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THE BONOBO *PAN PANISCUS* (MAMMALIA: PRIMATES: HOMINIDAE) NESTING PATTERNS AND FOREST CANOPY LAYERS IN THE LAKE TUMBA FORESTS AND SALONGA NATIONAL PARK, DEMOCRATIC REPUBLIC OF CONGO

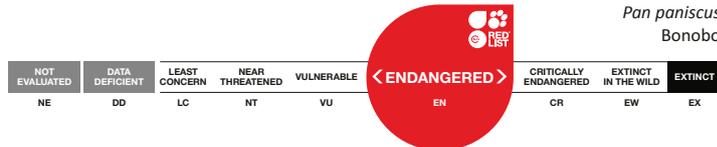
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Abstract: The description and differentiation of habitat types is a major concern in ecology. This study examined relationships between Bonobo *Pan paniscus* nesting patterns and forest structure in the Lake Tumba Swampy Forests. Data on presence of fresh Bonobo nests, canopy cover, canopy structure, tree densities and tree basal areas were collected systematically along 134 transects at 400m and 800m intervals, and the leaf-covered area (LCA) was calculated for each of seven forest types. I observed a significant correlation between bonobo nests and mixed mature forest/closed understory forest type ($r=-0.730$, $df = 21$, $p < 0.05$), but not mixed mature forest/open understory, old secondary forest and young secondary forest. Basal areas of non-nesting trees along transects did not differ significantly from those in sites where bonobos nested. Higher LCA (55% and 55%) occurred in nesting sites when compared with non-nesting sites (39% and 42%) at elevations 4–8 m and 8–16 m above the soil. There was greater leaf cover in the understorey at sites where bonobos did not nest, while there was greater leaf cover in the mid-storey at sites where bonobos did nest.

Keywords: Bonobos, canopy cover, nesting site, Lake Tumba Swampy forests.



Pan paniscus
Bonobo



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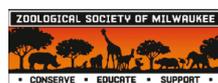
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For French Abstract, see end of this article.

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INTRODUCTION

The Bonobo *Pan paniscus* (Schwarz, 1929) was taxonomically described in 1929 as distinct from the Common Chimpanzee *Pan troglodytes*. Historically, the species was known as the Pygmy Chimpanzee because of its comparatively slender physical stature compared with the Common Chimpanzee. Bonobos occur only within the Democratic Republic of Congo (DRC) (Fig. 1; Image 1). To the north their distribution is defined by the southern bend of the Congo River, while to the south their distribution is limited by the Kwango-Kasai-Sankuru rivers system. The heart of the species distribution is in the area of the Salonga National Park (SNP), the massive the tropical forest zone that was set aside in 1969 as the first protected area to preserve the species (IUCN 1992). Since the recognition of Bonobos as a species studies have been conducted in several sites (Lomako, Yalosidi, Wamba, SNP and Lukuru), most concentrated on feeding ecology, population surveys and behavior. A few studies included habitat descriptions, but rarely were physical aspects of habitats described. This study is one of the first to investigate this important component of habitats. I compared data from the SNP and the Lake Tumba Swampy Forest (LTSF), a comparison that is important because SNP is a forested habitat that has been considered to be the most appropriate for Bonobos, while the LTSF habitat is a mosaic of savannah-forest complex like that of Lukuru.

The accurate description and differentiation of habitat types is a major concern of ecological research (Sutherland 1996). However, many studies of habitat types are limited to floristic aspects. Measurements of the vertical structure of vegetation are critical for the description of forest habitats, and for understanding the relative availability of terrestrial and arboreal food (McDiarmid & Wilson 1996; Dubayah & Drake 2000). Vertical and horizontal measures of vegetation are particularly important for arboreal species such as great apes, because such parameters increase understanding of their positional behavior space (Williamson 1993). The complex combinations of vegetation in different vertical strata can help us understand the adaptive and evolutionary processes that act on great apes (Furuichi et al. 2001).

Forest structure parameters are important because physical elements of the habitat such as canopy cover, under-storey composition, tree distribution and density, and foliage density play an important role in habitat selection by species (Anderson & Ohmart 1986). Important quantitative parameters for any



Image 1. Bonobo *Pan paniscus*

detailed habitat assessment should include structural characteristics such as canopy stratification and canopy cover, tree densities and basal areas (Dubayah & Drake 2000). Consequently, this paper examines possible relationships between Bonobo distribution assessed from nest presence and quantitative measures in the LTSF. Data from the LTSF Landscape are compared with those from additional studies in the SNP, made with identical protocols. Tree densities between these two sites are compared with the Lomako Forest where similar data have been published by Boubli et al. (2004). More globally, the findings of this study are discussed in the framework of other studies on the nesting ecology of Bonobos.

METHODS

Study sites

The LTSF (80,000km²; Fig. 1) is located in the Democratic Republic of Congo on the border with the Republic of Congo. It is part of a complex and diverse botanical region that occupies most of the Central Congo Basin. With vascular plants numbering 1500 to 2000 species (10% endemic), the region belongs to Guineo-Congolian center of endemism (White 1983). Two distinguishable ecosystems characterize the landscape: 60–65% of the landscape (north of 1°30'00''S) is a vast zone of seasonally-inundated swamp forest. The remaining 35–40% of the area comprises mixed terra firma forest types, including mature (ombrophile and semi-deciduous) and secondary forests along valleys and on small hills. These occur mostly between major river systems. Ombrophile and semi-deciduous forest types are composed of leguminous tree species

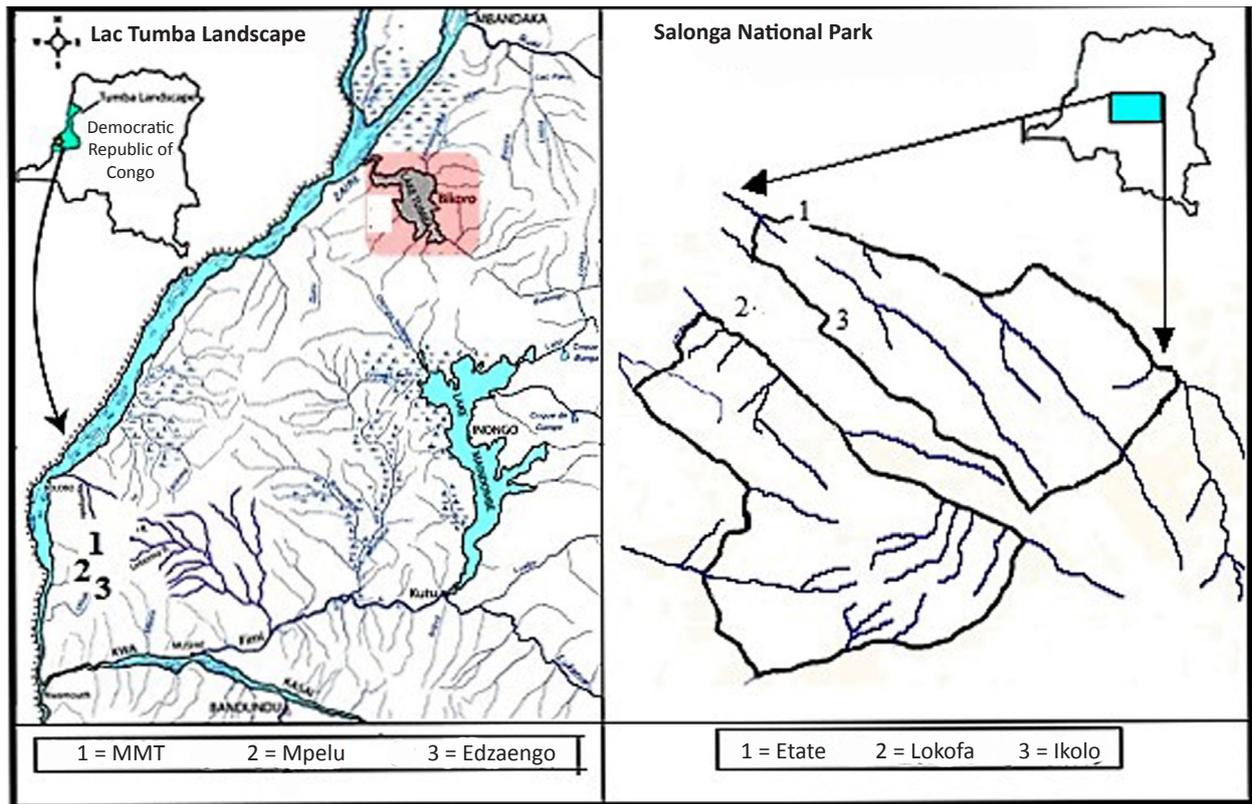


Figure 1. Lake Tumba landscape and Salonga National Park, Democratic Republic of Congo

such as hardwood timber species *Staudtia stipitata*, *Polyalthia suaveolens*, *Scorodophloeus zenkeri*, as well as large-fruit species as *Anonidium mannii* and *Parinari glaberrimum*, which serve as important fruit and seed sources for wildlife and humans (Twagirashyaka & Inogwabini 2009; Inogwabini 2013a). *Gilbertiodendron dewevrei* dominated forest spots occur between the Ubangi and the Ngiri rivers, and provide an important fruit and seed source for Elephants *Loxodonta africana*, Buffalo *Syncerus cafer nanus*, Forest Pigs *Potamocheirus porcus*, Duikers (*Cephalophus* sp.), rodents and other mammals. In addition to Bonobos, seven other species of diurnal primates occur in these forests, including the Angolan Pied Colobus *Colobus angolensis*, Allen's Swamp Monkey *Allenopithecus nigroviridis*, Black Mangabey *Lophocebus aterrimus*, Salonga Red Colobus *Piliocolobus tholonii*, Red-tailed Monkey *Cercopithecus ascanius*, De Brazza's Monkey *Cercopithecus neglectus* and the Wolf's Monkey *Cercopithecus mona wolfi* (Gautier-Hion et al. 1999). According to local communities, the Golden-bellied Mangabey *Cercocebus chrysogaster* was also present at the edges of Maindombe, which concurs with the species distribution map compiled by Gautier-Hion et al. (1999). However, heavy hunting pressure has

since resulted in the local extirpation of this species. The zone south of $1^{\circ}30'00''S$ is an eco-tone of forest-savannah of the Plateau de Bateke, a relatively drier area that connects the southern savannahs and the forest block of the central Congo basin. Savannah-adapted species share their habitats with forest-adapted ones, making the region one of the most diverse in the DRC (Inogwabini 2013a,b).

The Salonga National Park (SNP; 36,000km²; Fig. 1) is located between $1^{\circ}25'00''-2^{\circ}45'00''S$ & $20^{\circ}20'00''-21^{\circ}30'00''E$ (Inogwabini 2006). The western-most parts of SNP are also in the central Congo basin, whose main characteristics are a flat topography and low altitude (300m). It is predominantly mixed mature lowland tropical forest (Evrard 1968; Kortlandt 1995; Gautier-Hion et al. 1999), encompassing areas of seasonally-flooded and permanently-inundated zones characterized by an open understory and composed of communities of *Guibourtia demeusi*, *Raphia sese*, *Pandanus*, *Uapaca guineensis*, and *Uapaca heudelotii* (Evrard 1968; Gautier-Hion et al. 1999; Inogwabini 2005; Inogwabini 2006; Reinartz et al. 2006). The *terra firma* forest of SNP is characterized by plant species such as *Scorodophloeus zenkeri*, *Anonidium mannii*, *Polyalthia suaveolens* and

Diospyros sp., Patches of *Gilbertiodendron dewevrei* also occur, although in less extensive unbroken areas (Evrard 1968; Kortlandt 1995). *Marantaceae* stands (e.g., *Haumania librechtsiana* and *Megaphrynium macrostachii*) are frequent in understories and, in some parts of the northern sector constitute mono-dominant stands (van Krunkelsven et al. 2000; Reinartz et al. 2006). Wildlife species of the SNP are those typical of all the African lowland forests and include forest elephants, buffaloes, and several species of duikers. Primate species include Allen Swamp Monkey, Angola Pied Colobus, Red-tail Monkey, and the Bonobo.

Data collection and analysis

Physical metrics on forests consist of canopy cover, canopy structure, tree densities and tree basal areas. These were sampled systematically along each transect at 400m and 800m intervals. Data from the LTSF were collect from 86 transects of 1km each (Inogwabini et al. 2007) while those from the SNP were collected from 48 multi-length transects totaling 67.8km of effort (Reinartz et al. 2006). In both sites, transects were laid in such a way that they crossed different habitat types, categorized into seven forest types: permanent swamp forest, mature seasonally flooded forest, mixed mature forest/closed understory, mixed mature forest/open understory, old secondary forest, young secondary forest and fallows (Table 1 and 2); fallows were included because Bonobos used them in the LTSF. Fallows were defined as canopy-free land, which is left unseeded during a growing season but still containing growths of staple species such bananas, sugarcanes, uncultivated manioc, etc. These seven forest types have been defined in previous studies, including Evrard (1968), Letouzey (1982), Dowsett-Lemaire (1995), Lejoly (1996), van Asbroeck (1997), White & Abernethy (1997), White & Edwards (2000), Reinartz et al. (2006), and Inogwabini et al. (2012).

Leaf-covered areas at different canopy layers

Physical canopy structure was characterized using the point-contact method (Anderson & Ohmart 1986). A 4m high stick was held vertically in a 20m x 20m grid, at horizontal intervals of 10m, starting out from the center of the grid. At each point, one person scored contact between the stick and any live vegetation up to a height of 4m, and estimated contacts above 4m, up to an estimated height of 32m. The vertical intervals for which contacts were estimated were: layer 1 = 0–1 m; layer 2 = 1–2 m; layer 3 = 2–4 m; layer 4 = 4–8 m;

layer 5 = 8–16 m; layer 6 = 16–32 m, and layer 7 > 32 m. Scores of 1 and 0 were assigned for contact or no contact respectively for each horizontal or vertical interval. A Geographic Resource Solutions (GRS) Densitometer was used to measure the canopy cover at each point-contact. At each point, a score of 1 or 0 was used to indicate whether or not a leaf was seen through the densitometer. These measurements helped calculate the leaf-covered area (LCA) for each forest type.

All LCA scores were summed together for each canopy layer for each forest type. Percentage canopy cover (area covered by live leaves) was calculated at each vertical layer in a grid of 400m² by first summing up contact-points for each layer. The totals for each layer were then divided by N x 9, the number of sampled units for each forest type, using the formula (Anderson & Ohmart 1986)

$$LCA = \frac{\sum [P - C (\text{vertical layer})]}{9N} \text{ (Expressed in \%)}.$$

This equation expresses the LCA as a function of P-C representing the numbers of point-contacts where the stick 'touches a live leaf', and N = number of sampled units for each forest type. Partial correlation coefficients (Siegel 1956; Sokal & Rohlf 1995; Ennos 2000) were used to examine whether there was a correlation between tree density and mean canopy cover for each forest type. Partial correlations were run on mean LCAs Bonobos nesting sites and % canopy cover per sites to determine if canopy cover related with Bonobo distribution nesting patterns (Fig. 2).

Tree measurements

Trees ≥ 10 cm in diameter at breast height (i.e., at 1.30 m) above the ground were counted within a radius of 5.64m ($A = 100\text{m}^2$), and their diameter at breast height (DBH) was measured. Mean tree densities for each forest type were calculated using the standard formula (Cottam et al. 1953; Greig-Smith 1964; Kershaw 1966), i.e., by dividing the total by the total area of plots (A) in each forest type:

$$d = \frac{\sum \text{Trees (forest)}}{N}$$

Total basal areas per forest type were calculated by simple addition. Basal areas (BA_i) were calculated using the standard formula (Cottam et al. 1953; Greig-Smith 1964; Kershaw 1966):

$$BA_i = \pi \left(\frac{1}{2}\right) (\text{DBH})^2$$

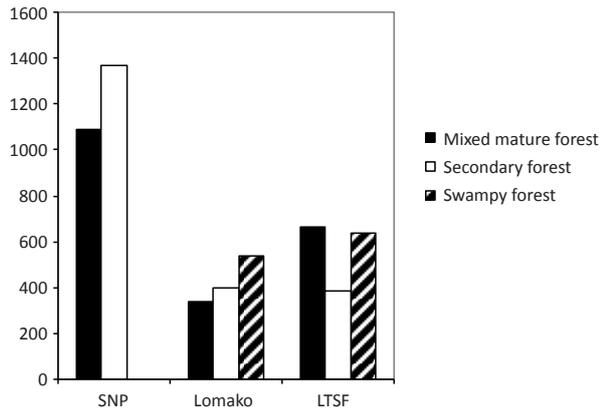


Figure 2 Mean tree density (trees/ha) per forest type at LTSF, SNP and Lomako (Boubli et al. 2004).

From BA_i the mean basal areas BA were obtained as the simple arithmetic mean: $BA = \sum BA_i / N_i$, where N_i = total area of plots per forest type. Mean tree densities were compared between sites, using a t-test between higher and lower indices of bonobo presence, to explore possible differences that might explain the influence of basal areas on the distribution of bonobos in the LTSF.

Bonobo nest heights and nest site spread

Bonobos typically make a nest each night for sleeping, and they may also construct day nests for resting. Nests are constructed by lacing together branches from one or more trees to form a platform, with smaller leafy twigs arranged in an interwoven solid structure that can be spotted from the ground. Nests can be identified as fresh (i.e., containing green leaves) or old (containing dried or brown leaves), and only fresh nests were considered in this study. Nests were categorized by height above the ground: 1–5 m, 6–10 m, 11–15 m, etc., and mean nest heights were calculated for each forest type. Mean nest heights, inclusive of single nests, were

first classified in relation to forest metrics, and then compared to determine the influence of forest structure on where Bonobos build nests, and in turn on Bonobo distribution. Mean heights were compared between different forest types using one sample t-tests. These categories were compared using a one-way ANOVA to examine possible relationships between nest height categories and different forest vertical strata (Upton & Cook 2004; Hawkins 2005). The group center $G (G_x, G_y)$ was calculated using $G_x = \sum d_i / n$ [a], and $G_y = \frac{1}{2} [Y_1 + Y_2]$ [b]. In these equations d_i is the perpendicular distance between nest i and the transect line; n is the total number of nests in each site. Nests to the left of the transect line were scored with negative values and those on the right with positive values. Y_1 is the distance of the first nest measured along a transect, and Y_2 is the distance of the last nest at the site. The site radius δ is the measure of the distance between the group center and the farthest individual nest n from the center. δ is the largest radius of a theoretical circular area within which all the nests of a given site would fall. To compare the surface area occupied by sites, the group spread was calculated as $A = \pi \delta^2$. Sites with single nests were excluded from this analysis because nesting site spread of one single nest site would be equal to a single point. Pair-wise comparisons were used to compare group spreads across the sites in the LTSF (Nkala (MMT), Mpelu and Edzaengo (Fig. 3a) whereas mean values of group spread were compared between LTSF and SNP using one-way ANOVA. Sites in the LTSF are inter-connected forest galleries while those in the SNP are separated by the extensive river networks that characterize the SNP. The straight line distance between LTSF and SNP is about 100km (Inogwabini & Leader-Williams 2012a). This stretch of forest is relatively heavily populated and has been cultivated for millennia (Inogwabini et al. 2007).

Table 1. Canopy cover (%) at different canopy heights compared between non-nesting sites and Bonobo nest sites in LTSF

		Transect							Bonobo nesting sites						
Forest layers	Forest types	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	> 32 m	19	3	33	2	0	11	28	-	-	26	6	22	-	-
	16–32 m	47	22	50	27	13	61	28	-	-	61	19	40	-	-
	8–16 m	55	27	42	51	48	67	28	-	-	55	21	51	-	-
	4–8 m	57	25	39	64	44	61	67	-	-	55	19	27	-	-
	2–4 m	57	30	69	47	33	72	72	-	-	42	16	56	-	-
	0–2 m	67	37	97	56	52	100	89	-	-	72	33	84	-	-

Forest types are defined as: 1 = permanent swamps, 2 = mature seasonally flooded forest, 3 = mixed mature forest/closed, 4 = mixed mature forest/open; 5 = old secondary forest, 6 = young secondary forest, and 7 = fallows
 Partial correlation coefficients significant only for mixed mature forest with closed under-storey ($r = -0.730$) while non-significant for any other forest type respectively $r = 0.490$, $r = 0.380$, and $r = 0.370$ for mixed mature forest with open under-storey, old secondary forest, young secondary forest.

Table 2. Tree densities in non-nesting sites along transects and Bonobo nesting sites in LTSF

	Forest types	Plots	Area (Ha)	# Trees	\bar{X} tree/Ha	\bar{X} Basal
Transects	Permanent swamp forest	16	0.16	50	312.5	2649.2
	Mature seasonally flooded forest	37	0.37	121	327.0	1015.3
	Mixed mature forest/closed	4	0.04	15*	375.0*	892.1**
	Mixed mature forest/open	11	0.11	37	336.4	852.4
	Old secondary forest	6	0.06	17*	283.3*	726.7**
	Young secondary forest	5	0.05	5	100.0	1346.4
	Fallows	2	0.02	5	250.0	387.8
Bonobo nesting sites	Permanent swamp forest					
	Mature seasonally flooded forest					
	Mixed mature forest/closed	18	0.18	77*	427.8*	1168.6**
	Mixed mature forest/open	16	0.16	85	531.3	417.7
	Old secondary forest	5	0.05	18*	360.0*	760.8**
	Young secondary forest	1	0.01	6	600.0	512.0
	Fallows					

* Non-significant differences ($t = -2.307$, $df = 3$; $p > 0.05$; $t = -2.005$, $df = 3$; $p > 0.05$; $t = 0.969$, $df = 3$; $p > 0.05$).

** Significant difference (One-way ANOVA: $F_{6, 249} = 3.45$, $p < 0.05$).

Table 3. Bonobo nest heights in the LTSF

Forest Type	N	\bar{X} heights (m)	Height range (m)
Mixed mature close	65	13.5 (SD =6.0)	[4–22]
Mixed Mature open	56	18.7 (SD =3.0)	[16–22]
Old secondary forest	62	17.0 (SD =3.3)	[10–25]
Overall	183	15.2 (SD = 5.1)	[4–25]

RESULTS

Bonobos nested in two types of mixed mature forest and in old secondary forests (Table 1, Table 2 and Table 3). Therefore, structural comparisons were undertaken between these forest types to examine possible differences between non-nesting sites and nesting sites. Transect LCA were highest (LCA = 100%) at the lowest layer of mixed mature forest and these values were greater than the highest (LCA = 84%) found in nesting sites at the lowest layer of old secondary forest (Table 1). There were significantly more Bonobo nests in forests where the mid-canopy LCA was higher (Table 1). For mixed mature forest, old secondary forest and young secondary forest the LCA was consistently higher in LTSF than in SNP (for the SNP data see Reinartz et al. 2006; Inogwabini 2010). Both young and old secondary forests differed significantly between LTSF and SNP while there was no significant difference for mixed mature forests between the two sites (Inogwabini 2010). Tree numbers varied consistently between transects and

bonobo nesting sites (Table 2). While basal areas differed significantly between different forest types (one-way ANOVA: $F_{6, 249} = 3.45$, $p < 0.05$), there were no significant differences between mixed mature forests and old secondary forests, tree densities, and mean basal areas with regards to nesting and non-nesting sites ($t = -2.307$, $df = 3$; $p > 0.05$), $t = -2.005$, $df = 3$; $p > 0.05$), and $t = 0.969$, $df = 3$; $p > 0.05$, respectively) (Table 2). By comparison with other sites, the LTSF and Lomako had consistently fewer trees/ha than SNP (one-way ANOVA: $F_{2, 7} = 6.400$, $p < 0.05$) (Fig. 3). Nests in mixed mature forest with open understory and old secondary forest were higher than those in mixed mature forest with closed understory, with heights in the range = [4–25] m differing significantly between forest types (Table 3). The largest group spreads in the LTSF were in old secondary forest (2400m²) and mixed mature forests (2088m²); pairwise comparisons indicated significant variation of group spreads across the three sites within LTSF and mean values of group spread were consistently larger in the LTSF than in SNP (Fig. 3b) but with no significant difference.

DISCUSSION

Bonobos nested most where the mid canopy leaf cover was greatest (Table 1). This result indicated that foliage layout in the vertical structure of forests influenced nesting patterns. Two factors might explain

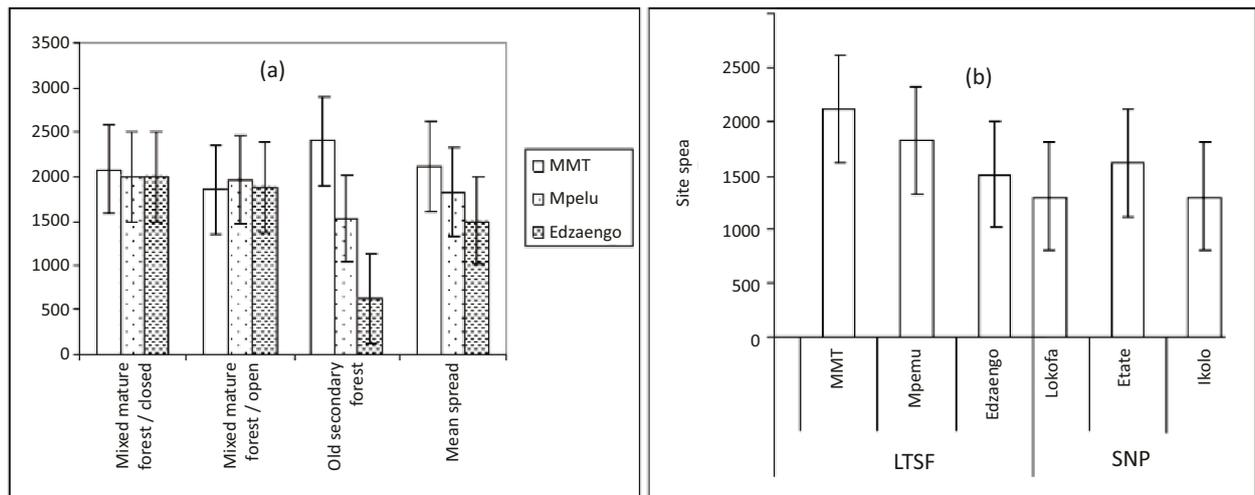


Figure 3 (a) Bonobo nest group spreads (m²) in three zones of LTSF shown according to different forest types, and against the overall mean spread for comparison and (b) mean group spreads compared between LTSF and SNP.

Pair-wise comparison showed significant difference in group spread across the sites (2a): Mpemu-MMT ($t = 0.265014$, $df = 2$; $p < 0.05$), Edzaengo-MMT ($t = 0.260377$, $df = 2$; $p < 0.05$) and Mpelu – Edzaengo ($t = 0.518706$, $df = 2$; $p < 0.05$). Mean values of group spread were larger in the LTSF than in SNP (2b) but with no significant difference; one-way ANOVA ($F_{1,5} = 8.451$, $p > 0.05$).

these trends. First, nests are built in trees that offer suitable foliage for constructing a comfortable pad on which to sleep. Second, Bonobos choose tree layers that provide good cover, to avoid being detected by potential predators at night. While the first option is straightforward, the influence of predation-risk on the nesting of great apes has been also reported in the nesting behavior of gibbons (Reichard 1998). Leopards (D'Amour et al. 2006), pythons and lions are potential sympatric predators of Bonobos at LTSF (Inogwabini, unpublished data). All three predators hunt at night, so building nests in trees with thicker foliage may be essential for security while sleeping. Humans and their dogs represent an additional risk from hunting or disturbance.

Other studies (Fruth & Hohmann 1993; Kano 1983) of bonobo nesting show that the patterns observed in LTSF are similar to those found at other sites. The overall mean nest height (15.2m) was higher than that previously reported from one small area within the wider LTSF region. Horn (1980) reported a height range of bonobo nests near Lake Tumba from 7–12 m. However, Horn's (1980) results were based on a very small sample size from a 1km² study area, and so cannot be extrapolated to the entire LTSF. The mean height of bonobo nests throughout LTSF was very similar to nest heights reported from Yalosidi, where 78% of nests had heights ≤ 15 m (range = [2–50] m) (Kano 1983). The highest nests were reported from Lomako, where recorded values ranged from 3–60 m above the ground

(Fruth & Hohmann 1993). No comparable studies to those reported here have been undertaken on the use of forest vertical layers by bonobos. Nevertheless, all these reported nest heights fall in the strata expected to support more foliage cover, or are higher still. This reinforces the predator security hypothesis as an explanation for choice of nest height by bonobos.

Nest site spread may indicate the level of perceived threat felt by bonobos, and may reflect the 'security in numbers' principle: threatened Bonobos would be expected to nest in tighter groups for greater security. Nest sites were most compact in the Ikololo region, where Reinartz et al. (2006) documented most signs of human activity. At the other extreme, the widest spread of nest sites in the LTSF was found at the Nkala site where local communities did not hunt Bonobos (Inogwabini & Leader-Williams 2012b). Hence hunting pressure may influence nesting group spreads. Data collected on the eastern lowland gorillas from Kahuzi-Biega National Park, DRC showed the same trend (Inogwabini et al. unpublished data set).

The finding that LTSF supports more leaf cover at ground level than seen at other bonobo study sites is also of great conservation importance. Great apes use herbs as fallback foods when fruits become scarce (Marshall & Wrangham 2007; Conklin-Britain et al. 2001). This could explain why densities of bonobos were greater at LTSF than SNP (Inogwabini et al. 2007), with implications for the persistence of this threatened species.

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French Abstract: La description et la différenciation de types d'habitat est une question majeure pour l'écologie. Cette étude fut un examen des relations entre les structures de nids des bonobos *Pan paniscus* et la structure des forêts dans la zone des forêts inondées du Lac Tumba. Les données sur les nids frais des bonobos, la canopée, la structure de la canopée ainsi que les aires de base des arbres furent systématiquement collectées sur 134 lignes de transect à 400m et 800m d'intervalles et l'Aire de Couverture par le Feuillage (ACF) fut calculée pour chacune de 7 types forestiers. J'ai observé une corrélation significative entre les nids de bonobos et les forêts matures mixtes à sous-bois fermé ($r = -0.730$, $df = 21$, $p < 0.05$) mais pas avec les forêts matures mixtes à sous-bois ouverts et les vieille et jeune forêts secondaires. Les aires de base des arbres des sites sans nids sur les lignes de transect n'ont pas différencié significativement avec les sites où on a observé les nids de bonobos. Les valeurs plus élevées des ACF (55% et 55%) furent observées dans les sites avec les nids des bonobos, en comparaison les valeurs plus faibles (39% et 42%) dans ceux sans nids aux hauteurs respectives de 4-8 m et 8-16 du sol. Il y avait plus de couverture par feuillage dans les sous-bois où les bonobos n'avaient pas construit les nids alors qu'il y avait une couverture plus importante par feuillage dans la moyenne canopée dans les sites avec les nids de bonobos.

