

## REVIEW ARTICLE

## Chimpanzee Nesting Patterns in Savanna Habitat: Environmental Influences and Preferences

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Data on chimpanzee (*Pan troglodytes*) nesting patterns were collected in Issa, Ugalla, western Tanzania. Ugalla is one of the driest, most open, and seasonal habitats inhabited by chimpanzees. We investigated the physical characteristics of nests and trees used for nesting to understand environmental influences on nest building and identify the characteristics preferred by the chimpanzees and the basis for such preferences. We analyzed 2,167 nests and 1,523 nesting trees. Most nests were built in the middle section of the tree crown and close to the tree trunk, and used a single tree in construction. Some physical characteristics of nests (e.g., distance from tree trunk) seemed to be the result of constraints imposed by tree structure. Issa chimpanzees preferred tall trees with high first branches for nesting supporting the hypothesis that elevated height of a sleeping place is a predator defense strategy. The height from the ground to the first branch showed less variation than either tree height or crown height and correlated weakly with tree height, suggesting that height from the ground to the first branch may be a more important factor than tree height alone in selecting a tree in which to nest. As in other study sites, the chimpanzees used tree species in proportions that did not correspond to their abundance suggesting tree species preference. We report for the first time that chimpanzees directionally oriented their nests and propose that this may be to maximize sunlight. We compare our data to those of other chimpanzee study sites. *Am. J. Primatol.* 9999:1–16, 2013. © 2013 Wiley Periodicals, Inc.

**Key words:** nesting; savanna chimpanzees; environmental influences; preferences; predation

## INTRODUCTION

Chimpanzees, like other great apes, build structures of bent and broken, woven vegetation called nests (also called beds or platforms) for sleeping at night and sometimes for resting during the day. Each weaned individual builds a new nest every evening, usually in a different location from that used the previous night. Sometimes chimpanzees reuse previously made nests by adding fresh vegetation. To construct a nest takes only a few minutes but the resulting structure is sturdy and remains identifiable even after many months. Chimpanzee nests and nesting behavior have been studied directly and indirectly from the earliest field studies to the present [Nissen, 1931; Bolwig, 1959; Goodall, 1962, 1965, 1968; Schaller, 1963; Reynolds and Reynolds, 1965; Izawa and Itani, 1966; de Bournonville, 1967; Jones and Sabater Pi, 1971; Baldwin, 1979; Baldwin et al., 1981, 1982; Anderson et al., 1983; Sabater Pi, 1984, 1985; Ghiglieri, 1984; Tutin and Fernandez, 1984; Sept, 1992, 1998; Wrogemann, 1992; Fruth 1990 in Fruth and Hohmann, 1994; Marchesi et al., 1995; Furuichi et al., 1997, 2001; Ogawa et al., 1997, 2006, 2007; Plumptre and Reynolds, 1997; Furuichi

and Hashimoto, 2000, 2004; Brownlow et al., 2001; Basabose and Yamagiwa, 2002; Hunt and McGrew, 2002; Ham 1998 in Kormos et al., 2003; Humle, 2003; Llorente-Caño, 2003; Poulsen and Clark, 2004; Ogunjemite et al., 2005, 2010; Hernandez-Aguilar, 2006, 2009; Morgan et al., 2006; Koops et al., 2007, 2012a,b; Petre et al., 2007; Sanz et al., 2007; Stewart

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et al., 2007, 2011; Pruetz et al., 2008; Stanford and O'Malley, 2008; Granier, 2011; Sousa et al., 2011; Samson, 2012; Samson and Hunt, 2012]. Despite such studies and although nesting is a daily behavior of the great apes, the environmental constraints of nesting remain poorly understood. Here we present detailed information on the physical characteristics of nests and also trees used for nesting by the chimpanzees at Issa. The physical characteristics of a nesting tree, the place within the tree where the nest was constructed, and the materials used should elucidate both the environmental constraints faced by the chimpanzees and their preferences.

The data presented here include only night nests. Generally, chimpanzee day nests are not carefully constructed and are structurally simpler [Goodall, 1962, 1965, 1968; Plumptre and Reynolds, 1997; Brownlow et al., 2001]. Nests that were not carefully made or solid were considered day nests. Damaged or incomplete nests were excluded in the present analysis. The structural integrity of a nest was easily observed in new nests. But even for old nests, for which some or most of the leaves were gone, it was possible to see a clear and complex weaving of branches, suggesting it had been a solidly built structure. Goodall [1968] reported a higher number of day nests made in the rainy season compared to the dry season. Chimpanzees during our study were seen resting on branches and on the ground during the day without making nests, even in the rainy season. Ground nests were never found.

Primates seem to choose sleeping sites based on features that reduce the likelihood of predation, including the difficulty a predator would have reaching the sleeping site (by, e.g., sleeping as far from the tree trunk as body weight allows; reviewed in Anderson [1984]). One proposed function of arboreal nest building in chimpanzees is the avoidance of nocturnal predators [Goodall, 1962; Baldwin et al., 1981; McGrew, 1992, 2004]. It has been proposed that chimpanzees make nests higher in trees in habitats with predators, in order to avoid predation [Baldwin et al., 1981]. Pruetz et al. [2008] found support for this hypothesis by comparing nest heights from two chimpanzee sites (Assirik vs. Fongoli) inhabiting similar habitats in Senegal but differing in predator presence. Similarly, Fruth and Hohmann [1993] interpreted the height of bonobo nests as an anti-predator tactic. It has been suggested that the height from the ground to the lowest branch of a nesting tree and not only the total height of a nest is important to avoid ground predators in chimpanzees [Goodall, 1962] and bonobos [Fruth, 1995]. Although perhaps a less important evolutionary force on chimpanzees than on other primate species [Zuberbühler and Jenny, 2002] chimpanzees do suffer predation. Leopards prey on chimpanzees [Boesch, 1991; Henschel et al., 2005], chimpanzees have encountered leopards in trees [Gandini and Baldwin, 1978], and lions eat

chimpanzees [Tsukahara, 1993]. Here we investigate if the elevated heights of nests and of the first branch of nesting trees reflect an antipredation strategy.

Although basic nest design and construction patterns are similar for all chimpanzees, differences in nest building between study sites are important for identifying chimpanzee cultural variation [Baldwin et al., 1981; McGrew, 1992, 2004; Fruth and Hohmann, 1994]. Many differences in nest building emerge when chimpanzee populations are compared but it is unknown if any of these have cultural explanations [McGrew, 2004]. Baldwin et al. [1981] explained differences in the physical characteristics of nests and nesting trees between two chimpanzee populations living in distinct habitats as the result of environmental factors. To test whether behavioral differences across chimpanzee study sites are culturally influenced, it is important to rule out ecological explanations [Baldwin et al., 1981; McGrew, 1992; Whiten et al., 1999]. This cannot be done by simple comparisons (e.g., "tall" vs. "short" trees in forests and savanna habitats, respectively); instead it requires systematic testing and elimination of numerous potential environmental factors. The present study is a step forward in this direction.

In this paper we analyze the physical characteristics of nesting trees and the placement of nests within the trees to (1) identify environmental constraints in nest building, (2) elucidate the patterns of chimpanzees' selection, and (3) test the anti-predator hypotheses of arboreal nesting. We compare our data to those of other chimpanzee study sites.

## METHODS

### Study Area and Subjects

The study area, Issa, was located in the western part of the Ugalla region and comprised 48 km<sup>2</sup>. The Ugalla region is east of Lake Tanganyika in western Tanzania. It is bordered by the Malagarasi River on the north, the Niamanzi (Ilumba) basin on the south, the Uvinza-Mpanda road on the west, and the Ugalla River on the east. The region is about 3,300 km<sup>2</sup>, with several broad valleys broken up by steep hills that generally have flat plateau summits [Kano, 1972; Moore, 1994], elevation ranges from 900 to 1,800 m. The Malagarasi and Ugalla Rivers are perennial but are far from the Issa study area. Within the region there are only streams, mostly seasonal [Kano, 1972; Moore, 1994; Hernandez-Aguilar, 2006]. The research camp was established near the center of the study area (05°23.34S, 30°35.04E). During the study, average daily maximum temperature was highest in August (34°C) and lowest in November (28°C). Average daily minimum temperature was highest in January (17.2°C) and lowest in August (14.4°C).

Annual rainfall was 955 mm. There is a rainy and a dry season [a dry month was defined as having <100 mm of rainfall, Hernandez-Aguilar, 2006]. The dry season lasted from May to October and yielded only 7.7% of total annual rainfall. The vegetation of the Ugalla region is “miombo” woodland, with *Brachystegia* and *Julbernardia* (Fabaceae) as the dominant tree genera. The canopy is generally open with a grassy understory, except for 2% of the region which is evergreen forest. Vegetation types within the Issa study area are open (woodland, wooded grassland, grassland) and closed (gallery and thicket forests) (for description of vegetation types, see Hernandez-Aguilar [2009]). Fauna included hartebeest, roan antelope, eland, elephant, zebra, and four potential predators of chimpanzees: lion, leopard, spotted hyena, and African wild dog. Ugalla is one of the driest, most open and seasonal habitats inhabited by chimpanzees [Kano, 1972; Itani, 1979; Nishida, 1989; Moore, 1992, 1994, 1996; Hernandez-Aguilar, 2006, 2009; Ogawa et al., 2007]. Savanna will be used in this paper synonymously with dry habitat.

Issa chimpanzees were neither habituated nor provisioned. The chimpanzees were never observed by researchers or reported by local people to crop-raid. However, there are only a few small human settlements (mostly composed of a single family farm) in peripheral areas of the Ugalla region, all far (>20 km) from the study area. Community and range sizes were unknown at the time of this study. Based on nest counts, researchers have been concluded that different areas in Ugalla have different densities of chimpanzees, with estimations varying from 0.03 to 0.14 ind/km<sup>2</sup>; the maximum density came from our study area, Issa [Hernandez-Aguilar et al., 2006]. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

### Data Collection

We collected data from October 2001 to June 2003, systematically and repeatedly walking the study area searching for nests on transects, along topographic contours, and opportunistically while carrying out other research activities. For flat areas (valleys and plateaus) we walked along straight transects and for slopes along topographic contours. Both transects and contours were separated by about 20–50 m, depending on the density of trees, in order to ensure visibility of nests. Since forest vegetation types had a higher density of trees and denser and higher canopies than other vegetation types, walking lines were separated by 3 m. Examinations of the study area to search for nests were repeated every 3–4 months. When a nest or concentration of nests was found, a radius of 100 m was searched for other nests.

A total of 5,354 nests were found in the study area [Hernandez-Aguilar, 2009] of which 2,167 nests and 1,523 nesting trees were measured. The number of nesting trees included those containing the 2,167 nests, plus a small number of trees in the same nesting sites that were recorded with nests, but these nests were no longer clearly recognizable when we returned to measure them (e.g., those broken during strong storms). The 2,167 nests analyzed here represent 40% of the total number of nests found within the study area. The remaining 3,187 nests (60%) and the trees containing them were not measured but were described (see Hernandez-Aguilar [2009], for the analysis of their distribution on the landscape).

The following variables for nests and nesting trees were recorded (modified from Baldwin et al. [1981], Sabater Pi [1985], Sept [1992], Fruth [1995], Plumptre and Reynolds [1997]).

### Nesting trees

1. *Diameter at breast height (DBH)*: Circumference at breast height (1.30 m) was measured in the field. DBH was calculated using the formula  $\text{Diameter} = \text{Circumference}/\pi$ .
2. *Tree height (TH)*: From the ground at the base of the tree to the top of the tree.
3. *Lowest branch height (LBH) or crown base height*: From the lowest branch to the ground.
4. *Crown height (CH)*: Subtracting the crown base height from the tree height. Lowest branch height and crown height were measured for a subset of the data (we aimed for the subset to be at least 10% of the total number of nesting trees measured for height and DBH; we measured the last trees that were found to contain nests in our study period), and as a result the *N* for these two variables (182) is smaller than the 1,523 nesting trees measured.
5. *Species*: Determined in the field by local name (Kitongwe or Kiswahili) and later identified by botanists.
6. *Number of nests per tree*: Including nests of all ages.

### Nests

1. *Nest height (NH)*: From the base of the nest to the ground at the base of the tree.
2. *Vertical position within the crown*: Calculated by obtaining the height from the lowest branch of the tree to the base of the nest, dividing the height of the crown by 3, and determining if the nest fell within the top, middle, or bottom section of the crown.
3. *Distance from the base of the tree trunk*: Horizontal distance from the tree trunk to the center of the

nest. When the nest was exactly on top of the base of the tree trunk, the distance was considered 0.

4. *Orientation within the tree*: Measured the horizontal angle relative to magnetic north of the nest direction with respect to the base of the tree trunk. When the nest was exactly on top of the tree trunk base, the value was 0.

For variables 3 and 4, nests were considered exactly on top of the base of the tree trunk even if the trunk was not vertical but inclined, in order to homogenize criteria.

5. *Slope orientation*: Direction in which the slope went down hill from where the nest was constructed (north, north-east, east, south-east, south, south-west, west, and north-west).
6. *Orientation within the tree for nests constructed on slopes*: Nests constructed on slopes were used here to investigate if there was a difference in the orientation within the tree of nests made on east-facing versus west-facing slopes, to test if the chimpanzees preferentially oriented their nests in relation to sunlight. Nests were considered to be oriented east of the trunk if they were between  $>22.5^\circ$  and  $\leq 167.5^\circ$ , and oriented west if they were between  $>202.5^\circ$  and  $\leq 337.5^\circ$ . Nests oriented north (between  $>337.5^\circ$  and  $\leq 22.5^\circ$ ), and south (between  $>167.5^\circ$  and  $\leq 202.5^\circ$ ) were excluded from this analysis, as were those constructed in flat areas.
7. *Integrated nests*: Number of trees used in the construction of a single nest: Included main or primary and secondary trees. Primary trees were those which provided the main support for the nest. The other trees that contributed to construction were defined as secondary.
8. *Cover*: Described as present, absent, or partial. A nest was considered covered when it had vegetation above, open when only the sky was above, and partially covered when about half of the nest had vegetation above. It was also noted if the cover came from (a) the same tree where the nest was made, (b) other tree or trees, or from a combination of (a) and (b).
9. *Relative age*: Scored on a scale of 1–5 according to the degree of decay. Nests of age-class 1 were vacated the same morning when they were found. Nests were assigned to age-class 2 when they were more than 1-day-old but still all green. Nests belonging to age-class 3 were complete but more than half of their leaves were dry and brown. Nests of age-class 4 were beginning to lose leaves or had lost less than half of the leaves. Nests of age-class 5 had lost half or more of their leaves but the woven structure still was clearly recognizable. With the exception of age-class 1, these scores are not absolute estimations of age, because nests made in different species of trees or vegetation types and during different seasons decay at different rates [Stewart et al., 2011].

We used the following equipment: hand-held GPS unit (Magellan 315) for location, 50 m measuring tape to determine horizontal distances, compass (Silva Ranger 15) to get the horizontal angle from magnetic north, Clinometer (Suunto PM-5/360PC) to obtain heights (see Hernandez-Aguilar [2006] for details on calculation methods), and Nikon Travelight V 8:24 × 25 zoom binoculars to inspect nest details. Botanical specimens from nesting species were identified by Yahya Abeid from the National Herbarium of Tanzania and Roy Gereau from the Missouri Botanical Gardens.

#### *Comparisons across chimpanzee study sites*

Nest and nesting tree variables were compared across chimpanzee study sites. Data not reported in metric units were converted. A more exhaustive comparison of nest height, nesting tree height and DBH was done across dry study sites.

#### *Data analysis*

ANOVA was used to determine the differences in the means of DBH and height between primary and secondary nesting trees. A regression analysis was employed to compare the frequency of tree species and the number of tree used for nesting. Poisson regression was used to test if the number of nests per tree was a function of tree height. Regression analyses were done to determine if DBH, crown height, and lowest branch height of nesting trees as well as nest height correlated with nesting tree height. Binomial tests were conducted to test if chimpanzees preferred to orient their nests east or west within the trees. One-way ANOVA was used to test for differences in the means of DBH, tree height and nest height for those dry study sites for which the necessary statistics to conduct this test have been published (see Table III).

## RESULTS

### **Nesting Trees**

1. The DBH for 1,523 trees used in nest construction had a mean of 35.2 cm (SD = 15.8, range: 5.4–147.4). Most nesting trees (96%,  $N = 1,465$ ) had one trunk at breast height, 56 trees (4%) had two trunks, 1 had 3, and 1 had 4. Primary trees had a mean DBH of 35.6 cm (SD = 15.8, range: 8.3–147.4,  $N = 1,451$ ) Table I. Secondary trees had a mean DBH of 27 cm (SD = 13.6, range: 5.4–71.9,  $N = 72$ ). The use of the formula  $\text{Diameter} = \text{Circumference}/\pi$  allowed for results of DBH to the nearest millimeter. Mean DBH differed significantly between primary and secondary trees (ANOVA:  $df = 1$ ,  $F = 20.65$ ,  $P < 0.0001$ ).
2. Tree height for 1,523 nesting trees had a mean of 17.63 m (SD = 5.70, range: 3.14–43.76). Only

TABLE I. Descriptive Statistics of the Variables Recorded for Nests and Nesting Trees

	Mean	Median	SD	Range	N
Nesting trees					
DBH (cm)	35.6	33.4	15.8	8.3–147.4	1,451
Tree height (m)	17.69	17.39	5.66	3.14–43.76	1,451
Lowest branch height (m)	8.11	8.15	2.97	1.13–17.09	182
Crown height (m)	10.88	10.18	4.96	1.59–24.64	182
Number of nests per tree	1.54	1	1.15	1–15	1,444
Nests					
Height (m)	12.15	11.93	4.19	1.17–33.02	2,164
Distance from tree trunk (m)	3.42	2.76	2.66	0–16	2,170
Number of trees per nest	1.06	1	0.24	1–33	2,225

one tree was shorter than 4 m, and 46 (3%) were less than 8 m. Primary trees had a mean height of 17.69 m (SD = 5.66, range: 3.14–43.76,  $N = 1,451$ ). Secondary trees had a mean height of 16.29 m (SD = 6.51, range: 6.04–34.02,  $N = 72$ ). Mean height differed significantly between primary and secondary trees (ANOVA:  $df = 1$ ,  $F = 4.15$ ,  $P < 0.05$ ).

- The height of the lowest branch for 182 primary nesting trees had a mean of 8.11 m (SD = 2.97, range: 1.13–17.09). Only 14 (8%) of these trees had the lowest branch below 4 m.
- The mean crown height for those 182 primary trees was 10.88 m (SD = 4.96, range: 1.59–24.64). (The height of the lowest branch and the crown height were measured only for a subset of the data, and as a result the  $N$  for these two variables is smaller than the 1,523 nesting trees measured.)

To calculate the actual heights we used the formulas provided by the clinometer manufacturer (see Hernandez-Aguilar [2006] for details). The resulting numbers included centimeters.

- Of the 1,523 nesting trees, all but 19 were taxonomically identified, but it was not always possible to distinguish between different species of *Brachystegia*. The taxonomy of the genus *Brachystegia* is confused, and hybridization may contribute to the complex pattern of morphological variation observed in several species of this genus [Chinuki, 1996]. It is therefore difficult to identify *Brachystegia* specimens to the species level [Roy Gereau, per. comm.]. Table II shows the number of stems recorded in 70 vegetation plots of 5 m-radius (see Hernandez-Aguilar [2006] for details) for each of the tree species used for nesting. There was no relationship between tree species frequency in vegetation plots and tree species frequency in nesting ( $R = 0.16$ ,  $N = 17$ ,  $P < 0.05$ ). *Brachystegia* was excluded from this analysis because the nesting frequency of each of the species belonging to this genus is not available. Only five times a liana was involved in nest construction but in all these cases it was tall and had a self-standing trunk resembling a tree. From the nesting species

taxonomically identified, only one was a liana (*Dalbergia malangensis*, see Table II). That virtually all nests were found in trees may be partially explained because the majority of nests reported in this study were constructed in woodland vegetation type where lianas and vines are

TABLE II. Frequency of Species Used for Nesting and Their Frequency in Seventy 5 m-Radius Plots of Vegetation Transects

Species	Frequency in nesting	Frequency in vegetation plots
<i>Brachystegia</i> sp.	550	66
<i>Julbernardia globiflora</i>	424	12
<i>Pterocarpus tinctorius</i>	184	8
<i>Isoberlinia tomentosa</i>	83	0
<i>Combretum molle</i>	61	6
<i>Julbernardia unijugata</i>	57	43
<i>Lannea schimperi</i>	28	1
<i>Pericopsis angolensis</i>	28	3
<i>Pterocarpus angolensis</i>	22	11
<i>Markhamia obtusifolia</i>	12	9
<i>Albizia antunesiana</i>	11	3
<i>Erythrophleum africanum</i>	7	0
<i>Parinari curatellifolia</i>	7	4
<i>Diplorhynchus condylocarpon</i>	6	24
<i>Pleurostylie africana</i>	4	0
<i>Sclerocarya birrea</i>	4	0
<i>Ficus exasperata</i>	2	0
<i>Azelia quanzensis</i>	1	0
<i>Anisophyllea boehmii</i>	1	2
<i>Dalbergia malangensis</i>	1	0
<i>Garcinia huillensis</i>	1	4
<i>Manilkara mochisia</i>	1	2
<i>Monotes adenophyllus</i>	1	3
<i>Monotes</i> sp.	1	0
<i>Ochna mossambicensis</i>	1	0
<i>Ozoroa insignis</i>	1	0
<i>Pseudolachnostylis maprouneifolia</i>	1	9
<i>Sterculia</i> sp.	1	0
<i>Stereospermum kunthianum</i>	1	0
<i>Zanha africana</i>	1	1
<i>Zanthoxylum chalybeum</i>	1	0

**TABLE III. Physical Characteristics of Nests and Nesting Trees for Dry Study Sites**

Study Site	Location	DBH of tree (cm)					Tree height (m)					Nest height (m)					Refs.
		Mean	Median	SD	Range	N	Mean	Median	SD	Range	N	Mean	Median	SD	Range	N	
Kasakati	Tanzania						19				5–40	491				Izawa and Itani [1966]	
Assirik <sup>a</sup>	Senegal						14.22 <sup>f</sup>	5.46 <sup>f</sup>	2–40	163	11.3	5.16 <sup>f</sup>	2–40	163	2.9 <sup>h</sup>	Baldwin [1979]	
Assirik <sup>b</sup>	Senegal										11			252		Baldwin et al. [1981]	
Assirik <sup>c</sup>	Senegal	42								13	11			252		Hunt and McGrew [2002]	
Assirik <sup>d</sup>	Senegal						14.47	4.39		252	13.55	4.24		694	0.92	Pruetz et al. [2008]	
Lwazi	Tanzania	37	29.7–47.6				21				16–30	16		16		Ogawa et al. [1997]	
Ishasha	DRC	54 <sup>g</sup>	11–301	49		67	20 <sup>g</sup>	9	7–40	67	13.5	6.1		101	6.5 <sup>h</sup>	Sept [1992, 1998]	
Semliki	Uganda	45	6–197	405			11	14			11	5.81	1.5–47.8	324		Hunt and McGrew [2002]	
Fongoli	Senegal						11.15	4.42		870	8.33	4.13		1,665	2.8	Pruetz et al. [2008]	
Ntakata/ Kakungu	Tanzania						19		4–35	136	13.9		4–30	136	5.1 <sup>h</sup>	Ogawa et al. [2006]	
Ugalla	Tanzania	36.9	4.3–121.3	19.3		549	19.8	5.5	5–35	549	13.4	5.1	3–30	549	6.4 <sup>h</sup>	Ogawa et al. [2007]	
Issa <sup>e</sup>	Tanzania	35.6	8.3–147.4	15.8		1,451	17.69	5.66	3.14–43.76	1,451	12.15	4.19	1.17–33.02	2,164	5.76	This study	

<sup>a</sup>Data collected from 1976 to 1978.

<sup>b</sup>Data collected from 1976 to 1979.

<sup>c</sup>Data collected in 2000.

<sup>d</sup>Data collected in different study sites within the Ugalla region, except for Issa.

<sup>e</sup>Calculated from data in Baldwin [1979, Table 2, Chapter 9].

<sup>f</sup>Mean for nesting trees ( $n = 67$ ) found in primary forest, no mean for the total number of nesting trees found ( $n = 72$ ) is reported [Sept, 1998, Table II].

<sup>h</sup>Calculated from data in source reference. Blank spaces, no data reported; NPFTT, nest position from tree top.

uncommon. Furthermore, the preferred species for nesting in forest vegetation types where lianas and vines are more common was *Jubernardia unijugata*, a tree. Shrubs may not be used for nesting because they are simply too short.

- The number of nests per tree was counted for 1,444 primary trees. These trees had a mean of 1.54 nests (SD = 1.15, range: 1–15). Most of the trees (1,003 or 69%) had only one nest, 426 (30%) trees had 2–5 nests, and only 15 (1%) trees had 6–15 nests. Trees that were secondary for the construction of some nests were sometimes primary for the construction of others. Taller trees had significantly more nests (Poisson regression: regression coefficient,  $\beta = 0.017$ , standard error = 0.004,  $P$ -value =  $5.19 \times 10^{-6}$ ).

## Nests

- Mean height of 2,164 nests was 12.15 m (SD = 4.19, range: 1.17–33.02). Only 16 nests were  $\leq 4$  m high. Two nests were unusually low 1.17 and 1.20 m.
- Vertical position within the crown was calculated for 337 nests within primary trees. One hundred fifty-three (45%) were constructed in the middle section, 124 nests (37%) in the lower section, and 60 nests (18%) in the top section of the crown.
- Horizontal distance from the tree trunk was measured for 2,170 nests. The mean distance was 3.42 m (SD = 2.66, range: 0–16). Of these, 1,435 (66%) nests were made within 4 m of the base of the trunk, and 42 (2%) were exactly above the base of the tree trunk.
- Orientation within the tree was taken for 2,167 nests. Of the total, 960 (44%) nests were made between 181° and 315° or to the south-west and west of the tree trunk.
- Of 2,167 nests, 813 (38%) were constructed in flats or valleys. For the other nests, 487 (22%) were built on east-facing slopes (N-E, E, S-E) and 867 (40%) on west-facing slopes (N-W, W, S-W). None of the measured nests was made on N or S facing slopes. The hills in the Issa study area run mainly from north to south and comparatively little area consists of north and south facing slopes. Thus, when nesting on slopes they preferred to nest on the downslope side of the tree, opposite to the hillside.
- Of nests made on east-facing slopes, 67% ( $N = 325$ ) were oriented east and 33% ( $N = 162$ ) were oriented west from the tree trunk: chimpanzees preferred to place their nests in the east part of the tree (Binomial test:  $P < 1.3 \times 10^{-13}$ ). Of nests constructed on west-facing slopes, 73% ( $N = 631$ ) were oriented west and 27% ( $N = 236$ ) were oriented east: chimpanzees preferred to place their nests in the west part of the tree (Binomial test:  $P < 2.7 \times 10^{-42}$ ).

- Mean number of trees used per integrated nest was 1.06 (SD = 0.24, range: 1–3,  $N = 2,225$ ). Most of the nests, 2,104 (95%), used only one tree for construction, 116 (5%) used two trees, and only five integrated three trees. When multiple trees were used to make a nest, these trees were significantly shorter and had a significantly smaller DBH than the trees used singly for nest building.
- Presence/absence of cover was recorded for 2,164 nests, of these 864 (40%) were covered, 318 (15%) were partially covered, and 982 (45%) were open or uncovered. Of covered nests, 591 (68%) were covered by the nesting tree, 130 (15%) by the nesting tree plus other tree(s), and 143 (17%) by a tree(s) other than the one in which the nest was constructed. Of partially covered nests, 250 (79%) were covered by the nesting tree, 20 (6%) by the nesting tree plus other tree(s), and 48 (15%) by a tree(s) other than the nesting tree.

The correlation between DBH and height of nesting trees was statistically significant ( $R = 0.45$ ,  $N = 1,523$ ,  $P < 0.0001$ ), but low: the height accounted for only 20% of the variation in the DBH of nesting trees. The correlation between crown height and total height of nesting trees was statistically significant ( $R = 0.88$ ,  $N = 185$ ,  $P < 0.0001$ ), with height of the trees accounting for 77% of the variation in the height of the crown. The correlation between height of the lowest branch and nesting tree height was also statistically significant ( $R = 0.59$ ,  $N = 185$ ,  $P < 0.0001$ ), but the height of the trees accounted for only 35% of the variation in the height of the lowest branch. There was a statistically significant correlation between height of the nest and height of the nesting tree ( $R = 0.67$ ,  $N = 2,164$ ,  $P < 0.0001$ ), the height of nesting trees accounted for 45% of the variation in the height of the nests.

## Comparisons Across Chimpanzee Study Sites

Table III presents data on nest height, nesting tree height and DBH for dry or savanna sites and Table IV for forested sites. At dry sites overall mean ranges for nest height were 8.33–21 m, for nesting tree height were 11.15–20 m, and for DBH were 35.6–54 cm. At forested sites overall mean nest height ranged from 7.8 to 23.2 m, nesting tree height from 12.2 to 24.18 m, and DBH from 20 to 42.4 cm.

The means of DBH, tree height and nest height differed significantly between dry study sites: DBH (ANOVA:  $F = 31.02$ ,  $df = 2$ ,  $P < 0.0001$ ), tree height (ANOVA:  $F = 244.47$ ,  $df = 5$ ,  $P < 0.0001$ ), and nest height (ANOVA:  $F = 190.86$ ,  $df = 6.56$ ,  $P < 0.0001$ ).

## DISCUSSION

### Nest Height, Nesting tree Height, DBH

In comparing nest height across chimpanzee study sites several problems emerge (see Tables III

TABLE IV. Physical Characteristics of Nests and Nesting Trees for Forested Study Sites

Study Site	Location	DBH of tree (cm)				Tree height (m)				Nest height (m)				Refs.		
		Mean	Median	SD	Range	N	Mean	Median	SD	Range	N	Mean	Median		SD	Range
Kindia	Guinea										11.7				100	Nissen [1931]
Near Fort Portal, Rwenzori	Uganda										16.5				25	Bolwig [1959]
Gombe	Tanzania										11			4.6–24.4	384	Goodall [1962]
Kayonza	Uganda													0 to >30.5	259	Schaller [1963]
Budongo	Uganda															Reynolds and Reynolds [1965]
Rio Muni	Republic of Guinea											10		2–24	184	de Bournonville [1967]
Rio Muni	Equatorial Guinea										10.015	9	6.08	0–40	195	Baldwin et al. [1981]
Sapo	Equatorial Guinea											12			62	Groves and Sabater Pi [1985] <sup>i</sup>
	Liberia	52				62	18								62	Anderson et al. [1983]
	Gabon										8.7			2–32	1,741	Tutin and Fernandez [1983] <sup>j</sup>
Ngogo, Kibale	Uganda										12.2			2–35	472	Ghiglieri [1984]
Kanyawara, Kibale	Uganda										10.8			5–23	148	Ghiglieri [1984]
Tai		42	33		6–168						23.2	20		5–45	154	Fruth [1990] <sup>j</sup>
Lopé	Gabon	34.6	25		5–400						11.7	10		2–45	523	Wrogemann [1992]
Petit Loango	Gabon										12.5				323	Furuichi et al. [1997]
Several Sites	Guinea										17.65			0–37	923	Ham [1998] <sup>k</sup>
Budongo	Uganda	26.4				411					12.1				601	Brownlow et al. [2001]
Tishibati, Kahuzi-Biega <sup>a</sup>	DRC	35.3	21.9			94	12.6		4.3		9.8				94	Basabose and Yamagiwa [2002]
Tishibati, Kahuzi-Biega <sup>b</sup>	DRC	24.9	13.3			104	12.1		5.5		9.4				104	Basabose and Yamagiwa [2002]
Bossou	Guinea	32.1	20.5		5.1–114.6	218					13	12.5	5	2.5–32.5	245	Humle [2003]
Seringbara, Nimba	Guinea	28.7	28.4		4.7–135	157					12.5	12.5	7.9	2.5–37.5	169	Humle [2003]
Yealé, Nimba	Ivory Coast	42.4	34.8		1.9–150	192					18.7	17.5	10.7	2.5–42.5	222	Humle [2003]
Kanyawara, Kibale Forest	Uganda	20	18.1		1.6–216.4	1,245	12.2		5	3–35	1,234	11.3	4.9	0–32	937	Llorente-Caño [2003]
Lac Télé <sup>c</sup>	Congo										9.3		6.21	1.2–50	329	Poulsen and Clark [2004]
Lac Télé <sup>d</sup>	Congo										18.9		9.07	3–42	55	Poulsen and Clark [2004]
Lac Télé <sup>e</sup>	Congo										12.5		8.68	3–30	79	Poulsen and Clark [2004]

TABLE IV. Continued

Study Site	Location	DBH of tree (cm)			Tree height (m)			Nest height (m)			Refs.	
		Mean	Median	SD	Range	N	Mean	Median	SD	Range		N
Lac Télé <sup>f</sup>	Congo						10.7	2.10	2.10	7–15	15	Poulsen and Clark [2004]
Ise-Forest Reserve	Nigeria	20.64	4.14		24.18	5.86	19.14	6.75	6.75		61	Ogunjemite et al. [2005]
Pongara	Gabon						13.4			4–34	111	Petre et al. [2007]
Gouloungou Triangle, Congo							17.3	7.4	7.4		247	Sanz et al. [2007]
Nouabalé-Ndoki												
Bwindi	Uganda						16.06	15	6.202	0–46	3,414	Stanford and O'Malley [2008]
German-Fort, Gashaka-Gumti <sup>g</sup>	Nigeria	40.25			8.75		7.1				83	Ogunjemite et al. [2010]
German-Fort, Gashaka-Gumti <sup>h</sup>	Nigeria	83.13			11.09		9.48				83	Ogunjemite et al. [2010]
Gouéla II, Nimba	Guinea						7.8	4.6	4.6		337	Granier [2011]
Cantanhez	Guinea-Bissau						19.72	2.94	2.94	5–30	718	Sousa et al. [2011]
Seringbara, Nimba	Guinea						11.3	10.5	6.3		1,376	Koops et al. [2012a]

<sup>a</sup>Secondary forest.<sup>b</sup>Primary forest.<sup>c</sup>Swamp forest.<sup>d</sup>Seasonally flooded forests.<sup>e</sup>Mixed forest terra firma, low water.<sup>f</sup>Mixed forest terra firma, high water.<sup>g</sup>Rainy season.<sup>h</sup>Dry season.<sup>i</sup>Calculated from data in Table 5b, p. 30.<sup>j</sup>In Fruth and Hohmann [1994].<sup>k</sup>In Kormos et al. [2003].

Blank spaces, no data reported.

and IV). First, the descriptive statistics reported in the literature are not uniform: while some studies provided the mean, standard deviation, and range, others gave only the range or the median. Some studies presented results by season or by vegetation type but figures for the total number of nests analyzed per site were not provided. Importantly, it is difficult to evaluate the significance of nest height variation across sites without complementary data on nesting tree height. Although it has long been suspected that the height of the tree had an effect on the height of the nest [Goodall, 1962; Reynolds and Reynolds, 1965; Izawa and Itani, 1966], few studies have actually measured the height of nesting trees or of trees in the habitat. Nest height has been shown to have a significant positive correlation with nesting tree height [Sept, 1998; Ogawa et al., 2007; this study], thus chimpanzees in some sites may not be able to make higher nests because the available trees are short. Ghiglieri [1984] speculated that the difference between average nest heights in Ngogo and Kanyawara in Kibale was a product of the greater number of tall trees at Ngogo, but he could not test this assumption because trees were not measured.

Studies of chimpanzee nesting have used DBH of nesting trees as a proxy for their height, but this may be problematic. At Seringbara, a forested site, Koops et al. [2012a] found a strong correlation between DBH and height of nesting trees, but at Issa, a savanna site, the correlation between these two variables was statistically significant but low (less than what it would be desirable as a proxy for height). Although the allometric relationship between tree height and DBH is commonly known, it is not simple and constant. Tree height for a given diameter may vary significantly among and within species and within and across sites [Horn, 1971; Kira, 1978; Rich et al., 1986; Feldpausch et al., 2011]. This variability is such that Feldpausch et al. [2011] concluded that the assumption of the height:diameter ratio being constant is not longer valid. Using tree DBH as a proxy for tree height may not provide accurate measures in studies of chimpanzee nesting behavior. For example, chimpanzee preferences to nest in trees with large DBHs may reflect a choice for older, not necessarily higher, trees with thicker branches more able to support the chimpanzees' weight.

It is thus not surprising that differences in DBH across study sites do not reflect a proportionate difference in nesting tree height (see Tables III and IV). Means rather than medians were available for more chimpanzee study sites and thus below we focus comparisons on means. When DBH and nesting tree height were compared for the three dry study sites for which data are available, Ishasha trees showed a larger DBH than is expected from the comparison with Ugalla and Issa. Nesting tree heights were almost identical at Ishasha and Ugalla,

while DBH at Ishasha was 1.5 times larger than at Ugalla. Although in Issa most nests came from woodland, in Ugalla and Ishasha nests came from the same vegetation type, forest. Thus differences in the physical characteristics of trees across forest vegetation types at Ishasha and Ugalla may account for this dissimilarity.

Differences in nesting tree height across dry sites (see Table III) may in part relate to the height of trees in the different vegetation types where nests occur. Trees in forest are higher than in woodland in Ugalla [Hernandez-Aguilar, 2006] as in other dry chimpanzee habitats [Baldwin, 1979; Pruett et al., 2008]. Thus, nesting trees in Issa being lower than in other study areas within Ugalla may be because at Issa more than 90% of nests were found in woodland [Hernandez-Aguilar, 2009], while in the other study areas most nests came from forest [Ogawa et al., 2007]. Although it can be said that Issa chimpanzees extensively used the woodland for nesting throughout the annual cycle, preference for woodland or forest cannot be concluded without measuring the actual availability of nesting spots between the two vegetation types [Hernandez-Aguilar, 2006, 2009]. Similarly, nesting trees in Ishasha being higher than those in Issa may be because nests in Ishasha also were found in gallery forest. Nesting trees found in Ugalla were almost the same height as those in Ishasha, and, as mentioned above, nests at these two sites occurred mainly in forest vegetation types. Nesting tree height was the second lowest of all dry sites in Assirik. During early studies at this site more nests were found in open (woodland and grassland) than in closed (forest) vegetation types [Baldwin, 1979; Baldwin et al., 1981] but a later study found the opposite [Pruett et al., 2008]. These differences can be because Pruett et al. [2008] collected data only during the late dry season at Assirik (February to April) while the year-round Baldwin's [1979] study found that at the end of the dry season Assirik chimpanzees nested more frequently in gallery forests than in woodland and grassland. However, despite the difference in the vegetation types where nests were found, the two periods showed remarkably similar nesting tree heights (14.22 m vs. 14.47 m). Baldwin [1979] and Pruett et al. [2008] concluded that chimpanzees in Assirik preferred the tallest trees in their habitat for nesting, suggesting that overall tree height in Assirik is lower than that at other dry sites except for Fongoli. When comparing tree physical characteristics in equivalent vegetation types across dry sites, specific vegetation physiognomy at each site needs to be taken into consideration to identify constraints imposed by vegetation and the chimpanzee's preferences. For example, even though nesting tree height at Assirik was lower than at Issa, chimpanzees at both sites used for nesting taller trees than the average tree

height in their habitat suggesting preference for tall trees [Baldwin, 1979; Hernandez-Aguilar, 2006; Pruett et al., 2008]. In contrast, chimpanzees in Fongoli nested in low trees (the lowest of all dry sites) despite availability of higher trees [Pruett et al., 2008]. Thus, habitat tree height may constrain nesting tree height in Assirik but not in Fongoli, depending on the tree height preferred by the apes in each site.

Data from Table III support the hypothesis that the construction of elevated nests is an adaptation against predation: at all dry sites, where predators are present, chimpanzees made higher nests than at Fongoli, where predation pressure is almost absent. Accordingly, Fongoli is the only dry site for which nocturnal ground nests have been reported [Pruett et al., 2008]. Furthermore, for those dry sites for which the mean height of both nests and nesting trees is provided (Fongoli excluded) nesting tree height ranged from 14.22 to 20 m while nest height showed less than half of that variation (11.3–13.55 m). Thus, in support of the anti-predation function of high nests, nest height appears more constant than nesting tree height across dry study sites where predators exist.

Regression results indicate that nesting tree height in Ishasha and Issa accounted for 45% [Sept, 1998; this study], and in other areas within the Ugalla region for 25% [Ogawa et al., 2007] of the variation in nest height. As nesting tree height explains about half or less of the variation in nest height, chimpanzees at these sites may select not only tall trees for nesting, but also a height for nest construction and thus provides further support for the hypothesis that elevated sleeping places are an anti-predation strategy.

### Height of the Lowest Branch

Goodall [1968] noted that trees with lowest branches less than 3 m from the ground were not usually used for nest construction in Gombe. In Lopé, the height to the lowest branch of nesting trees ranged between 3 and 6 m [Wrogemann, 1992]. The mean lowest branch height of nesting trees was 5.6 m in Kibale [Llorente-Caño, 2003] and 8.11 m in Issa. At Assirik 54 of 163 nests (33%) were constructed in trees with lowest branches less than 3 m in height [Baldwin, 1979], while at Issa only 7 of 182 (4%) were. That Assirik chimpanzees construct nests in trees with low branches almost 10 times more often than their Issa counterparts, given that predators are present at both dry sites, requires explanation. Height of nesting trees at Issa is greater than at Assirik, so the difference in lowest branch height may be related to this, but the difference in nesting tree height does not explain completely the difference in the height of the lowest branch between these two sites.

Our results suggest that height of the lowest branch is an important variable for the chimpanzees' selection of trees in which to nest. In our study the height of the nesting tree accounted for 77% of the variation in the height of the crown but only for 35% of the variation in the height of the lowest branch. This means that if a chimpanzee chose a tree for nesting based only on its height, this tree would have a high lowest branch only about 1/3 of the time. Our results differ, as 92% of the nesting trees had a high lowest branch (>4 m). No comparable data for crown height and height of the lowest branch of nesting trees have been published for chimpanzees, but Fruth [1995] reported similar data from her analysis of nest building by bonobos at Lomako, Democratic Republic of Congo. There nesting tree height accounted for 68% of the variation in crown height and for 30% of the variation in the height of the lowest branch. She concluded that both the height of the lowest branch and the height of the crown are positively correlated with nesting tree height but she did not discuss the difference between nesting tree height accounting for 30% and 68% of variation in height of the lowest branch and crown height, respectively. It is important to note that Lomako, like Issa, had predators (leopards: Fruth [1995]). Koops et al. [2012a] concluded that chimpanzees of Seringbara preferred nesting trees with low first branches, predation at the site is low or absent.

Gandini and Baldwin [1978] reported a young leopard climbing the vertical trunk of a tree with a lowest branch of 8 m. Despite felines' ability to climb, they may need to work harder to climb a tree with high lowest branches (we were unable to find research comparing the energetics of felid vertical climbing vs. branch-to-branch leaping ascent). Nesting at greater heights would allow chimpanzees greater opportunity for detecting the presence of a predator, as the higher a feline has to climb, the longer the time a chimpanzee has for hearing it or sensing its movement. Being aware of the presence of a feline in a tree gives an advantage to chimpanzees, for fleeing or for confrontation.

Although the data presented here support the hypothesis that elevated height of nests, nesting trees and lowest branches are a response to predator pressure in chimpanzees, to test more adequately this hypothesis systematic comparisons are needed of physical characteristics of trees used for nest construction versus trees not used for nesting despite being suitable. Nesting trees had significantly greater total height and lowest branch height than non-used suitable trees at Issa [Hernandez-Aguilar, 2006, 2009, in prep.].

### Tree Species Preference

Baldwin [1979] was the first to report nesting tree species preference based on the lack of

correlation with the frequencies of the tree species in vegetation transects. Since then, species preference for nesting has been noted for other chimpanzee study sites [Ghiglieri, 1984; Wrogemann, 1992; Hashimoto, 1995; Brownlow et al., 2001; Hunt and McGrew, 2002; Furuichi and Hashimoto, 2004; Bababose and Yamagiwa, 2002; Humle, 2003; Ogawa et al., 2007; Petre et al., 2007; Sanz et al., 2007; Stanford and O'Malley, 2008; Koops et al., 2012a].

The frequency with which some species were used for nesting in the present study did not correspond to their availability, and this may indicate the chimpanzees' preference. For example, *Isobertinia tomentosa* was one of the most frequent nested-in species, although it is not abundant: no individuals from this species were present in vegetation plots. *I. tomentosa* grows in isolated groves where it is a dominant species, mainly in the woodland in flat areas or valleys, and it was frequently used for nesting during the dry season when other species in woodland were leafless (each species drops its leaves at a different period during the dry season).

It is not accurate to conclude species preference by taking into consideration only species abundance, rather one must evaluate the physical characteristics of each individual species before preference by the chimpanzees can be concluded. For example, even though *Diplorhynchus condylocarpon* was one of the most frequent species in vegetation plots only 6 of 1,504 nesting trees were *D. condylocarpon*. However, when the typical height of this species is taken into account, this is not surprising. *D. condylocarpon* is an understory tree in woodland and most trees of this species are short, individuals from vegetation plots averaged only 3.74 m and none was above 6 m [Hernandez-Aguilar, 2006], while only 4 of 1,523 nesting trees in Issa were 6 m tall or less. The six *D. condylocarpon* used for nesting averaged 17.70 m (range 15.44–22.62). Thus, although chimpanzees may prefer *D. condylocarpon* for nesting, they may simply not find individuals tall enough to make nests. In this sense even though *D. condylocarpon* is a common species, the individuals that can actually be used for nesting are extremely rare and as such it could be considered a preferred species.

### Number of Nests per Tree

For the number of nests per tree Baldwin et al. [1981] reported that the median in Equatorial Guinea was 1 while in Assirik it was 2, and hypothesized the difference to be due to fewer suitable nesting trees available at Assirik because it was a dry site in comparison with Equatorial Guinea. The median number of nests per tree in Issa was 1. In order to know if this hypothesis explains the difference between Assirik and Issa, both dry sites,

data on suitable tree availability for both sites need to be compared.

### Vertical Position of the Nest Within the Crown

Izawa and Itani [1966] reported that most nests were constructed near the tree top in Kasakati. In Assirik nests were built in the top part of the crown during different study periods [Baldwin, 1979; Baldwin et al., 1981; Pruett et al., 2008]. Issa chimpanzees nested more frequently in the middle part of the tree crown. No data on crown height are given for other dry sites and nest position within the three segments of the crown (top, middle, bottom) cannot be calculated. However, the position of nests below the top of the tree crown is available from several dry sites and the difference ranged from 0.92 to 6.5 m (see Table III). For forested sites, Goodall [1962, 1968] noted that when Gombe chimpanzees used short trees (<9 m), nests were made near the top of the tree; the middle third of the crown was most often used for nesting both in Lopé [Wrogemann, 1992] and Seringbara [Koops et al., 2012a].

### Distance From the Tree Trunk

The nest distance from the tree trunk seemed to be linked to the physical characteristics of nesting trees. Most nests were made close to the trunk although the percentage volume of the crown increases at longer distance away from the trunk. This may reflect a preference for the thicker/stronger branches that grow closer to the trunk since they would be more able to support the chimpanzee's weight. Horizontal branches are expensive for trees to produce because of gravity and need to be thicker close to the trunk [Horn, 1971]. Thus, the distance from the tree trunk to the nest is likely constrained by the availability of branches able to support a chimpanzee's weight.

### Orientation

In Equatorial Guinea, Jones and Sabater Pi [1971] found that when on slopes, more nests were made on east-south facing slopes than on west-north facing slopes (63% vs. 15%); the remaining 22% of nests were made in flat terrain. They hypothesized that chimpanzees in Equatorial Guinea oriented their sleeping sites to obtain the thermal benefit from the sun. However, Sabater Pi [1985] and Groves and Sabater Pi [1985] later analyzed the same data and found no support for this hypothesis. In these data from Equatorial Guinea the orientation of a nest was defined as the orientation of the slope where the nest was constructed, but no data on the orientation of the nest within the tree were reported. Reynolds and Reynolds [1965] mentioned that day nests

in Budongo during the long wet season seemed to be made in “sunny spots of trees” [p.386], but they gave no numbers. To our knowledge, no data on the orientation of nests with respect to the trunk of the tree have been published, so the present report is the first. Hernandez-Aguilar [2009] analyzed the location of the total number of nests found within the Issa study area and confirmed that the chimpanzees preferred to nest on slopes. The data presented here were used to see if there was a difference in the orientation within the tree for nests constructed on west-facing slopes versus nests built on east-facing slopes. Our results show that when on west-facing slopes, the chimpanzees preferred to orient their nests west within the tree, and when on east-facing slopes they preferred to orient their nests east within the tree. Since the sun goes down in the west, these data suggest that when on west-facing slopes chimpanzees preferred to make nests in the west part of the tree perhaps to have light a little bit longer for nest construction or to use the warmer part of the tree. When they nested on east facing slopes they preferred to orient their nests eastwards perhaps to receive the first sun in the morning. Stewart [2011] found support for the hypothesis that nests function in thermoregulation, providing insulation, at Fongoli, where overnight temperatures drop to 7°C. Similarly, in Issa the lowest temperature recorded during the present study was 8°C. Issa is overall less cold than Fongoli: mean monthly minimum temperatures of 14.4 and 11°C, respectively [Hernandez-Aguilar, 2009; Stewart, 2011]. However it still might be advantageous for Issa chimpanzees to gain some warmth when the sun goes down or during the early morning when temperatures are lower than later during the day. Koops et al. [2012a] also found support for the hypothesis that nests function in thermoregulation, as a strategy to avoid humidity. An alternative hypothesis to the Issa chimpanzees’ preference in nest orientation is that because of light foliage within a tree is denser in the side of the tree exposed to either morning or evening sun. This last hypothesis remains to be tested.

### Integrated Nests

Few data on the percentage of integrated nests (i.e., those made with more than one tree) have been published for chimpanzees. Goodall [1962] mentioned that nests made with more than one tree were rare, but gave no numbers. At Lopé, less than 10% of nests integrated more than one tree and the maximum number of trees used was 2 [Wrogemann, 1992]. Humle [2003] reported that nests made with more than one tree comprised 9.8% at Bossou (maximum four trees), 17.4% at Seringbara (maximum seven trees), and 12.6% at Yealé (maximum four trees). At Issa only 5% of nests were integrated (maximum three trees). McGrew

[2004] suggested that frequency of nests made with more than one tree might reflect density of individual trees and degree of canopy closure. The different percentages of integrated nests between Issa and the forested sites of Lopé, Bossou, Seringbara, and Yealé may reflect differences in tree density. Rainforests have a higher density of young trees than do dry habitats [Horn, 1971]. In Bossou, Seringbara, and Yealé, Humle [2003] found that the primary tree in integrated nests had a smaller DBH than trees used singly for nest making and also found a significant negative correlation between the DBH of the main tree and the number of trees used in the construction of an integrated nest. She said that when using a tree of small DBH, branches and leaves from neighboring trees may be needed to make a structure of adequate support. At Issa we found that when trees were integrated into a nest, these trees were shorter and less wide than the trees used singly for nest construction. Fruth [1995] hypothesized that the high percentage of integrated nests in Lomako (40%, maximum six trees) was a consequence of a bonobo trying to be closer to another individual when bigger trees were not available in the vicinity of the desirable companion. She concluded that bonobos may integrate more trees in nest making than chimpanzees because of the difference in social lives of the two ape species. More data are needed to test Fruth’s hypothesis, mainly from chimpanzees living in habitats with similar tree density and vegetation physiognomy to that of the forest of Lomako.

### Cover

At Issa, 45% of nests were open, versus 40% covered and 15% partially covered. For most sites nests were categorized only as covered or open. At Assirik 75% [Baldwin et al., 1981] and at Semliki 38% of nests were open [Hunt and McGrew, 2002]. That a lower percentage of nests at Semliki than at Issa are open may be because all nests at Semliki were found in gallery forest [Hunt and McGrew, 2002], where canopy density is higher than in more open vegetation types [Samson and Hunt, 2012]. The difference in cover percentage between Assirik and Issa is interesting because 105 of 252 (42%) of the nests analyzed for cover in Assirik occurred in gallery forest (<3% of habitat) [Baldwin et al., 1981], while only 6% of the nests analyzed for cover in Issa occurred in forest despite the similar percentage of gallery forest (2%). At both study sites, forest vegetation types had higher stem density than open ones [Baldwin, 1979; Hernandez-Aguilar, 2006] and there was denser canopy in forests than in open vegetation types. Woodland at Issa [92%, Pintea and Hernandez-Aguilar, unpublished data] covers more of the study area than in Assirik [37%, Baldwin, 1979]. Thus vegetation in Assirik may be thinner overall than in Issa. At Assirik, gallery forests in general occurred in

long, narrow and steep-sided clefts in plateau [Baldwin, 1979]. In these narrow strips the edges of the strip (which have no trees to cover them) make up a larger proportion than the even spatial distribution of woodland trees in Issa. Thus, distribution could be responsible for some of the differences in percentages of open versus covered nests between Assirik and Issa and not overall density of trees in these sites. At Assirik, nests were made closer to the tree top while at Issa they were built in the middle part of the crown (see above) and this may also account for the higher percentage of covered nests in Issa. In forested study sites, reported percentages of open nests are 17% in Equatorial Guinea, 21% in Sapó [Anderson et al., 1983], 38% in Lopé [Wrogemann, 1992], 45% in Kibale [Llorente-Caño, 2003], and 20% in Seringbara [Koops et al., 2012a]. Baldwin et al. [1981] explained the much lower percentage of open nests at Equatorial Guinea versus Assirik as an effect of the vegetation being thinner in Assirik. However, that almost half of nests in Kibale are open, despite it being a forested site, indicates that habitat type alone cannot explain percentages of covered vs. open nests. At Seringbara [Koops et al., 2012a] and Issa most nests were built in the middle and lower parts of the crown and percentages of nests made in the top part of the crown were similar for both sites (23% and 18%, respectively), but percentage of open nests differ between the two sites. To explain differences in nest cover across study sites not only data on tree and canopy densities are needed, but also on tree morphology (including crown shape), position of nests within the crown, and distance of the nest from the tree trunk.

## CONCLUSION

The chimpanzees chose physical characteristics of trees and made their nests in specific spots or sections in order to obtain benefits in coping with their environment. Nests functioned as shelters [sensu Stewart, 2011]. The apes directionally oriented their nests within the tree possibly to take advantage of sunlight. Our findings provided support for the hypothesis that arboreal nest building is an antipredator strategy: Issa chimpanzees preferred to built nests not only in taller trees but also in trees with higher first branches. Studies of nesting in chimpanzees need to present statistical data in a systematic way, including all descriptive statistical values for the total number of nest analyzed and not just for sub-sets of data by vegetation type or season. Additionally, greater efforts need be made to accurately measure heights not only of nests, but also of nesting tree variables using a clinometer or a similar precision instrument. This is a time-consuming task, even more so in forested habitats where clear views of tree crowns are not easy to achieve, but getting these data for at least a representative sub-sample of all the

nesting trees analyzed is of vital importance if we are to systematically compare nesting variables across study sites. Thus in order to analyze chimpanzee nesting behavior and adequately evaluate environmental determinants, patterns of selection, and potential cultural differences we need to obtain data on the physical characteristics of nesting trees and not just nests, on the availability of nesting material (selected vs. suitable), and to make exhaustive comparisons of vegetation physiognomies across study sites.

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## REFERENCES

- Anderson JR. 1984. Ethology and ecology of sleep in monkeys and apes. *Adv Study Behav* 14:165–229.
- Anderson JR, Williamson EA, Carter J. 1983. Chimpanzees of Sapó Forest, Liberia: density, nests, tools and meat-eating. *Primates* 24:594–601.
- Baldwin PJ. 1979. The natural history of the Chimpanzee (*Pan troglodytes verus*), at Mt. Assirik, Senegal [Ph.D. Dissertation]. Stirling: University of Stirling.
- Baldwin PJ, Sabater Pi J, McGrew WC, Tutin CEG. 1981. Comparison of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates* 22:474–486.
- Baldwin PJ, McGrew WC, Tutin CEG. 1982. Wide-ranging chimpanzees at Mt. Assirik, Senegal. *Int J Primatol* 3:367–385.
- Basabose AK, Yamagiwa J. 2002. Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric gorillas. *Int J Primatol* 23: 263–282.
- Boesch C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 16:1–16.
- Bolwig N. 1959. A study of the nests built by mountain gorilla and chimpanzee. *South African J Sci* 55:286–291.

- 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* 55:45–55.
- Chinuki A. 1996. Species delimitation problems in *Brachystegia* Benth (Caesalpinioideae-Leguminosae). *Oxford Plant Syst* 4:8–9.
- de Bourmonville D. 1967. Contribution à l'étude du chimpanzé en République de Guinée. *Bull Inst Fundam Afrique Noire* 29A:1188–1269.
- Feldpausch TR, Bani L, Phillips OL, et al. 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences* 8:1081–1106.
- Fruth B. 1995. Nests and nests Groups in Wild Bonobos (*Pan paniscus*): ecological and behavioral correlates [Ph.D. Dissertation]. München and Starnberg: Ludwig-Maximilians-Universität München and Max-Planck-Institut für Verhaltensphysiologie Seewiesen. Aachen: Shaker.
- 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: McGrew WC, de Waal FBM, Wrangham RW, Heltne P, editors. *Chimpanzee cultures*. Cambridge: Harvard University Press. p 109–128.
- Furuichi T, Hashimoto C. 2000. Ground beds of chimpanzees in the Kalinzu Forest, Uganda. *Pan Africa News* 7:26–28.
- Furuichi T, Hashimoto C. 2004. Botanical and topographical factors influencing nesting-site selection by chimpanzees in Kaliunzu Forest, Uganda. *Int J Primatol* 25:755–765.
- Furuichi T, Inagaki H, Angoue-Ovono S. 1997. Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: employing a new method to distinguish between nests of the two species. *Int J Primatol* 18:1029–1046.
- Furuichi T, Hashimoto C, Tashiro Y. 2001. Extended application of a marked-nest census method to examine seasonal changes in habitat use by chimpanzees. *Int J Primatol* 22:913–928.
- Gandini G, Baldwin PJ. 1978. An encounter between chimpanzees and a leopard in Senegal. *Carnivore* 1:107–109.
- Ghiglieri MP. 1984. *The Chimpanzees of the Kibale forest: a field study of ecology and social structure*. New York: Columbia University Press.
- Goodall J. 1962. Nest building behavior in the free ranging chimpanzee. *Ann N Y Acad Sci* 102:455–467.
- Goodall J. 1965. Chimpanzees of the Gombe Stream reserve. In: de Vore I, editor. *Primate behavior*. New York: Holt, Rinehart and Winston. p 425–447.
- Goodall J. 1968. The behavior of free-living chimpanzees in the Gombe stream reserve. *Anim Behav Monographs* 1: 163–311.
- Granier N. 2011. Chimpanzees in the eastern part of the Nimba Mountains Biosphere Reserve: Gouéla II and Déré Forest. In: Matsuzawa T, Humle T, Sugiyama Y, editors. *The chimpanzees of Bossou and Nimba*. Tokyo: Springer. p 289–299.
- Groves CP, Sabater Pi J. 1985. From ape's nest to human fix point. *Man* 20:22–47.
- Hashimoto C. 1995. Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. *Primates* 36:477–488.
- Henschel P, Abernethy KA, White JT. 2005. Leopard food habits in the Lope National Park, Gabon, Central Africa. *African J Ecol* 43:21–28.
- Hernandez-Aguilar RA. 2006. *Ecology and Nesting Patterns of Chimpanzees (Pan troglodytes) in Issa, Ugalla, Western Tanzania* [Ph.D Dissertation]. Los Angeles: University of Southern California.
- 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.
- Hernandez-Aguilar RA, Moore J, Stewart F, Piel A, Ogawa HA, Pintea L. 2006. Surveys of ugalla and masito. In: Moyer D, Plumtre AJ, Pintea L, et al., editors. *Surveys of chimpanzees and other biodiversity in Western Tanzania*. Wildlife Conservation Society, the Jane Goodall Institute and the United States Fish and Wildlife Services. p 24–31.
- Horn HS. 1971. *The adaptive geometry of trees*. Princeton, NJ: Princeton University Press.
- Hunt KD, McGrew WC. 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant LF, editors. *Behavioural diversity in chimpanzees and bonobos*. Cambridge: Cambridge University Press. p 35–51.
- Humle T. 2003. *Culture and variation in wild chimpanzee behaviour: a study of three communities in West Africa* [Ph.D. dissertation]. Stirling: University of Stirling.
- Itani J. 1979. Distribution and adaptation of chimpanzees in an arid area. In: Hamburg DA, McCown ER, editors. *The Great Apes*. Menlo Park, CA: Benjamin/Cummings. p 55–71.
- Izawa K, Itani J. 1966. *Chimpanzees in Kasakati Basin, Tanganyika: ecological study in the rainy season 1963–1964*. *Kyoto Univ African Stud* 1:73–156.
- Jones C, Sabater Pi J. 1971. Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. *Bibliotheca Primatol* 13:1–96.
- Kano T. 1972. Distribution and adaptation of chimpanzees on the eastern shore of Lake Tanganyika. *Kyoto Univ African Stud* 7:37–129.
- Kira T. 1978. Community architecture and organic matter dynamics in tropical lowland rain forest of Southeast Asia with special reference to Pasoh Forest, West Malaysia. In: Tomlinson PB, Zimmermann MF, editors. *Tropical trees as living systems*. Cambridge University Press. Cambridge: p 561–590.
- Koops K, Humle T, Sterck EHM, Matsuzawa T. 2007. Ground nesting by the chimpanzees of the Nimba Mountains, Guinea: environmentally or socially determined? *Int J Primatol* 69:407–419.
- Koops K, McGrew WC, de Vries H, Matsuzawa T. 2012a. Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and antivector hypotheses. *Int J Primatol* 33:356–380.
- Koops K, McGrew WC, Matsuzawa T, Knapp LA. 2012b. Terrestrial nest-building by wild chimpanzees (*Pan troglodytes*): implications for the tree-to-ground sleep transition in early hominins. *Am J Phys Anthropol* 148:351–361.
- Kormos R, Boesch C, Bakarr MI, Butynski TM. 2003. *West African chimpanzees: status survey and conservation action plan*. Gland and Cambridge, UK: IUCN/SSC Primate Specialist Group.
- Llorrente-Cañó M. 2003. *Estudio comparado de la conducta nidificadora de los chimpancés (Pan troglodytes schweinfurthii) de la comunidad de Kanyawara (Parque Nacional de Kibale, Uganda)* [Ph.D. dissertation]. University of Barcelona: Barcelona.
- Marchesi P, Marchesi N, Fruth B, Boesch C. 1995. Census and distribution of chimpanzees in Cote D'Ivoire. *Primates* 36: 591–607.
- McGrew WC. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.
- McGrew WC. 2004. *The cultured chimpanzee: reflections on cultural primatology*. Cambridge: Cambridge University Press.
- Moore J. 1992. "Savanna" chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford MP, de Waal FBM, editors. *Topics in*

- primatology: human origins. Tokyo: University of Tokyo Press. p 99–118.
- Moore J. 1994. Plants of the Tongwe East Forest Reserve (Ugalla), Tanzania. *Tropics* 3:333–340.
- Moore J. 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew WC, Marchant LF, Nishida T, editors. *Great Ape societies*. Cambridge: Cambridge University Press. p 275–292.
- Morgan D, Sanz C, Onononga JR, Strindberg S. 2006. Ape abundance and habitat use in the Goulougo Triangle, Republic of Congo. *Int J Primatol* 27:147–179.
- Nishida T. 1989. A note on the chimpanzee ecology of the Ugalla area, Tanzania. *Primates* 30:129–138.
- Nissen HW. 1931. A field study of the chimpanzee. *Compar Psychol Monogr* 8:1–122.
- Ogawa H, Kanamori M, Mukeni SH. 1997. The discovery of chimpanzees in the Lwazi River area, Tanzania: a new southern distribution limit. *Pan Africa News* 4:1–3.
- Ogawa H, Moore J, Kamenya S. 2006. Chimpanzees in the Ntakata and Kakungu areas, Tanzania. *Primate Conserv* 21:97–101.
- Ogawa H, Gen'ich I, Moore J, Pintea L, Hernandez-Aguilar RA. 2007. Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. *Int J Primatol* 28:1397–1412.
- Ogunjemite BG, Afolayan TA, Agbelusi EA. 2005. Habitat structure of chimpanzee community in Ise-Forest Reserve, Ekiti State, South-western Nigeria. *African J Ecol* 43:396–399.
- Ogunjemite BG, Ashimi TA, Okeyoyin OA. 2010. The chimpanzee community of German-Fort, and the potentials for the development of tourism-base management of Gashaka-Gumti National Park, Nigeria. *J Sust Dev Africa* 12:107–115.
- Petre CA, Huynen MC, Beudels-Jamar R. 2007. First assessment of chimpanzee (*Pan troglodytes troglodytes*) density and bedding behaviour in the Pongara National Park, Gabon. *Pan Africa News* 14:22–27.
- Plumptre AJ, Reynolds V. 1997. Nesting behavior of chimpanzees: implications for censuses. *Int J Primatol* 18:475–485.
- Poulsen JR, Clark CJ. 2004. Densities, distributions, and seasonal movements of gorillas and chimpanzees in swamp forest in northern Congo. *Int J Primatol* 25:285–306.
- Pruetz JD, Fulton SJ, Marchant LF, et al. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. *Am J Primatol* 70:393–401.
- Reynolds V, Reynolds F. 1965. Chimpanzees on the Budongo forest. In: De Vore I, editor. *Primate behavior*. New York: Holt, Rinehart and Winston. p 368–424.
- Rich PM, Helenurm K, Kearns D, et al. 1986. Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest. *Bull Torrey Bot Club* 113:241–246.
- Sabater Pi J. 1984. Gorilas y chimpancés del África Occidental: estudio comparativo de su conducta y Ecología en Libertad. México: Fondo de Cultura Económica.
- Sabater Pi J. 1985. *Etología de la vivienda humana: de los nidos de los gorilas y chimpancés a la vivienda humana*. Barcelona: Editorial Labor.
- Samson DR. 2012. The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve, Uganda. *Primates* 53:357–364.
- Samson DR, Hunt KD. 2012. A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. *Am J Primatol* 74:811–818.
- Sanz C, Morgan D, Strindberg S. 2007. Distinguishing between the nests of sympatric chimpanzees and gorillas. *J Appl Ecol* 44:263–272.
- Schaller BG. 1963. *The Mountain Gorilla: ecology and behavior*. Chicago: University of Chicago Press.
- Sept J. 1992. Was there no place like home? A perspective on early hominid archaeological sites from the mapping of chimpanzee nests. *Curr Anthropol* 33:187–207.
- Sept J. 1998. Shadows on a changing landscape: comparing nesting patterns of hominids and chimpanzees since their last common ancestor. *Am J Primatol* 46:85–101.
- 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.
- Stanford CB, O'Malley RC. 2008. Sleeping tree choice by Bwindi chimpanzees. *Am J Primatol* 70:642–649.
- Stewart FA. 2011. Brief communication: 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.
- Tsukahara T. 1993. Lions eat chimpanzees: the first evidence of predation by lions on wild chimpanzees. *Am J Primatol* 29:1–11.
- Tutin C, Fernandez M. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *Am J Primatol* 6:313–336.
- Whiten A, Goodall J, McGrew WC, et al. 1999. Cultures in chimpanzees. *Nature* 399:682–685.
- Wrogemann D. 1992. *Wild chimpanzees in Lope, Gabon census methods and habitat use* [Ph.D. Dissertation]. Bremen: Bremen University.
- Zuberbühler K, Jenny D. 2002. Leopard predation and primate evolution. *J Hum Evol* 4:873–886.