Comparative Analyses of Nest Building Behavior in Bonobos and Chimpanzees

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Introduction

One trait thought to separate nonhuman primates from other mammals is cognitive ability (Harcourt 1988). This ability can be expressed in a variety of ways. One way, which we will discuss, is the modification and/or utilization of physical objects or tools. Although reports on tool use and object manipulation are available for a large number of species, many of those reports concern captive animals, and corresponding reports from the field are limited in many cases to a few species performing single tasks of goal-oriented manipulation of objects. The only species known to utilize and manufacture a number of different tools both in captivity and in the wild is the chimpanzee *(Pan troglodytes)*. Moreover, the tools used by different chimpanzee populations vary in both number and quality (McGrew 1992).

Traditionally, nest building has been treated separately from tool use (Beck 1980; Tuttle 1986). However, this separation has been disputed (Galdikas 1982; McGrew 1992) although some of the arguments appear arbitrary. Whatever the case may be, nest building is certainly the most pervasive form of object manipulation among the Pongidae. Nest building differs from other forms of tool use in several ways: it is common practice in all Pongidae species while, at the same time, a practice that is absent in all other simian primates; it occurs daily, performed by all mature males and females with similar frequencies; and it is characterized by specific combinations of different objects.

Nest building shows variation both between and within species: while gorillas often build their nests close to or at the forest floor, orangutans, chimpanzees, and bonobos build their nests almost exclusively within trees

(Schaller 1963; Galdikas 1982; Goodall 1962; Kano 1992). Furthermore, this species-specific preference in nesting sites persists in areas where chimpanzees and gorillas are sympatric, that is, where gorillas and chimpanzees occur in the same range, strongly suggesting that this preference may not be exclusively related to environmental conditions. Another possible species-specific difference in nest building concerns the habit of improving nests by adding soft twigs and leaves, a behavior widely reported for chimpanzees (Goodall 1962) and bonobos (Kano 1992), but apparently absent in mountain gorillas (Schaller 1963).

Within one species, nest-building behavior seems to be comparatively uniform, and variations have been mostly attributed to ecological differences. While comparison of nests for two distinct chimpanzee populations revealed significant variation within and between populations, all structural differences were most likely related to environmental factors such as seasonality, predator pressure, and available vegetation, demonstrating adaptive responses to changes in environmental conditions (Baldwin et al. 1981). At Gombe, chimpanzees use oil palms for nest building (Goodall 1968). According to Wrangham (1975), this habit seems merely to reflect seasonal

Table 1
Habitat and nest characteristics of chimpanzees.

Country		Senegal		Republic of Guinea		Liberia	Ivory Coast		Gabon	
Study site		Mt. Assirik				Sapo	Taï		Lopé	
Author		Baldwin et al. 1981	1982	Nissen 1931[a]	de Bournonville 1967[a]	Anderson 1983	Boesch 1978	Fruth 1990[b]	Tutin and Fernandez 1983[c]	Wrogemann 1992
Habitat		SW	SW	SW	—	SW	RF	RF	RF	RF
Nests	N	252	4,478	100	184	67	146	154	1,741	523
Height in meters:										
	average	—	—	11.5	—	—	—	23.2	8.7	11.7
	median	11	—	—	—	12	—	20	—	10
	range	0–44	5–22	4–31.5	2–24	6–20	3.5–15	5–45	2–32	2–45
	%	100	94	100	100	81	82	100	100	100
DBH in centimeters:										
	average	—	—	—	—	—	—	42	—	34.6
	median	39–45	—	—	—	52	—	33	—	25
	range	—	—	—	—	6–25	—	6–168	—	5–400
	%	—	—	—	—	93	—	100	—	—

Notes: a. study site not specified. b. four different study sites. c. nationwide. SW = savanna-woodland (dry); RF = rain forest; GWF = mosaic of grassland-woodland and forest; % = percentage of the nests the range is referring to; DBH = diameter breast high. * (Tuttle 1986).

variation in available materials. However, the fact that palm trees are used for nest building at Gombe but not at other study sites suggests that culture might be a factor in variation (McGrew 1985).

These examples show different factors involved in variations (Reynolds and Reynolds 1965). Accordingly, identification of the factors responsible for differences and similarities requires several kinds of comparison. By incorporating data from additional chimpanzee populations and from other closely related species into a comprehensive analysis, we may be able to identify the links between environmental conditions and nest building, to weigh the magnitude of single factors as, for example, hunting pressure on particular aspects of this behavior (nest height), and to select those features that most likely represent local culture.

We had precisely such a scheme in mind when we started to work on this chapter. Available data on nest building for the chimpanzee *(Pan troglodytes)* include all three subspecies and a wide range of habitats occupied by this species (see table 1) (Tuttle 1986). Moreover, the nest building behavior of the bonobo *(Pan paniscus),* has been investigated at four study sites (see table 2) and, thus, provides sufficient data for comparative analyses. However, during an initial survey of the literature, it became evident that

Equatorial Guinea		Uganda			Tanzania		Zaire	
		Budongo	Ngogo	Kanyawara	Gombe	Ugalla	Lake Kivu	Virunga
Jones and Sabater Pi 1971[a]	Baldwin et al. 1981[a]	Reynolds and Reynolds 1965	Ghiglieri 1984[a]	Ghiglieri 1984[b]	Goodall 1968	Itani 1979	Rahm* 1967	Sept 1992
RF	RF	RF	RF	RF	GWF	GWF	RF	GWF
195	195	259	372	63	384	491	?	101
—	—	—	12.2	10.3	—	19	—	13.5
10	10	—	—	—	—	—	—	—
0–20	0–40	3–45	2–35	5–23	12–24	5–40	10–25	—
96	—	100	100	100	57	100	100	—
—	—	—	—	—	—	—	—	—
—	13–19	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—

this refers to date of publication!!

Table 2
Habitat and nest characteristics of bonobos.

Country		Zaire				
Study Site		Lomako		Lake Tumba	Yalosidi	Wamba
Author		Badrian and Badrian 1977[a]	Fruth and Hohmann 1993[b]	Horn 1980	Kano 1983	Kano 1992
Habitat		RF	RF	RF	G/RF	RF
Number of nests		174	1,155	107	2,380	3,353
Height in meters:						
	average	—	16.6	—	—	—
	median	—	16	—	—	13[c]
	range	5– >35	3–50	4–28	0–50	0– >40
	%	100	100	100	100	100
DBH in centimeters:						
	average	—	23.8	—	—	—
	median	—	18	—	—	—
	range	—	2–137	1–36	>0–>40	—
	%	—	100	100	100	—

Notes: a. unspecified community. b. eyengo community. c. night nests only. RF = rain forest; G/RF = mosaic of grassland and rain forest. % = percentage of the nests the range is referring to.

the majority of data sets for the two *Pan* species were highly incommensurate, that is, lacking a common basis for comparison. For example, in many studies, data on nest building were collected for only short periods of time (less than one year) and, with very few exceptions, the data were collected from abandoned, anonymous nests of unknown age. After selecting only studies containing compatible information, the comparative data boiled down to a few structural characteristics of nests and nest trees. Because most of the studies have reported on nests and not on nest-building behavior, data on the social context or the manner of use are almost nonexistent.

Consequently, we had to abandon our first scheme and create a more realistic scheme. These comparisons now involve only a small number of studies that provide the most comprehensive information on some of the major aspects of nest-building behavior. Many categories of data we would have liked to compare were available from only a few sites or from only one site but not the others. Therefore, in spite of better intentions, our comparisons of nest building in the two *Pan* species remain fragmentary and preliminary.

This chapter presents data on the following three topics: single nests, considering morphological and ecological characteristics of nests; nest groups, considering the number of nests per group and the changes in party size during day and night; and the ethology of nest building, considering ontogeny, sex differences, context, and social significance.

Methods

The data for comparison appear in table 3. Whenever possible, the data are presented in their original form and physical dimension. For reasons of compatibility some data was modified or rearranged. For example, absolute values were transformed into percentages and measurements of structural parameters of nests and nest trees using different scales such as feet, yards, or meters were standardized. If not specified otherwise, data from Lomako was derived from our 14-month study of bonobos conducted between August 1990 and June 1992 (Fruth and Hohmann 1993). The Lomako study site is described in detail by Badrian and Badrian (1977, 1984), White (1988), and Malenky and Stiles (1991).

Table 3
Structural features of nests for chimpanzees and bonobos.

Species		*Pan Troglodytes*				*Pan Paniscus*		
Country		Senegal	Liberia	Gabon	Equatorial Guinea	Zaire		
Study Site		Mt. Assirik	Sapo	Lopé	a.	Lomako	Yalosidi	Wamba
Nest	N	252	67	523	195	1,156	2,380	3,353
Uncovered	%	75.0	21.0	38.2	17.0	50.4	—	—
Covered	%	25.0	79.0	61.8	83.0	49.6	—	—
Nests/Tree	N	2	?	+	1	+	+	+
Trees/Nest	max	—	—	2	—	6	5	6
Int. Nests	%	—	—	8.4	—	37.1	14.6	32.8
Ground	%	—	—	—	—	—	+	+
ID species	N	—	—	86	—	80	—	—
Used	N	—	—	45	—	24	100	108
UNT	N	—	—	321	—	476	2,142	—
TTT	%	—	—	61.2	—	75.6	63.9	72.0
Nest Groups	N	83	58	66	127	456	—	—
Nests/Group	range	1–18	1–10	1–26	1–12	1–24	—	—
Nests/Group	median	4	1	1	2	7	—	—
NN-Nest	N	224	—	284	33	—	—	—
NN-Distance	m	4	—	6	4	—	—	—

Note: a. study site not specified. Nest N = total sample size; Uncovered = percent of nests not covered by upper vegetation; Int. nests = percent of integrated nests; ID species = total of identified species in the sample area; Used = number of species used for nest construction; UNT = number of individual trees used for nesting from which the rate of used species was calculated; TTT = percent of all UNT representing the 10 tree species most often used for nesting; Nest Groups = number of obscured nest groups; NN-Nest = total number of nests occurring in nest groups for which NN-distance was computed; NN-Distance = mean distance between next neighbors for all nests in a given group.

Results: Single Nests

Type of Construction

The technique of nest building has been described for chimpanzees by Bolwig (1959) and Goodall (1968) and for bonobos by Horn (1980) and Kano (1979). Despite individual, age, or species variations, all nests combine plant materials into three nest components: a solid foundation, or frame; a central mattress; and a lining made of additional leafs and twigs (McGrew 1992).

From the available descriptions of nest building by chimpanzees, we have information from six sites on the median number of nests observed in one tree (see table 3). However, with the exception of data from Lopé (Wrogemann 1992), little has been mentioned about whether nests incorporate parts of more than one tree. At Gombe, for example, integrated nests constructed of materials from more than one tree seemed to be the exception rather than the rule (Goodall 1962).

In contrast, data about bonobo populations at Yalosidi, Wamba, and Lomako have demonstrated that nests commonly incorporate parts of more than one tree (see table 3) (Kano 1983, 1992; Fruth and Hohmann 1993). At Lomako, almost 37% of all bonobo nests consisted of parts of two or more trees, with a maximum of six trees involved in a single nest. The only available source for comparison is the study on chimpanzees conducted at Lopé, Gabon (Wrogemann 1992). At Lopé, less than 10% of the total sample (N = 523) of nests incorporated parts of more than one tree, and the maximum number of trees constituting a nest was two.

Height of Nests

Tables 1 and 2 present data on nest height above forest floor from 23 studies of chimpanzees and bonobos. All values on nest height indicate a large range of variability within populations. Height varied most (3 to 45 meters) at Budongo (Reynolds and Reynolds 1965) and least (3.5 to 15 meters) at Taï (Boesch 1978). There is no evidence for a correlation between the height of nests and the type of habitat (savanna-woodland versus rain forest) or a correlation between the height of nests and their affiliation to forests (West versus Central Africa). However, the variation found within a given population was always greater than that found between populations. This is true for both chimpanzees and bonobos.

Diameter of Nest Trees

Trees used for nest construction had a minimum diameter of five centimeters for chimpanzees at Lopé (Wrogemann 1992) and one centimeter for bonobos at Lake Tumba. The values for the two populations of bonobo fit well within the range given for chimpanzees (see tables 1 and 2). As mentioned before, bonobos often combine trunks of several different trees into their nests. This technique may enable them to use saplings, which could never support a nest alone. Consequently, at least in bonobos, the diameter of trees does not seem to be a limiting factor, although height of trees and the height of the nest remains important.

Seasonal Differences

Speculation about the reasons for differences between populations or between sites has often overshadowed the magnitude of variation within one population or one site. However, studies across seasons demonstrate variations in characteristics such as the height and the position of nests. Both chimpanzees (Baldwin et al. 1981; Wrogemann 1992) and bonobos (Fruth and Hohmann unpubl. data) build their nests higher during the rainy season. In Equatorial Guinea, Senegal, and Gabon, chimpanzees build fewer nests with covers during the rainy season than during dry months (Baldwin et al. 1981; Wrogemann 1992). Thus, for chimpanzees, seasonal variation appear to be consistent across habitats. At Lomako, the ratio of uncovered to covered bonobo nests remained steady throughout the year (47% versus 49%; N = 995), with a tendency to cover more in the wet season.

Day and Night Nests

The fact that chimpanzees and bonobos build nests not only at night but also during the day is well established (Nissen 1931; Goodall 1968; Kano 1983). Descriptions of day nests of chimpanzees have been published by Goodall (1962) and Hiraiwa-Hasegawa (1989), but the data reported permits only general comparisons with night nests. More detailed analyses have been conducted for bonobos at Wamba (Kano 1992) and at Lomako. At Lomako, it became apparent that day nests differed in four respects from night nests, time of construction, duration of use, mode of construction, and nest sites.

Time of construction: on average, bonobos needed 4.2 minutes to build a night nest, or roosting site, (M = 4, range 1–7 minutes, N = 35) but less than 1 minute to build a day nest (M = 0, range 0–5 minutes, N = 105). These patterns are significantly different (U-test; $p < .001$).

Duration of use: in the mean, day nests were used for 31.3 minutes (M = 25, range 2–120 minutes, N = 134), while the estimated time spent in night nests was 10 to 12 hours.

Mode of construction: out of 110 day nests, 96% incorporated material from only a single tree, but 41% of all night nests (N = 595) combined parts of several trees. Hence, the number of trees incorporated in a day nest differed significantly from the number used in a night nest ($\chi^2 = 57.7$, $p < .001$).

Nest sites: day nests were built considerably higher in the trees (x=20.4 meters, SD=8.5, range 5–50 meters, N = 102) than night nests (x=15.4 meters, SD=4.8, range 3–35 meters, N = 595) (t=8.47, df=695, p <.001). These data on differences between bonobo day and night nests at Lomako correspond with the results published by Kano at Wamba (1992).

Another important difference seems to exist concerning the use of feeding trees for nest building: corresponding to our data from Lomako, Kano (1983) observed that of 19 day nests, 11 were built within a tree previously used for feeding.

Most of these features may be compared for both species when a comparable set of detailed data becomes available for chimpanzees.

At Gombe and Mahale, the rate of day-nest construction by chimpanzees seems to be very low (Goodall 1962, Hiraiwa-Hasegewa 1989). However, chimpanzees at Kibale and bonobos at Lomako and Wamba apparently build day nests frequently (Wrangham pers. com.; Kano 1983). Therefore, the frequencies of day-nest construction appears to be habitat-specific rather than species-specific.

Nesting Site Selection

Chimpanzees and bonobos spend half their lives or more in nests. Therefore, it is reasonable to assume that nesting sites are carefully chosen. Various studies have hinted about preferences regarding nesting sites, but those studies often refer only generally to the size of the trees or the position of the nests within trees (Reynolds and Reynolds 1965; Jones and Sabater Pi 1971; Badrian and Badrian 1977; Horn 1980).

The studies providing more systematic data on nest building and the location of nesting sites suggest the following: first, nest groups are not randomly distributed but located in particular areas of the home range. At Lomako, traces of old nests indicate that some nesting sites are reused by generations of bonobos (Fruth and Hohmann in press) Studies of chimpanzees at Sapo, Liberia (Anderson et al. 1983); Equatorial Guinea (Baldwin et al. 1981); and Ishasha, Zaire (Sept 1992) and of bonobos at Yalosidi (Kano 1983) and Lomako have demonstrated that, if available, primary forest and gallery forest are the two most preferred habitat types for nest building. At Mount Assirik, Senegal, nests were found in equal proportion in woodland and gallery forest (Baldwin et al. 1981), and at Ugalla, Tanzania, most chimpanzee nests were found in dry open woodland but not in gallery forest (Itani 1979). With the exception of Ugalla, the data indicate that chimpanzees and bonobos preferred to build their nests in areas of dense, high vegetation.

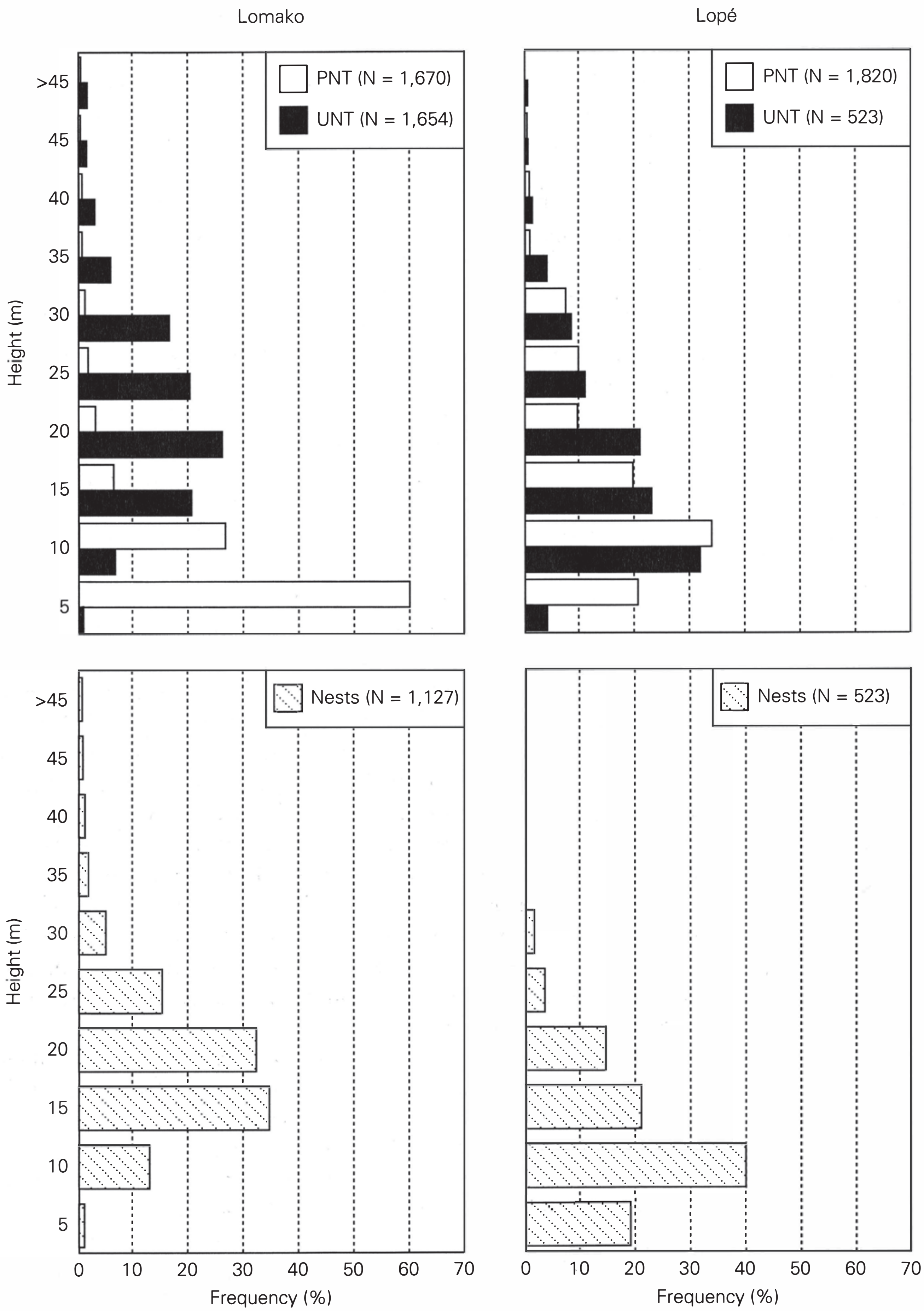
Second, chimpanzees and bonobos tend to select particular tree species for nest building. For example, when nesting in the grassland, chimpanzees at Mount Assirik choose two species *(Spondias mombin* and *Adansonia* *digitata)* as a nesting tree (Baldwin et al. 1981), and chimpanzees at Ishasha, Zaire, have been reported to prefer *Cynometra alexandrii* as a nesting tree (Sept 1992). Kano (1983, 1992) found that bonobos at Yalosidi and Wamba show a high preference for a single species *(Leonardoxa romii),* accounting for 45% of all trees chosen for nest building at Yalosidi and 34.5% at Wamba.

Third, chimpanzees and bonobos rarely build their night nests within trees offering ripe fruit or other food but rather in neighboring trees (Goodall 1962; Kano 1992; Fruth and Hohmann unpubl. data). Although analyses of our data from Lomako are still in progress, it appears that feeding trees are used for night nests at other times of the year, such as when the tree is not in fruit. Hence, the state of a tree may be another criterion for selection of nesting sites.

Conclusions regarding the use of selection criteria (height of nesting trees) for particular trees by chimpanzees and bonobos must take into account the abundance and distribution of trees of different height. This information has only recently been sought. Earlier reports, while pointing to possible selection criteria, do not have the full range of data to be conclusive.

More extensive quantitative data on the selection of nesting trees have been collected in independent studies, one on chimpanzees at Lopé, Gabon (Wrogemann 1992) and the other on bonobos at Lomako. In both studies, evaluation of choices for nesting trees were based on the relationship between the used nesting trees (UNT) and the potential nesting trees (PNT). At Lopé, the characteristics of PNT were obtained by the following sampling method: At 100-meter intervals along several paths, the height of the 10 nearest trees over 5 centimeters DBH (diameter at breast height) was estimated. The heights were arranged into 5-meter classes. At Lomako, data were taken from 10 forest plots, each of 400 square meters, containing nesting sites. The height of all trees with a minimum diameter of 2 centimeters and a minimum height of 5 meters were measured. In order to obtain data on the selection of particular species as preferred nesting sites, 15 plots randomly placed along standardized transects were compared to 17 plots containing nesting sites.

The results of these studies can be summarized as follows. Bonobos at Lomako built their nests in tall trees more often than expected. The majority of nests (82%) were located in trees of the middle forest layer (11–30 meters above the forest floor); in contrast, only 12% of the potential nesting trees were this high. The difference between potential and used nesting trees in this forest layer, then, is highly significant (U-test; $p < .001$). Chimpanzees at Lopé select UNT that have a height distribution quite similar to PNT (see figure 1.) In general, nests at Lopé are constructed slightly lower.


Lomako
Lopé
PNT (N = 1,670)
UNT (N = 1,654)
PNT (N = 1,820)
UNT (N = 523)
Nests (N = 1,127)
Nests (N = 523)
Height (m)
>45
45
40
35
30
25
20
15
10
5
0
10
20
30
40
50
60
70
Frequency (%)

◀ Figure 1
Top left and right: Height of potential nesting trees (PNT) and used nesting trees (UNT). Bottom left and right: Frequency of nest heights for bonobos at Lomako (left) and chimpanzees at Lopé (right).

At Lomako, the species of 83% of 476 UNT have been identified, compared to 1052 PNT of which 91% have been identified into 80 species. Of these 80 species of PNT, bonobos have used 24 species as nesting trees. Of the 10 tree species most frequently chosen at Lomako, five were used with much higher frequencies than expected by chance. In contrast, at Lopé, the species of 63% of 321 UNT have been identified, compared with 1092 PNT of which 77% have been identified into 86 species. Of the 86 species of PNT, 56 have been chosen for nest building. Chimpanzees at Lopé focused their nest building efforts on seven out of the 10 most frequently used species.

Overall, bonobos appear to be more selective about tree height than chimpanzees. This difference, however, might be caused by the high frequency of the shortest class of PNT at Lomako (an artifact of including trees of DBH down to 2 centimeters) and the high frequency of bonobo day nests, which are constructed considerably higher than bonobo night nests.

Groups of Nests

The term *nest group* is restricted to clusters of nests thought to be built by different individuals at the same time. When construction was not directly observed, a nest group was inferred when the nests were close together and were similar in the degree of decomposition. Most of these studies dealt with single nests or clusters of nests of unknown age.

Comparing the ranges of the number of nests per group from different studies (see table 3), it would appear that chimpanzees and bonobos form sleeping groups of similar size. However, differences become evident when comparing the median number of nests per group for bonobos (M = 7) and for chimpanzees (M = 1–4). Data collected for chimpanzees at Lopé (Wrogemann 1992) and for bonobos at Lomako strongly support this difference in the size of nest groups. At Lopé, single nests accounted for more than 53% of all chimpanzee nest groups whereas at Lomako, more than 96% of all bonobo nest groups consisted of two or more nests, with most groups consisting of 2 to 13 nests (see figure 2).

Further, at Lomako, nest groups of bonobos are always larger than daytime travel parties (see figure 3). Data collected during a third field trip (1993) verify the tendency for fusion of parties at night. In contrast, data collected by Wrangham and Smuts (1980) at Gombe show that chimpanzees do not gather to form large sleeping groups. However, observations from chimpanzees who live in a rain forest are required to decide whether this variation in the size of sleeping groups is related to environmental

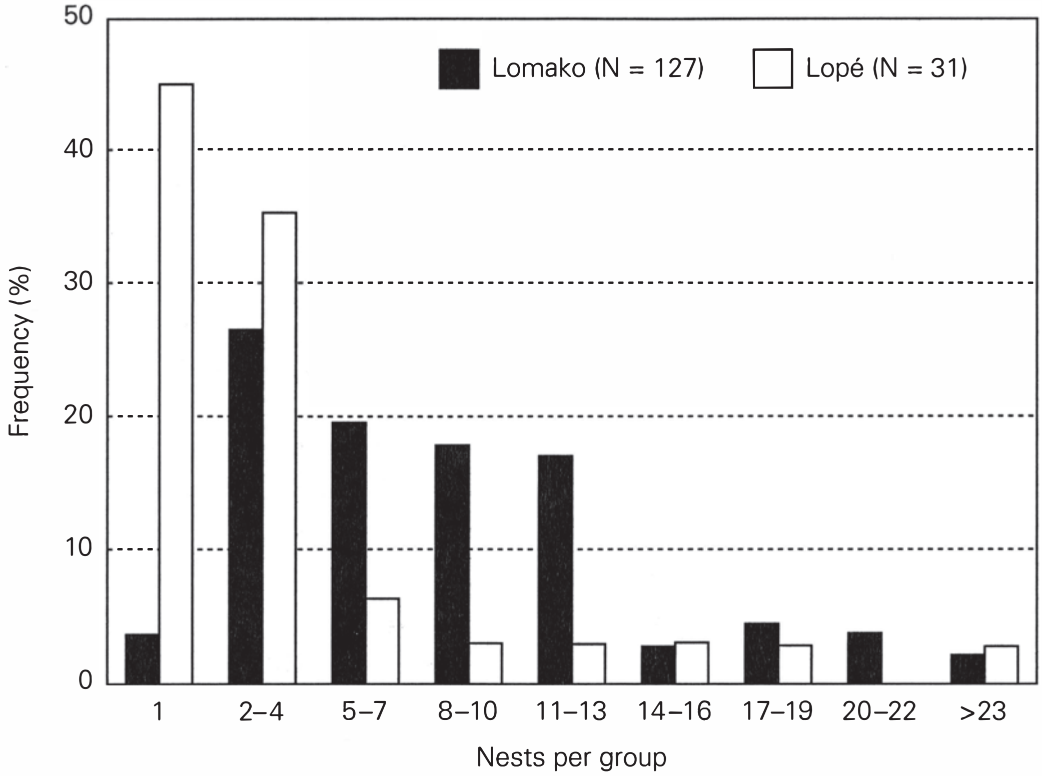


Figure 2
Comparison of nest group size (= number of nests per group) between bonobos at Lomako and chimpanzees at Lopé.

conditions or represents a species-specific pattern. If this disparity in grouping patterns can be confirmed, this would be another striking difference between the two *Pan* species.

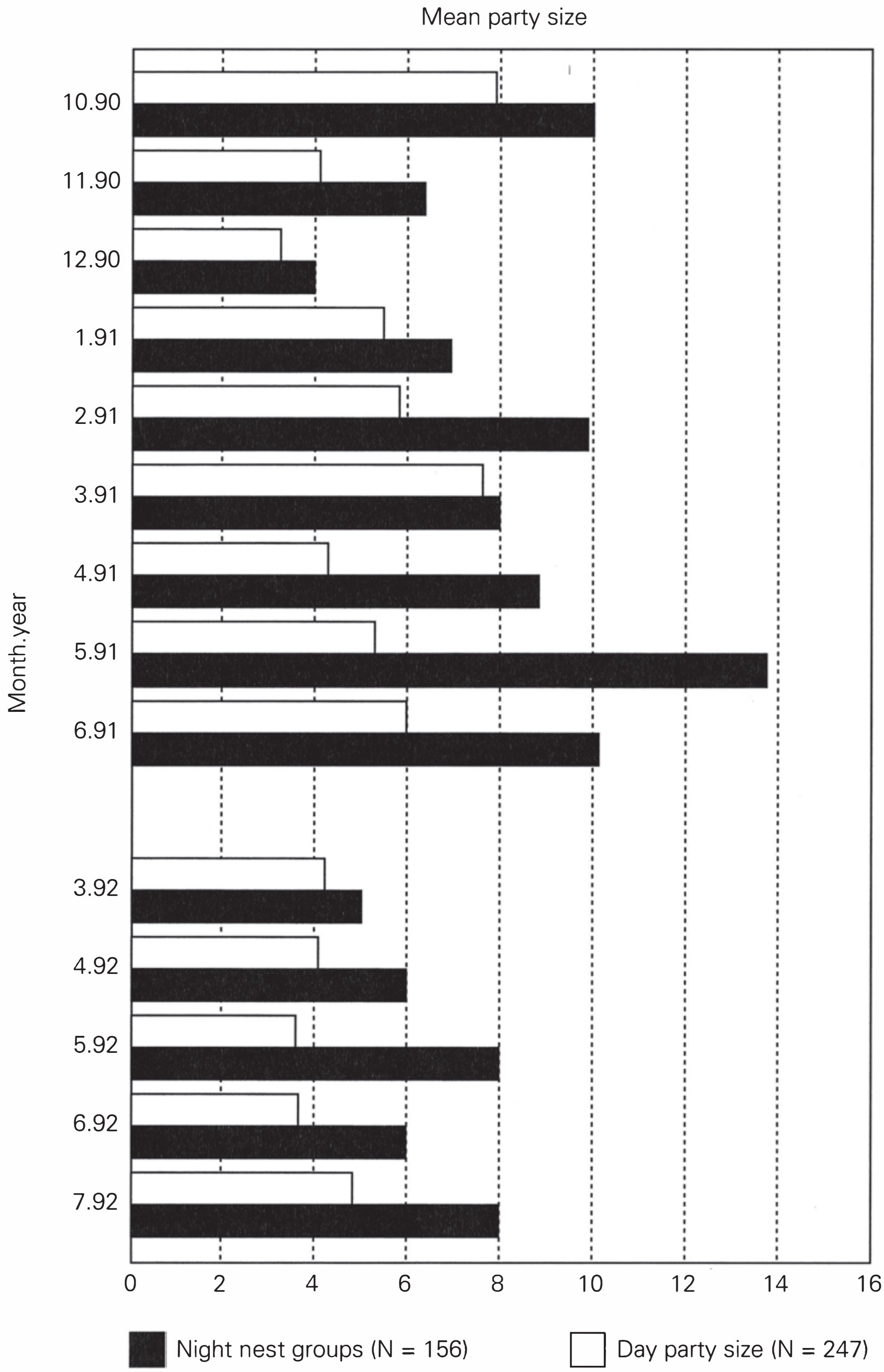
Ethology

Ontogeny

Chimpanzees and bonobos build nests every day, and individuals of all age-sex groups participate. Despite the regular and frequent occurrence of nest building, very little is known about the ontogeny of this behavior. Captive chimpanzees separated from mothers soon after birth make only incomplete nests (Bernstein 1961). On the other hand, wild-born immature chimpanzees captured and subsequently raised by human beings have demonstrated the regular occurrence of nest-building activities (Reynolds 1967). Observations suggest that chimpanzees acquire nest-building skills through learning (Bernstein 1961; Baldwin et al. 1981; Goodall 1962), but this proposal remains to be demonstrated by systematic research.

At Lomako, immature bonobos frequently make day nests not by standing in the center of the prospective nest (as adults do), but by bending and folding leaves and twigs in front of them. Moreover, day-nest construction by infants was rarely related to nest-building activities of mature individuals; instead day-nest building by infants occurred when other party

Figure 3
Mean party size of bonobos at Lomako during the day (white bars, N = 247) and at night (black bars, N = 156).



members were feeding or resting. With few exceptions, infants used their day nests not for rest but for solitary or social play. However, observations from Gombe (Goodall 1962) and Lomako show that an infant may participate in the building of a night nest with their mother.

In chimpanzees, the first attempts at nest building were seen at the age of 8 months at Gombe (Goodall 1968) and at 12 to 14 months at other sites (Plooji 1984; Hiraiwa-Hasegawa 1989). Goodall's (1968) description of nest building refers to attempts of an infant to build a ground nest out of twigs and grass blades. In Goodall's example, the infant built the nest not under, but on top of, its body. At Mahale, Hiraiwa-Hasegawa (1989) observed that, initially, infants did not break or bend branches but made nests out of a collection of loose material. Later, the quality and quantity of nest building steadily increased, and the frequency of day-nest construction reached a peak at the age of three (Hiraiwa-Hasegawa 1989). Thus, at Mahale, nest building becomes an important part of the daily behavior long before the infant is weaned.

At Lomako, older infants often approached their mothers while the mothers were resting in a day nest with the obvious intention of making physical contact. Usually, infants did not jump into the nest immediately but stopped at the fringe, making begging gestures (pout face) and related vocalizations (whimpering). In response, mothers usually permitted physical contact. However, the contact very often occurred outside the nest. Although quantitative data are still lacking, the prohibition of offspring from the maternal nest may be part of the weaning process, encouraging infants to build and occupy their own nests. Another example of nest building in response to weaning stress has been provided by Kummer (1991). This event involves a five-year-old female and its mother. When the mother put down the daughter who had been clinging to her body, the infant, "comforted herself by building a flimsy nest of twigs and sucking her toe" (Kummer 1991:80). It is tempting to conclude that, in this case, the nest may have served as a surrogate.

Sex-specific Differences

To investigate the possibility of sex differences in nest-building behavior of bonobos, only nests of mature individuals have been used. Generally, females started the daily process of nest building, while males began later. Considering all nests built by identified adults, males' nests were at an average height above the forest floor of 14.6 meters, significantly lower than the average height of 19.4 meters for female nests (t-test, $p < .01$). When day nests were analyzed separately from night nests, this difference became even more apparent. In addition, both the time required for nest building as well as the duration of use differed: males built day nests faster than females (0.1 minute versus 0.7 minute) and used the day nests for shorter periods of time (25 minutes versus 35 minutes). Finally, females built day nests more often than males (2.88 versus 0.71 per 10 hours of observation). Similar differences have been found by Hiraiwa-Hasegawa (1989) for chimpanzees at Mahale (females vs. males: 0.08 versus 0.01 per 10 hours). Unfortunately, these are the only data on sex differences in nest building of chimpanzees; a comparison between the chimpanzees and bonobos is not yet possible.

Nothing has been published on sex differences in nest building from other wild populations of bonobos, but a recent study of a captive group confirmed our field observations (Berle 1993). Not withstanding the low degree of sexual dimorphism in bonobos, the differences mentioned here seem to be related to environmental rather than social factors. Various explanations are possible: if the quality of potential nesting trees at a given site differs, whoever makes the first choice (females) can occupy the best places. The choice made by males, however, may represent a compromise between two distinct interests: the proximity to particular females and the quality of the nesting site. Another possible interpretation of the males' choice of lower nest sites is that guarding females against ground predators is part of their social task.

Social Context

The function of nests within a social context remains largely unexplored. The major function traditionally ascribed to nests is that they facilitate sleep and rest. This is certainly true for nests that individuals regularly occupy at dusk and, with few exceptions, continue to occupy until the next morning. However, this may not be the limit of nest function. As we know from our own species, beds may serve not only sleep, but a number of other, and often vital, functions. Very little is known about the nocturnal activity of the two *Pan* species, and that part of their life remains, literally, in the dark. What we do know points to important activity. Chimpanzees at Gombe and bonobos at Wamba have been observed to mate in night nests (Goodall 1968; Kano 1992), and chimpanzees are known to travel, and thus leave and, sometimes, reoccupy nests at night (Goodall 1968).

Some additional information on the social context of nest building is available from studies of animals that construct and occupy nests during the day. At Lomako, bonobos used day nests not only for rest but also for a number of other activities. Observations of 176 day nests revealed that only 53% of nest owners used their nests solely for rest. Other activities recorded were feeding (10%), mutual grooming (5%), and social play (3%). In the remaining cases (29%), the nests were occupied by mother-infant pairs, and at least one individual (mostly the infant) performed activities other than rest.

According to Reynolds and Reynolds (1965), unhabituated chimpanzees may build nests to hide from human observers; similar observations have been made for orangutans (Harrison 1962) and gorillas (Reynolds and Reynolds 1965). At Lomako we have observed bonobo nests serving as refuges during interactions between members of the Eyengo-community

(Fruth and Hohmann 1993). These cases (N = 13) occurred when females or immature individuals feeding on highly preferred food were approached by other adult male or female party members. Following the building and occupation of a nest by the first individual, the approaching individual made no further attempt to contact or displace the nest owner, and the nest owner consumed food undisturbed for extended periods of time. Only one case did not involve food. In that case, an adult male escaped a charging display of another adult male by climbing into a tree and building a rudimentary nest. In response, the charging male stopped at the base of the nesting tree and moved away, leaving a dragged branch which he used for display at the base of the nesting tree.

Several observations indicate the social significance of nests as a means of recognizing the presence of conspecifics (Wrangham 1975; Goodall et al. 1978). When, for example, adult chimpanzees encountered fresh nests at the periphery of their home range, they inspected the nests visually and olfactorily and then displayed at the nests destroying them partly or completely. Such instances of redirected aggression closely resemble the violent acts of human beings during conflict and warfare (Eibl-Eibesfeldt 1989). The examples given escape a quantitative approach but supply important anecdotal clues about the social significance of nest building. Neither the legendary goose Martina (Lorenz 1965) nor the Japanese macaque female Imo (Kawamura 1959) would fit the median of the normal distribution but both have lent tremendous input into our understanding of phylogenetic ingenuity (Sommer 1985).

Summary

This chapter deals with the ecological and behavioral differences in nest building of chimpanzees and bonobos. Data from 23 independent field studies have been reviewed. The major findings are organized into three subject categories: single nests, nest groups, and ethology.

Most of the structural characteristics of single nests were similar for both species. For example, chimpanzees and bonobos preferred to build their nests in areas of dense, high vegetation; favored particular tree species; and rarely built night nests in trees offering ripe fruit. Furthermore, nests of both species showed seasonal variations, appearing higher in trees during the rainy season. However, bonobos more often build integrated nests and include trees with small diameters than do chimpanzees. Data from bonobos showed that, as compared with night nests, day nests were higher, less sophisticated in structure, required less time for construction, and were used for shorter periods of time. Overall, structural characteristics of nests and

nesting trees for both species show large variation but not necessarily at the level of species specificity.

Comparisons between nest groups of chimpanzees and of bonobos revealed striking differences. While chimpanzees seemed to prefer to rest solitarily or in small groups, bonobos showed a tendency to gather at night, forming sleeping clusters consistently larger than daytime parties. If this pattern is not related to environmental conditions, which remains to be seen, it will represent a significant difference between the two *Pan* species.

Finally, regarding ethology, several points can be made. In both infant chimpanzees and infant bonobos, nest building becomes a daily routine long before weaning. Nesting female bonobos showed a spatial intolerance toward their dependent offspring keeping infants out of the nest, which appears to be part of weaning. Bonobos revealed a number of sex-specific differences: males constructed nests lower than females, males built day nests less frequently and faster, and males used their nests for shorter periods of time. These differences between males and females seem to be related to social rather than to environmental conditions.

Both bonobos and chimpanzees are known to build nests not only for rest but also to serve a number of other functions. Bonobos, for example, have been observed to build nests that served as refuges when potential or imminent conflicts arose. Nests are tools that the apes make to alter their environment and, sometimes, the behavior of conspecifics. Moreover, nests provide tools for humans who want to know more about the lives of their nearest relatives.

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