984, 2005; Groves and Sabater Pi 1985; McGrew 1992; Thorén et al. 2010). Therefore, this article adopts the functionally descriptive term “sleeping platform” (SP), originally used by Goodall (1962: 455) and described as more terminologically appropriate by McGrew (1992), when referring to chimpanzee nests or any sleeping substrate constructed in the manner employed by the extant great apes. The sleeping substrates among different primate taxa are functionally heterogeneous (Kappeler 1998), but ape sleeping platforms are functionally more closely related to human beds than nests made by other species (Fruth and Hohmann 1996; Kappeler 1998; Videan 2006); for example, the most common forms of bedding used by hunter-gatherers include a substrate on which to rest the body and often a covering for the substrate and the body itself (Worthman and Melby 2002). The Efe use materials such as leaves, a similar substrate to great ape nesting. The Alutiiq prepare the ground by first laying grass down and then layering mountain-goat and bear skins (Lantis 1938). The oldest evidence of bedding (generally a completely organic material) was discovered in situ in Israel, and dates to 23,000 years old (Nadel 2004); it was grass bedding, and consisted of stems and leaves covered by compacted clay. Therefore, sleeping platform construction in the Hominidae is a derived trait that evolved to serve other functions (Kappeler 1998).

McGrew (2004) noted that hypotheses purporting to explain the functions of SPs have yet to be rigorously tested. Among the proposed functions of SPs are: predation avoidance (Kortlandt 1992; Pruett et al. 2008), thermoregulation (McGrew 2004), pathogen or parasite avoidance (Fruth and Hohmann 1996; Anderson 1998; Nunn and Heymann 2005), and mental health or sleep quality (Fruth and Hohmann 1996; Sabater Pi et al. 1997; Anderson 1998). Houle and colleagues (2004) noted that gaining access to tree canopies would add a new dimension of information to primatological field research—this new knowledge being essential in order to test SP function. Research targeting the proximate cause of ape SP construction and location is burgeoning (Ancorenaz et al. 2004; Koops et al. 2007; Ogawa et al. 2007; Stewart et al. 2007; Hernandez-Aguilar 2009; Stewart 2011), including a concurrent study of SP architecture at Issa, Ugalla (Stewart et al. 2011). Unfortunately, due to the inherent difficulties of gaining access to arboreal SPs, little is empirically known about their structural morphology. For example, SP height varies greatly across field sites. Reported mean heights show that SP height ranges from 8.33 m (Pruett et al. 2008) in Senegal to 20 m at the Ivory Coast (Fruth and Hohmann 1994).

This study was conducted to generate quantitative data on the morphology of dry habitat chimpanzee SPs. In

addition, an analysis was performed to compare SP structures of different tree species and assess the relationships of SP morphology with associated environmental variables. This descriptive analysis provides the groundwork for future great ape cross-site comparisons of SP morphology by illustrating a safe and efficient method of accessing previously inaccessible arboreal sleeping sites. Finally, presenting empirical data on SP morphology may prove useful for enriching captive ape sleeping environments by informing researchers about the structure of wild ape sleeping substrates and applying these results to the sleeping platforms provided for individual sleeping enclosures.

Methods

Study area

Chimpanzees have been studied in the Toro-Semliki Wildlife Reserve (TSWR) in western Uganda since 1996. TSWR is northwest of Fort Portal, close to the eastern edge of the Great Rift Valley (0°50′–1°05′N, 30°20′–30°35′E), and encompasses 548 km². Semliki consists of strips of dry gallery forest (50–250 m wide) bounded and crosscut by watercourses; within these forests emergent trees reach as high as 50 m (Allan et al. 1996; Hunt and McGrew 2002). The chimpanzee study community range includes the Mugiri River and its tributaries, as well as open woodland and bushland on the escarpment near the northeastern reserve boundary. The biome is predominantly dry *Combretum ghasalense* savanna and *Borassus aethiopicum* palm savanna. The range of the Mugiri chimpanzees is limited to the northeast by tea estates and peasant holdings at the top of the escarpment. The chimpanzee community is heavily reliant upon fruiting species such as *Beilschmiedia ugandensis*, *Cynometra alexandri*, *Cola gigantea*, *Phoenix reclinata*, and *Tamarindus indica* (Hunt and McGrew 2002). Their community home range is the largest known at 72.1 km² (measured with the minimum convex polygon of any area where identified individuals have been observed), with the second and third largest home ranges being the dry-habitat sites of Fongoli at 64 km² (Pruett 2006) and Assirik at 50 km² (McGrew et al. 1996; Tutin et al. 1983). There are estimated to be 30 males, which suggests a community size of approximately 104 (estimated using the average sex ratio across *P. t. schweinfurthii* sites) (Stumpf 2007). Finally, chimpanzees within this community disproportionately select *Cynometra alexandri* as a sleeping tree (Hunt and McGrew 2002), but do also sleep in others (*Albizia grandibracteata*, *Cola gigantea*, *Combretum molle*, *Ficus mucoso*, *Phoenix reclinata*, and *Pseudospondias microcarpa*).

Data collection

From May to June 2008 and August 2010 to January 2011 I gathered data on 65 Semliki chimpanzee sleeping platforms using two methods: (1) if the SP was less than 10 m high and deemed safe enough to climb without equipment, I freeclimbed the tree to gain access to the SP; (2) if the SP was higher than 10 m, I used a double-rope technique (DRT) with arborist clog-ascending gear with rope, line, saddle, foot, and hand ascender equipment to gain access to the SP (Fig. 1; for a detailed description of climbing techniques, see Houle et al. 2004). The latter method required a throw bag (a 12 oz heavy-duty vinyl weight) attached to a line to be thrown over a branching fork above the target SP. Once the throw line was in place, a heavy-duty arborist rope was pulled through and over the fork by attaching it to the throw line. Using the DTR, I pulled myself up the line by attaching the saddle to the appropriate foot and hand ascenders by way of a dynamic Prusik knot (a friction hitch used to put a loop of cord around a rope) system. DTR allows for the greatest horizontal movement along tree branches, which is essential to gain access to SPs that are great distances from the main trunk.

Sleeping platforms were selected using multiple criteria. The primary criterion was safety. A safe climb was defined as having a branching fork above the SP with a limb diameter greater than 10 cm; an open line of sight from the ground to the SP was a prerequisite for a secure climb. Greater height can limit access to SPs, as branching fork limbs decrease in diameter as height of the target SP increases. Yet, in this study, SPs were quantified up to 20 m in height. This is within the range of field sites with

the highest SP height—illustrating the capacity for this method to be employed at all chimpanzee field sites. In addition, binoculars were used to assess the structural integrity of weak or rotting limbs associated with or near the SP, as well as to note whether biting insects or dangerous fauna (e.g., ants, bees, snakes, etc.) were to be disrupted and agitated by the climb. Age was also a criterion. The age of the SP was classified into one of three classes following methods employed in previous studies (Hashimoto 1995): (a) fresh vegetation green or not wilted; (b) recent vegetation dry and changing color; (c) old vegetation dead but SP still recognizable. Construction was never observed, but an effort was made to quantify fresh SPs within days of construction once a new SP cluster was identified.

The dimensional SP variables were recorded to the nearest centimeter using a folding wooden ruler (which could be easily maneuvered within the tree canopy and readily pierce the SP surface without disrupting the structure itself); the following were recorded for each SP accessed within the canopy (see Stewart and colleagues 2007 for greater detail on the complexity, comfort, and softness measures):

1. Length: semi-major axis (or longest diameter) length
2. Width: semi-minor axis (or longest line segment that runs perpendicular to the major axis) length
3. Radii (1–4): the length from the surface center to the rim edge 45° from the axis (measured in 4 quarters running from the center focal point to the rim)
4. Depth: the width of the concavity from the surface center to the parallel rim

Fig. 1 DRT tree climbing method using clog-ascending equipment that was employed to gain access to arboreal SPs within the riverine gallery forest of Semliki, Uganda. Photograph taken by W.C. McGrew in June 2008



5. Thickness: the ventral center to the dorsal underside of the SP
6. Edge thickness (1–4): measured (in four points forming a rectangle within the ellipsoid rim) from a standard distance from the SP edge (5 cm) down through the body to the outer ventral surface
7. Number of frame support branches (FSB): defined as a branch that is bent or cracked in the initial stages of SP construction and then roughly interwoven with or laid on top of additional FSBs to form the primary supporting structure on which the chimpanzee can lay across horizontally (Fig. 2)
8. FSB circumference: measured distally at each bend/break
9. Total number of potentially usable FSBs adjacent to the SP (see FSB utilization index below)
10. Distance from the SP to the main tree trunk
11. True SP height: measured from the dorsal aspect of the SP to the ground (using a tape measure)
12. Total mass (SPs were cut from all attaching limbs using pruning shears and then bagged and later weighed using a digital hanging scale)
13. SP complexity (1–4): using an ordinal scale of 1–4 where 1 = ill-defined circular SP shape, insubstantial construction and 4 = well-defined circular shape and substantial construction
14. Index of visual discomfort (1–7): using an ordinal scale of visible discomfort where 1 = visible part of any branch <5 cm in length and 7 = visible part of any branch >30 cm in length and with a circumference >7 cm
15. Softness: a percentage estimate of the leafy, soft area versus hard, woody area on the SP surface.

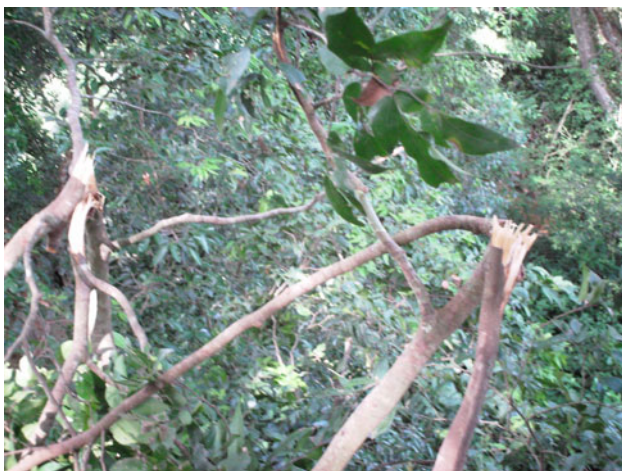


Fig. 2 FSBs from a *Cynometra* SP (12.3 m high) which have been cracked and manually weaved by a chimpanzee to frame a secure sleeping structure. Photograph taken by D.R. Samson in August 2010

After SP dimensions were recorded, I descended by repelling down the arborist rope. In addition, the following variables were recorded:

1. Tree species
2. Estimated distance of canopy above the SP (m).

Data analysis

The dimensional variables recorded in this study permit a typological assessment of SP structure. With the values generated, indices were calculated to further assess SP morphology. For example, a frame support branch utilization index was calculated to determine to what extent chimpanzees use the adjacent branches within range of the SP when weaving the supporting frame. FSBs are different from the additional SP materials (e.g., leafy twigs) added post-FSB construction to the SP. Therefore, the frame support branch utilization index is the number of FSBs used in SP construction divided by the total usable number of FSBs adjacent to the SP. The average circumference of an FSB is $4.86 \text{ cm} \pm 2.73$ ($n = 222$; range = 1–12 cm).

The SP perimeter was calculated with the formula for the perimeter of an ellipse (where a is the major axis and b is the minor axis):

$$\pi/2 \sqrt{(\sqrt{2a} + \sqrt{2b})^2}$$

Sleeping platform surface was calculated with the formula for an ellipse: πab (where a is the major axis and b is the minor axis). To determine whether there is a difference in SP characteristics between selected trees,

Table 1 Species analyzed in this study, as well as the number of times a whole SP was measured for this species

| Species | Number of SPs quantified |
|----------------------------------|--------------------------|
| <i>Cynometra alexandri</i> | 41 |
| <i>Combretum ghasalense</i> | 4 |
| <i>Pseudospondias microcarpa</i> | 4 |
| <i>Albizia grandibracteata</i> | 2 |
| <i>Dombeya mukole</i> | 2 |
| <i>Alangium chinense</i> | 1 |
| <i>Celtis wightii</i> | 1 |
| <i>Cola gigantea</i> | 1 |
| <i>Linociera leptopetala</i> | 1 |
| <i>Lovoa swynnertonii</i> | 1 |
| <i>Phoenix reclinata</i> | 1 |
| Unknown | 6 |
| Total | 65 |

Cynometra is a species that is highly preferred by Semliki chimpanzees; yet, alternative, less often selected tree species were sought to illustrate the variation between species

I compared species ($n = 11$; see Table 1) against several SP variables (one-way ANOVA); the ANOVA analysis passed Levene's test of homogeneity of variance and normality. Statistical tests were used to detect relationships between SP and environmental variables (Pearson correlation and Spearman's rho correlation for non-normally distributed data). All statistical tests were two-tailed, set at a significance level $\alpha = 0.05$.

Results

Sleeping platform morphology parameters are described in Table 2 and illustrated in Fig. 3. Of the 65 SPs investigated, a total of 81 % were fresh, 14 % were recent, and 5 % were old. The one-way ANOVA test comparing SP variables showed that leafy surface % ($F = 3.980$, $p = 0.006$), SP surface area (m^2) ($F = 3.479$, $p = 0.001$), and SP circumference (m) ($F = 2.665$, $p = 0.010$) significantly differ among tree species; all other variables were found to be nonsignificant.

Sleeping platform complexity correlates with several other SP variables (see Table 3). In addition, SPs located closer to the canopy are characterized by greater complexity ($n = 29$, Pearson correlation $r = -0.395$, $p = 0.034$). In addition, SPs located high in trees have a smaller surface area ($n = 62$, Pearson correlation $r = -0.301$, $p = 0.018$) and circumference ($n = 62$, Pearson correlation $r = -0.307$, $p = 0.015$), and therefore a smaller total size.

Table 2 Descriptive dimensional statistics defining SP morphology

| Variable | n | Mean and SD | Mode (categorical) | Range |
|----------------------------|-----|--------------|--------------------|-----------|
| Length (m) | 63 | 0.93 ± 0.16 | | 0.51–1.51 |
| Width (m) | 63 | 0.71 ± 0.12 | | 0.45–0.97 |
| Radii (cm) | 65 | 38.86 ± 6.88 | | 21.5–53.3 |
| Depth (cm) | 53 | 8.7 ± 6.3 | | 0–31 |
| Thickness (cm) | 61 | 34.32 ± 13.5 | | 11–81 |
| Edge thickness (cm) | 60 | 22.68 ± 8.78 | | 7–49 |
| Average FSBs per SP | 60 | 4.13 ± 1.11 | | 2–8 |
| Circumference (m) | 63 | 2.60 ± 0.41 | | 1.59–3.98 |
| FSB utilization index | 34 | 0.74 ± 0.20 | | 0.43–1 |
| SP to main trunk (m) | 64 | 0.94 ± 1.90 | | 0–12 |
| True SP height (m) | 62 | 8.84 ± 3.36 | | 3.24–19.5 |
| Mass (kg) | 32 | 3.12 ± 1.35 | | 0.77–5.56 |
| Surface area (m^2) | 65 | 0.51 ± 0.18 | | 0.00–1.15 |
| Complexity index | 30 | | 3 | 2–4 |
| Index of visual discomfort | 28 | | 3 | 1–7 |
| Softness (%) | 28 | 88.82 ± 8.83 | | 55–98 |

Discussion

Dry habitat chimpanzee SPs have a consistent and uniform morphology. The general outline of the SP is an elongated bowl. The rim shape is concave towards the ventral surface of the SP and is generally ellipsoid; the smaller the SP, the more circular the overall rim shape. Complexity correlates with several SP variables such as circumference, surface area, mass, visual discomfort, ratio of soft leafy material to hard woody material, and number of available FSBs used in its construction.

Brownlow and colleagues (2001:49) noted the importance of quantifying the variability of the products of SP manufacture behavior: “Examination of the sources of variation in the bed-building behavior of the great apes has both theoretical and applied significance. By assessing the impact of habitat variables on nesting parameters we can measure *flexibility* and *selectivity* in nesting behavior [emphasis is mine].” The argument has been made that variation in the structural differences in SPs are causally related to environmental determination (Baldwin et al. 1981); in contrast, a recent study has suggested that certain aspects of chimpanzee site selection and re-use may be due in part to “niche construction” or purposeful formation of good construction sites within trees (Stewart et al. 2011). Future research should use the presented climbing technique to perform cross-field site comparisons of SPs, tree selection, and niche construction. Additionally, morphologically unique species chosen for SP construction, such as oil palms that are commonly used for sleeping sites in Guinea-Bissau (Sousa et al. 2011), should be targeted for quantification to allow a direct comparison with more conventional tree species used. Using such methods may allow workers to sift out the variables that are related to differences between sexes, individuals, experience levels, and/or populations; in turn, once these variables can be controlled for, if the SP morphology differs amongst sites, it may support the suggestive possibility that SPs can be included within the greater umbrella of chimpanzee culture (Fruth and Hohmann 1994).

Interestingly, the closer the SP is to the top of the forest canopy, the more complex it is. It has been shown that wind speeds are greater in chimpanzee sleeping sites that are higher and have less canopy cover (Samson and Hunt in press). Therefore, it is hypothesized that in face of greater wind speeds, an individual would need to construct a more secure (using a greater number of FSBs) and therefore more complex SP to prevent falling from it while sleeping.

Workers have observed that male bonobos (*Pan paniscus*) (Fruth and Hohmann 1993, 1994) and common chimpanzees (Brownlow et al. 2001) site SPs significantly lower than females. Reynolds (1967) originally proposed that this was caused by sexual dimorphism in body mass.

Fig. 3 An illustration of the average dry habitat chimpanzee sleeping platform. Figure adapted from Stewart et al. (2007), personal communication

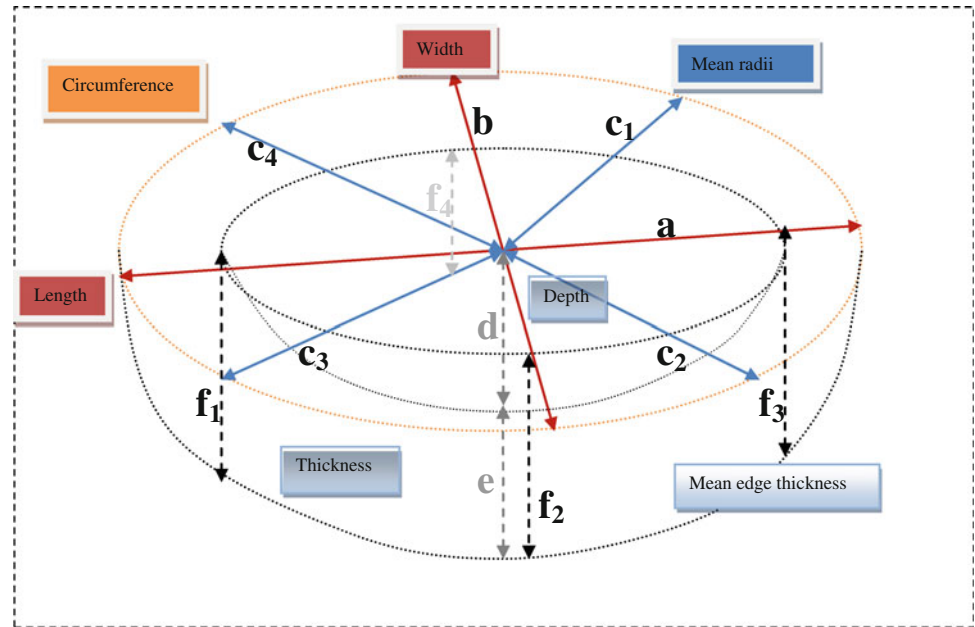


Table 3 SP complexity correlates with several SP dimensional variables

| SP categories | SP size | | | SP construction | | |
|---------------|---------------|-------------|--------------|-----------------------|----------------------------|-----------------|
| SP variables | Circumference | Mass | Surface area | FSB utilization index | Index of visual discomfort | Leafy surface % |
| Complexity | $n = 29$ | $n = 26$ | $n = 30$ | $n = 28$ | $n = 28$ | $n = 28$ |
| | $r = 0.588$ | $r = 0.538$ | $r = 0.509$ | $r = 0.398$ | $r = 0.744$ | $\rho = 0.744$ |
| | $p = 0.001$ | $p = 0.005$ | $p = 0.004$ | $p = 0.036$ | $p < 0.001$ | $p < 0.001$ |

Pearson correlation was used for normalized data, while Spearman’s rho correlation was used for non-normally distributed data (e.g., leafy surface was right-skewed)

At Semliki, the variables that relate to SP size are negatively correlated with the height of the SP (Fig. 4). Considering that Hunt (1994) found large chimpanzee males vertically climb less to limit daily energy expenditure, it is inferred that more massive males benefit by siting SPs lower than females by way of lesser energetic climbing costs and greater stability.

In regards to the evolutionary origins of ape SPs, Baldwin and colleagues (1981) proposed two competing hypotheses to explain the origin of SPs among the great apes. The cognitive hypothesis suggests that apes manufacture SPs because their great intelligence allows it. Thus, even though the ape SP increases personal comfort, it provides little selective advantage; rather, it is a byproduct of ape intelligence. Alternatively, the weight bearing hypothesis proposes that the great body weight of apes requires SPs, since balancing on branches during sleep is difficult for massive primates.

The study of primate cognition, especially object manipulation, derives from Piaget’s (1952) theory of sensory-motor development. Primate “intelligent tool use” is different from other forms of animal tool use in that there is

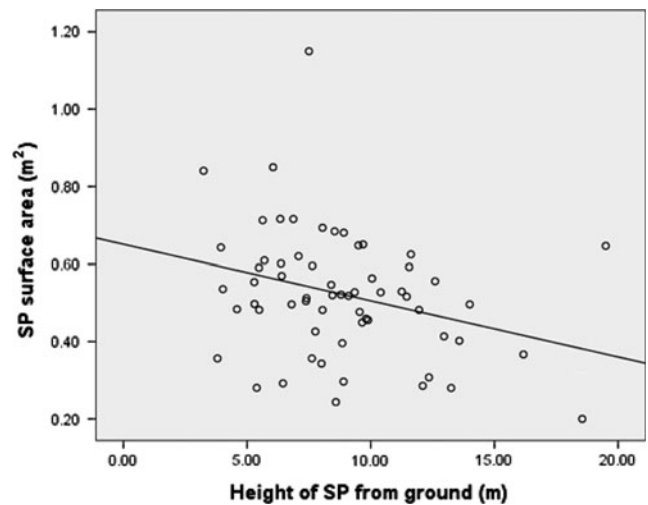


Fig. 4 Height of the SP from the ground is negatively correlated with the size of the surface of the SP ($r = -0.301$). The regression equation is stated as: surface area = 0.651 + 0.015 (height)

less overt trial-and-error learning and working and more mental representation (i.e., thinking and goal-directed insight; Parker and Gibson 1977). Therefore, although

Piaget's schemes are only one measure of cognition, primates are more readily applied to the Piagetian framework; see (Tomasello and Call 1997:57–99) for an in-depth discussion of primate understanding of tool use and causality within a Piagetian framework. The cognitive hypothesis can be rejected because two genera of non-ape primates exhibit cognitive abilities (Piagetian tertiary schemes where actions relate external entities to one another) analogous to SP building: *Cebus* (Parker and Gibson 1977; Fragaszy and Adams-Curtis 1991; Westergaard and Suomi 1994; Fragaszy et al. 2004) and *Papio* (Westergaard 1992, 1993). Capuchins and baboons have the intelligence to construct SPs, but there have been no recorded instances of such construction in the wild by either species.

In contrast to the cognitive hypothesis, the weight-bearing hypothesis is supported by this study. Throughout the Miocene, primate body size underwent positive selection from a smaller ancestral form (Fleagle 1999). With increases in size, extinct primates may have needed to build SPs to secure themselves from falling from lethal heights. The evolutionary origins of the SP may be explained by two aspects of the allometric effect: (1) branch size is relatively constant among species, so large-bodied primates must position themselves on relatively smaller supports; (2) even if larger primates positioned themselves on geometrically proportional supports, stress increases disproportionately—as body length increases, weight increases as the cube of length, whereas the surface of the body supporting the weight increases as only the square. As a result, large primates disproportionately stress the skin, connective tissue, and skeleton when lying horizontally. Therefore, as primate mass increased in the Miocene, the relatively constant size of the supporting branches that primates rely upon for safe and secure sleep would have no longer been appropriate for the task. Only extant primates above 32 kg build SPs in the wild. This threshold may be a terminal cut-off point at which selection pressure is too great for primates that weigh more than the threshold to forgo habitually making nightly SPs. Given that Semliki males are inferred to use larger SPs at lower heights and that SP complexity increases as individuals select areas with greater wind exposure, the data generated in this study supports the weight-bearing hypothesis as a primary function and a catalyst for the creation of SPs in early primate evolution.

In summary, greater SP complexity is argued to be a central component of increased stability and restraint in the face of greater wind speeds, thereby reducing the probability of falls. This observation may explain why males site SPs lower than females, and why SP diameters were greater for SPs sited lower in the canopy—due to the benefit attained by massive males from lesser climbing expenses and greater stability. In contrast, it also explains

why females, siting SPs higher in the canopy, manufacture more complex SPs in the face of greater wind speeds. These data support Baldwin and colleagues' (1981) hypothesis that the principal adaptive advantage (which facilitated the evolutionary origins of arboreal ape sleeping substrates) of SPs over open-branch sleeping sites is the greater stability required by large-bodied great apes.

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References

- Allan C, Sivell D, Lee T (1996) Semuliki (Toro) Game Reserve, Uganda: results of the Frontier-Uganda Biological Assessment (report no. 7). The Society for Environmental Exploration, London
- Ancrenaz M, Calaque R, Lackman-Ancrenaz I (2004) Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: implications for nest census. *Int J Primatol* 25:983–1000
- Anderson JR (1998) Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *Am J Primatol* 46:63–75
- Baldwin PJ, Sabater Pi J, McGrew WC, Tutin CEG (1981) Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates* 22:474–486
- Brownlow AR, Plumtre AJ, Reynolds V, Ward R (2001) Sources of variation in the nesting behavior of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Am J Primatol* 55:49–55
- Du Chaillu PB (1861) Explorations and adventures in equatorial Africa. Harper Brothers, New York
- Fleagle JG (1999) Primate adaptation and evolution. Academic Press, San Diego
- Fragaszy DM, Adams-Curtis LE (1991) Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). *J Comp Psychol* 105:387–397
- Fragaszy D, Izar P, Visalberghi E, Ottoni EB, Oliveira MGD (2004) Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am J Primatol* 64:359–366
- Fruth B, Hohmann G (1993) Ecological and behavioral aspects of nest-building in wild bonobos (*Pan paniscus*). *Ethology* 94:113–126
- Fruth B, Hohmann G (1994) Comparative analyses of nest building behavior in bonobos and chimpanzees. In: Wrangham RW, McGrew WC, de Waal FBM, Helme PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, pp 109–128
- Fruth B, Hohmann G (1996) Nest building behavior in the great apes: the great leap forward? In: Marchant LF, Nishida T (eds) Great

- ape societies. Cambridge University Press, Cambridge, pp 225–240
- Goodall J (1962) Nest building behavior in the free ranging chimpanzee. *Ann N Y Acad Sci* 102:455–467
- Goodall J (1968) The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim Behav Monogr* 1:161–311
- Groves CP, Sabater Pi J (1985) From apes nest to human fix-point. *Man* 20:22–47
- Hansell MH (1984) Animal architecture and building behaviour. Longman, London, p 324
- Hansell MH (2005) Animal architecture. Oxford University Press, Oxford, p 322
- Hashimoto C (1995) Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. *Primates* 36:477–488
- Hediger H (1977) Nest and home. *Folia Primatol* 28:170–187
- Hernandez-Aguilar RA (2009) Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *J Hum Evol* 57:350–364
- Houle A, Chapman CA, Vickery WL (2004) Tree climbing strategies for primate ecological studies. *Int J Primatol* 25:237–260
- Hunt KD (1994) The evolution of human bipedality: ecology and functional morphology. *J Hum Evol* 26:183–202
- Hunt KD, McGrew WC (2002) Chimpanzees in the dry habitats of Assirik, Senegal and at the Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioral diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 35–51
- Kappeler PM (1998) Nests, tree holes, and the evolution of primate life histories. *Am J Primatol* 46:7–33
- Koops K, Humle T, Sterck EHM, Matsuzawa T (2007) Ground-nesting by the chimpanzees of the Nimba Mountains, Guinea: environmentally or socially determined? *Am J Primatol* 69:407–419
- Kortlandt A (1992) On chimpanzee dormitories and early hominid home sites. *Curr Anthropol* 33:399–401
- Lantis M (1938) The mythology of Kodiak Island, Alaska. *J Am Folklore* 51:123–172
- McGrew WC (1992) Chimpanzee material culture: implications for human evolution. Cambridge University Press, Cambridge, p 277
- McGrew WC (2004) The cultured chimpanzee: reflections on cultural primatology. Cambridge University Press, New York, p 248
- McGrew WC, Marchant L, Nishida T (1996) Great ape societies. Cambridge University Press, Cambridge
- Nadel D (2004) Stone age hut in Israel yields world's oldest evidence of bedding. *Proc Natl Acad Sci* 101:6821–6826
- Nissen HW (1931) A field study of the chimpanzee. *Comp Psychol Monogr* 8:1–22
- Nunn CL, Heymann EW (2005) Malaria infection and host behavior: a comparative study of Neotropical primates. *Behav Ecol Sociobiol* 59:30–37
- Ogawa H, Idani G, Moore J, Pintea L, Hernandez-Aguilar A (2007) Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. *Int J Primatol* 28:1397–1412
- Parker ST, Gibson KR (1977) Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *J Hum Evol* 6:623–641
- Piaget J (1952) The origins of intelligence in children. Norton, New York
- Pruetz JD (2006) Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann G, Robbins M, Boesch C (eds) Feeding ecology in apes and other primates: ecological, physiological and behavioural aspects. Cambridge University Press, Cambridge, pp 161–182
- Pruetz JD, Fulton SJ, Marchant LF, McGrew WC, Waller MSM (2008) Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Am J Primatol* 70:393–401
- Reynolds V (1967) The apes: the gorilla, chimpanzee, orangutan, and gibbon: their history and their world. Dutton, New York, p 296
- Sabater Pi J, Veà JJ, Serrallonga J (1997) Did the first hominids build nests? *Curr Anthropol* 38:914–916
- Sept JM, Brooks GE (1994) Reports of chimpanzee natural history, including tool use, in 16th- and 17th-century Sierra Leone. *Int J Primatol* 16:867–878
- Shumaker RW, Walkup KR, Beck BB (2011) Animal tool behavior: the use and manufacture of tools by animals. Johns Hopkins University Press, Baltimore, p 282
- Sousa J, Barata AV, Sousa C, Casanova CCN, Vicente L (2011) Chimpanzee oil-palm use in Southern Cantanhez National Park, Guinea-Bissau. *Am J Primatol* 73:485–497
- Stewart FA (2011) Why sleep in a nest? empirical testing of the function of simple shelters made by wild chimpanzees. *Am J Phys Anthropol* 146:313–318
- Stewart FA, Pruetz JD, Hansell MH (2007) Do chimpanzees build comfortable nests? *Am J Primatol* 69:930–939
- Stewart FA, Piel AK, McGrew WC (2011) Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. *J Hum Evol* 61:388–395
- Stumpf R (2007) Chimpanzees and bonobos: diversity within and between species. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) Primates in perspective. Oxford University Press, New York
- Thorén S, Quietzsch F, Radespiel U (2010) Leaf nest use and construction in the golden-brown mouse lemur (*Microcebus ravelobensis*) in the Ankarafantsika National Park. *Am J Primatol* 72:48–55
- Tomasello M, Call J (1997) Primate cognition. Oxford University Press, New York
- Tutin CEG, McGrew WC, Baldwin PJ (1983) Social organization of savanna-dwelling chimpanzees (*Pan troglodytes verus*) at Mount Assirik, Senegal. *Primates* 24:154–173
- Videan EN (2006) Bed-building in captive chimpanzees (*Pan troglodytes*): the importance of early rearing. *Am J Primatol* 68:745–751
- Westergaard GC (1992) Object manipulation and the use of tools by infant baboons (*Papio cynocephalus anubis*). *J Comp Psychol* 106:398–403
- Westergaard GC (1993) Development of combinatorial manipulation in infant baboons (*Papio cynocephalus anubis*). *J Comp Psychol* 107:34–38
- Westergaard GC, Suomi SJ (1994) Hierarchical complexity of combinatorial manipulation in capuchin monkeys (*Cebus apella*). *Am J Primatol* 32:171–176
- Worthman CM, Melby MK (2002) Toward a comparative developmental ecology of human sleep. In: Carskadon MA (ed) Adolescent sleep patterns: biological, social, and psychological influences. Cambridge University Press, Cambridge, pp 69–117
- Yerkes RM, Yerkes AW (1929) The great apes: a study of anthropoid life. Yale University Press, New Haven