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Ecological and Behavioral Aspects of Nest Building in Wild Bonobos (*Pan paniscus*)

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Abstract

Data on nest building behavior were collected from free ranging bonobos (*Pan paniscus*). Considering the physical features of both nests and trees used for nest construction, bonobos appeared to show various preferences: (1) Trees with small leaves were chosen more frequently than expected; (2) The majority of nests were constructed in trees of the middle forest layer (15 to 30 m) and at a mean height of 16 m; (3) nests built during the day were located higher than night nests and differed in the general mode of construction (number of trees involved). Comparing nests made by mature males and females it became apparent that females (4) built nests higher, (5) constructed day nests more frequently and (6) used them for a longer time than males. Comparison of data collected at different study sites indicates site-specific differences concerning selection of trees and location of nesting sites. Behavioral observations made clear that nests were not only used for rest but also for other activities like feeding, social grooming and play. Moreover, the study provided the first evidence that bonobos build nests also in order to avoid potential or imminent conflicts with other party members. Field observations indicate that these nests symbolize a taboo zone and show another facet of the social abilities of bonobos for the solution of intra group conflicts. It is suggested that this behavior derives from the spatial intolerance shown by females during the process of weaning.

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Introduction

Amongst the great apes, members of both sexes and all ages (except dependent infants) build nests every night and sometimes during the day for the purpose of resting. Early descriptions of nest building trace back to the 18th century (MATTHEWS 1788, cited in YERKES & YERKES 1929) and were based on various anthropomorphic interpretations. In the last decades results of detailed

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field observations on nest building of chimpanzees (GOODALL 1962; WRANGHAM 1975), bonobos (KANO 1983, 1992), gorillas (SCHALLER 1963; CASIMIR 1979) and orang utans (MACKINNON 1974) became available and gave rise to various explanations concerning the selection of the nesting site (e.g. predator avoidance, human hunting pressure, adaptation towards climatic conditions). Recently nests have been used to design a new scenario of the possible formation of early archaeological sites, searching for ecological structures influencing the spatial patching of chimpanzee nesting sites (SEPT 1992). In addition nests have been used in census studies to facilitate evaluations of population densities (DAVIS & PAYNE 1981; ANDERSON et al. 1983; GHIGLIERI 1984; TUTIN & FERNANDEZ 1984).

In the case of pygmy chimpanzees or bonobos (*Pan paniscus*), nests have been mentioned in several field studies (NISHIDA 1972; BADRIAN & BADRIAN 1977; HORN 1980). The first detailed report was published by KANO (1983) from Yalosidi including structural and ecological aspects of nests. In spite of the number of studies dealing with this topic it seems that no other behavior known to exist in all the great apes has drawn so little attention as the ecology of nest building.

In order to provide more information on the etho-ecology of nest building in bonobos, a field study was conducted at Lomako, Equateur, Republic of Zaire. The study focused on the social aspects of nest building but included also the collection of metrical data. In this paper we present results from the initial part of the study.

The main aspects analysed in this study are:

1. Structural characteristics based on standard measurements of nests and nest trees;
2. the mode of construction of nests and their location within trees;
3. variation of structural patterns of nests in relation to time of construction and sex of the owner;
4. kind of utilization and social context of nest construction.

As far as possible data from Lomako were compared with those reported from two other study sites.

Methods

Study Area

Data on nest building were collected from Aug. 1990 to Jul. 1991 in Lomako, situated in the Tshuapa district of Equateur, Republic of Zaire. Observation of bonobos and investigation of nests were made in an area of approximately 11 km^2 consisting of primary lowland forest and swamp forest. For detailed descriptions of the flora, fauna, topography and climate of the Lomako study site see BADRIAN & BADRIAN (1977), BADRIAN et al. (1981), SUSMAN (1984), MALENKY & STILES (1991) and WHITE (1992).

Subjects

The bonobos involved in this study inhabited the eastern part of the Lomako study site and therefore were thought to be members of the "Eyengo community" described by BADRIAN & BADRIAN (1984) or "rangers" (THOMPSON-HANDLER et al. 1984; WHITE 1988; WHITE & BURGMAN 1990). From previous field studies (for a synopsis see SUSMAN 1984) members of the Eyengo community were habituated to the presence of human observers. However, at the beginning of the study, duration of observation was limited to those times subjects spent foraging or feeding high above the ground and most attempts to follow on the ground failed. Moreover, during the first months of the study, bonobos were reluctant to build their night nests in the presence of human observers. Employing observation techniques successfully used in another field study of common chimpanzees (BOESCH 1991), habituation improved progressively. From Jan. 1991 onwards, the first individuals tolerated us to follow them on the ground and did not hesitate to build their night nests within close proximity to the human observers. Until the end of the study (Jul. 1991), 22 adult community members could be identified using physical, morphological and behavioral traits.

Data Collection

Nest sites were located by (a) following and directly observing the animals, (b) searching at prospective nesting sites, and (c) incidental discovery. For 177 (23 %) of the nests analysed, details such as time, duration and technique of construction as well as sex and age of the animal involved were known. In the other cases (594), data on the aspects mentioned above were incomplete. Whenever possible the behavior preceding and following nest construction was registered in form of oral protocol using a dictaphone.

Nests varied tremendously in all possible dimensions, ranging from simple "cussions" consisting of a single twig to integrated platforms with sophisticated architecture. Therefore the following definition is considered being operational rather than descriptive: *Nests are constructions consisting of branches, twigs and/or leaves manipulated (bent, broken, transferred) by bonobos in order to establish a roosting site. Typically, the nest material is arranged from the periphery in centripetal direction towards the nest builder.*

The analyses of nests and nesting trees included the following criteria:

1. The *height of nests/trees* was measured with an altimeter (Silva, range 0—65 m).
2. *Diameters of nesting trees* were calculated by using the formula C/π where C is the circumference at breast height of the tree measured with a tape measure.
3. Four classes of *leaves of nest trees* were distinguished according to their relative size (width × length): small < 5.0 cm^2, medium 5.0—24.9 cm^2, large 25.0—64.9 cm^2, and extra large > 65 cm^2. In the case of leaves composed of several folioles (e.g. *Pancovia laurentii*) the size of a single foliole, and not the entire leaf, was considered.
4. For classification of the *type of nest construction*, a slightly modified version of the terminology introduced by KANO (1983) was used. The five different types distinguished are characterized by the number of trees involved and the position of the nest within the tree (Fig. 1).

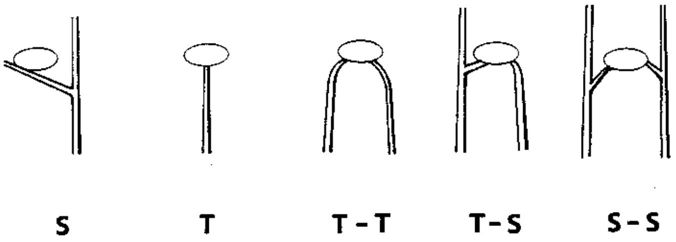

Fig. 1: Pictograms of the five different construction types (modified after KANO 1983). S = non-integrated nest on side branch; T = non-integrated nest on top of a tree; T-T = integrated nest combining two or more tree tops; T-S = integrated nest combining top and side branch; S-S = integrated nest combining side branches of two or more trees

5. *Evaluations of the selectivity* of bonobos in their choice for nest trees were assessed by the relation between potential nest trees and used nest trees. Systematic analyses derived from 10 forest plots of equal size (20 × 20 m) containing natural nesting sites. All trees with a minimum height of 5 m and a minimum diameter of 2 cm were considered as potential nest trees and sampled within each plot. Concerning height and diameter, the total sample was divided into a matrix of 12 size classes, with height ranging from 5 m to more than 55 m and diameter ranging from 2 cm to more than 55 cm. Limitation and size classes were choosen according to measurements taken from 1034 used nest trees.

Results

Nesting Trees

The aim of this part of the study was to determine the physical properties and abundance of nesting trees. A total of 1034 trees used for nest construction were compared with evaluations of 1673 potential nest trees recorded from 10 forest plots.

Height: Data from the 10 forest plots showed that the median for the height of potential nest trees was 5 m (range 2—52 m). Considering the middle layer these trees accounted for 12 %. In contrast the median for the height of the 1034 trees used for nest construction was 19 m (range 3—60 m). The maximum of these trees (79 %) belonged to the middle layer (range 10—30 m) of the forest (Fig. 2). The difference between potential and used nest trees of this forest layer is highly significant (Mann-Whitney U-test: $z = -7.0938$, $p < 0.001$).

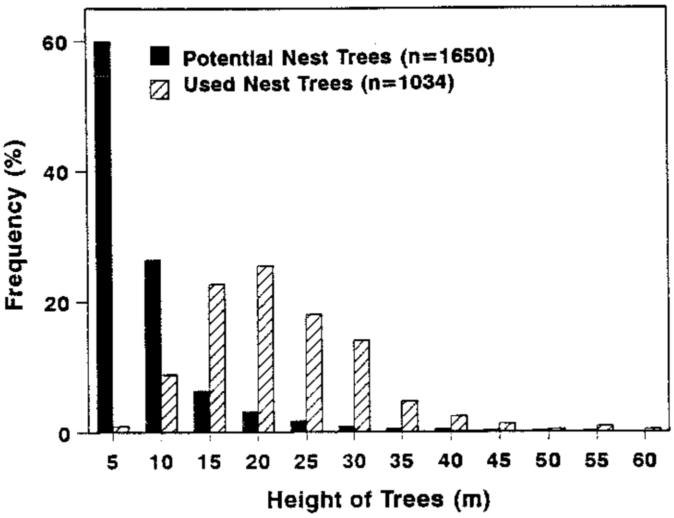

Fig. 2: Height of potential nesting trees and used nesting trees

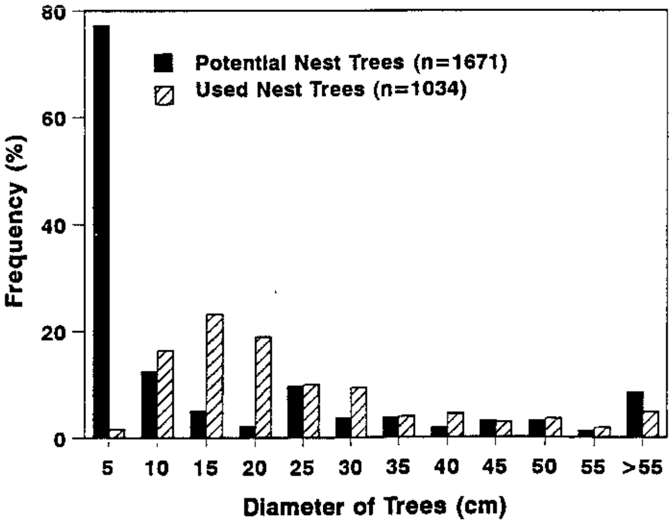

Fig. 3: Diameters of potential and used nesting trees

Diameter: Most of the potential nest trees (77 %) recorded had diameters between 2 and 5 cm ($\bar{x} = 3$ cm, range 2—137 cm). Fig. 3 shows the utilization of trees with different diameters used for nest construction. It shows that in more than 50 %, used nest trees had a diameter between 10 and 25 cm ($\bar{x} = 18$ cm, range 2—159 cm). Thus the diameter of used nest trees differed significantly from that of potential ones (Mann-Whitney U-test: $p < 0.001$).

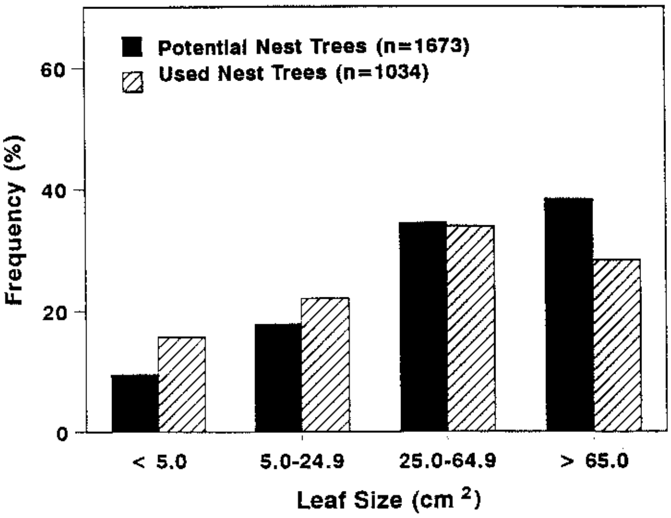

Fig. 4: Size of leaves collected from trees choosen by bonobos for nest construction and potential nesting trees

Leaf size: Fig. 4 compares the representation of the different classes of leaf size in potential and used nest trees. Small and medium sized leaves were choosen more frequently than expected (χ^2-test: < 5 cm^2: $p < 0.001$; 5.0—24.9 cm^2: $p < 0.01$). In the class 'large' availability and choice were rather balanced while the class 'extra large' was choosen less frequently than expected (χ^2-test: 25.0—64.9 cm^2: ns; > 65.0 cm^2: $p < 0.001$). Further inspection of the data revealed that 89 % of the samples from class 'small' came from a single species (*Scorodophloeus zenkeri*). The separation of *S. zenkeri* from the other species with small sized

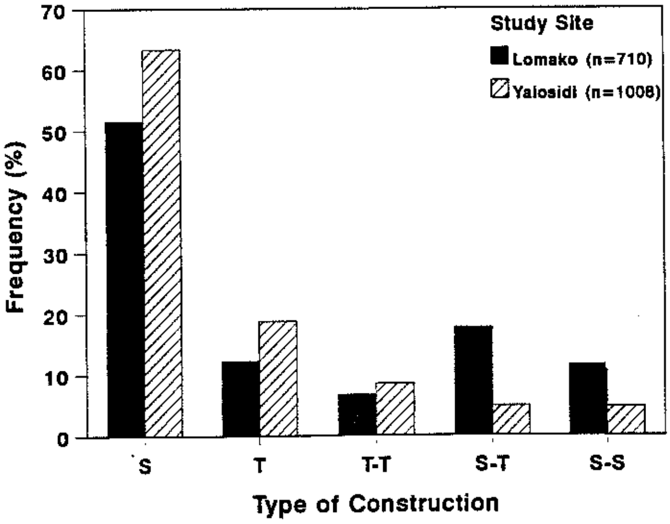

Fig. 5: Construction type of nests collected at Lomako (this study) and Yalosidi (KANO 1983). For description of different nest types see legend of Fig. 1

leaves showed that the pronounced asymmetry between availability and utilization of trees with small leaves is related to that single species.

Nests

Type of construction: Analyses of the type of construction involved 710 nests (Fig. 5). Non-integrated nests accounted for roughly ⅔ (65 %) of all nests. The rest (35 %) belonged to the class of integrated nests, combining parts of two (27.6 %), three (5.1 %), four (1.7 %), five (0.3 %) or six (0.1 %) trees.

Height of nests: Nests were built between 4 and 51 m above the ground ($\bar{x} = 16$ m, SD = 5.8 m) with the majority (83 %) being located in the middle layer (Fig. 6). During this study no evidence for construction of ground nests was found.

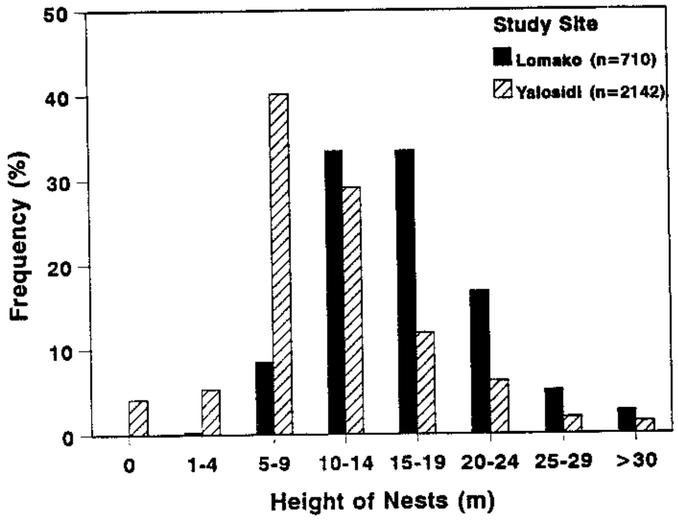

Fig. 6: Heights of nests recorded at Lomako (this study) and Yalosidi (KANO 1983)

Time of nest construction: Although nests were built during most hours of the day, two distinct peaks of nest building activity became apparent. The first corresponded with an extended period of rest at the late morning. The second peak — late in the afternoon — coincided with arrival to and occupation of the prospective night roosting site.

In all cases of nest building recorded late in the afternoon, observations lasted until the typical noises caused by construction of nests were no longer audible. Although systematic data on nocturnal activities of bonobos are not available, it was assumed that the subjects did not leave their nests before dawn. This was indirectly confirmed because individuals observed to have occupied a particular nest in the previous night were found in the same nest the following morning.

Duration of nest construction: The time required for building a nest varied between a few s and several min, but nests were often modified hours after occupation. To evaluate the duration of construction, the time between the first sign of nest building activity (bending or breaking branches) and its occupation was considered. Time scores were made to the nearest min. According to this assessment bonobos needed approximately 2 min for construction of nests ($\bar{x}$ = 1.7 min, SD = 1.92 min, range 0—7 min, n = 140).

Comparison of day nests and night nests: The *construction* of night nests required significantly more time than of day nests (Mann-Whitney U-test: $p < 0.001$) (Fig. 7). In average bonobos needed 4.2 min to build a night roosting site ($\tilde{x}$ = 4, range 1—7 min), whereas it took them less than 1 min to build a day nest ($\tilde{x}$ = 0 min, range 0—5 min). The median for the *time of utilization* of day nests was 25 min, range 2—120 min, n = 134, while the estimated time spent in night nests was 10 to 12 h.

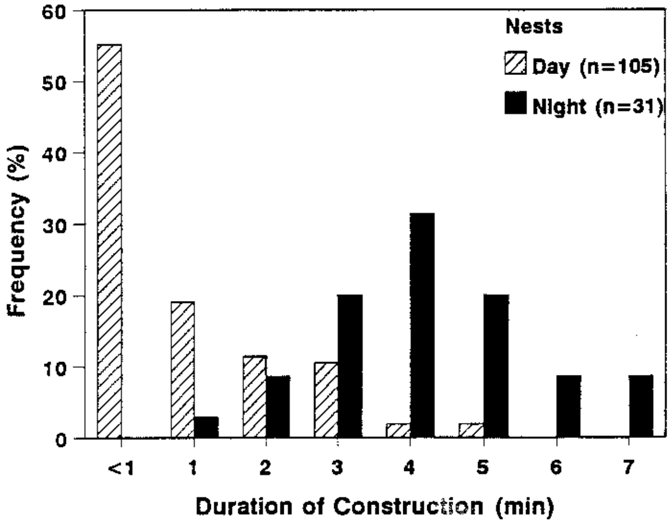

Fig. 7: Duration of construction of day nests and night nests

The difference in the duration of construction may be related to the *mode of construction*. Out of 110 day nests, 96.4 % involved material of only a single tree. In contrast, 41.0 % of all night nests (n = 595) integrated parts of more than one tree. Hence the number of trees contributing to a day nest or a night nest was significantly different (χ^2-test: $p < 0.001$).

Significant differences between the two groups of nests also existed concerning their mean *height*, with day nests being considerably higher ($\bar{x}$ = 20.4 m, SD = 8.5 m, range 5—50 m, n = 102) than night nests ($\bar{x}$ = 15.4 m, SD = 4.8 m, range 3—35 m, n = 595) (t-test: $p < 0.001$).

Sex-specific differences of nest building: To investigate the possibility of sex-differences in nest building behavior, only nests of mature individuals have been used. Concerning the *duration of construction*, the data obtained from males and females differed but not at a level of significance (males: $\bar{x}$ = 1.72 min, SD = 2.2 min, range 0—7 min, n = 30 vs females: $\bar{x}$ = 1.65 min, SD = 1.8 min, range 0—7 min, n = 104). Significant differences, however, were found concerning the *height* of nests. Males built nests lower ($\bar{x}$ = 14.6 m, SD = 5.0 m, range 8—26 m, n = 31) than females ($\bar{x}$ = 19.4 m, SD = 7.9 m, range 5—50 m, n = 106; t-test: $p < 0.01$).

When day nests were treated separately from night nests both the time required for nest building as well as the time of utilization differed: males built day nests faster than females did (0.1 min vs 0.7 min) and used them for a shorter period of time (24.8 min vs 35 min). While the difference in the duration of nest construction is significant (males: $\tilde{x} = 0$ min, range 0—1 min, n = 16 vs females: $\tilde{x} = 3$ min, range 0—3 min, n = 64; Mann-Whitney U-test: $p < 0.05$), the difference in the time of utilisation became not apparent at a level of significance (males: $\tilde{x} = 14$ min, range 3—64 min, n = 14; vs females: $\tilde{x} = 27$ min, range 4—120 min, n = 55; Mann-Whitney U-test: $p > 0.05$; Fig. 8).

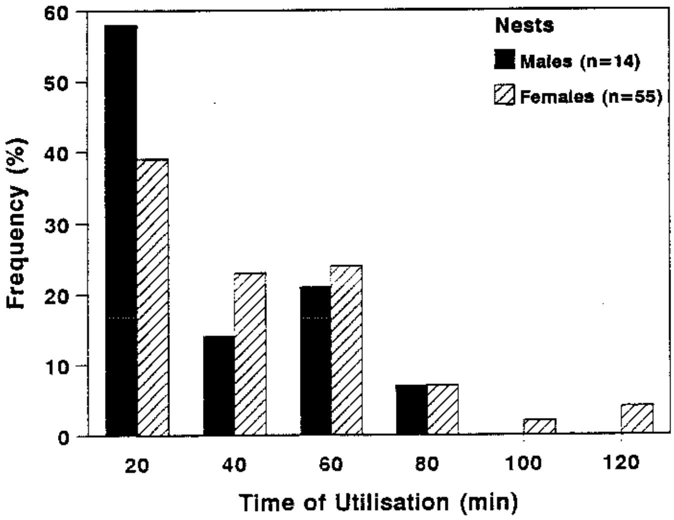

Fig. 8: Duration of utilization of day nests by mature males and females

Social activities of nest owners: Information on the behavioral activities related to construction and/or occupation of nests has derived from direct observations of 176 nests built during day time. Although rest seemed to be the main reason for nest construction (53 %), nest owners were also involved in other activities, like feeding (10 %), social grooming (5 %) and social play (3 %). Social interactions could precede or succeed a period of rest but in some cases nests were never used for rest but solely for other activities. The remaining sample (22 %) refers to mother-infant pairs, being excluded in this analysis since the offspring was considered to be dependent and almost all of these activities occurred within the same nest in frequent alternation and for very short periods of time.

Major factors inducing nest construction seemed to be the day time and the actual weather conditions. However, in 7 % of all samples, nest construction of one individual strongly coincided with an approach by another individual. The following example is representative and may illustrate these observations.

During the dry season, bonobos of the Lomako forest feed on fruits of *Pancovia laurentii*, an orange colored fruit with a sweet, juicy exocarp and edible seed. Occupation of fruiting trees is regularly accompanied by loud vocalizations and sometimes tension may escalate into severe aggression between group members. The high rate of displacements and other agonistic behaviors indicated strong competition between bonobos for places with large quantities of ripe fruits. On Feb. 24th, 1991 (07.45 h), an adolescent female enters a *Pancovia* tree and starts to feed on a branch bearing several bunches of large fruit. A few min later an adult male climbs into the same tree heading for the branch already occupied by the female. Looking in the direction of the approaching male, the female immediately bends a few branches and arranges them into a circular structure which includes some fruit-bearing twigs. Sitting in her nest the female feeds without further interruption. In spite of his initial intentions, the male makes no attempts to displace the female but invades another part of the same feeding tree.

All cases (n = 13) when nest building immediately followed approaches by other individuals had the following features in common: (1) nest construction was almost always related to food; (2) the individuals building a nest were either adult females or immatures; (3) the approaching individuals were either adult males or females; (4) following nest building the nest owner consumed food undisturbed for a longer period of time; and (5) the approaching individual made no further attempts to contact or displace the nest owner. There was no evidence for immediate involvement or participation of a third individual.

Differences between populations: Comparative data of bonobo nests are available from a previous study at Lomako (BADRIAN & BADRIAN 1977) as well as from two other study sites, Yalosidi (KANO 1983) and Lake Tumba (HORN 1980).

The differences between the three study sites are the following: (a) Nests and (b) nesting trees were higher in Lomako than in both Yalosidi and Lake Tumba (Fig. 6), (c) no ground nests were recorded in Lomako and (d) the number of integrated nests found in Lomako (35 %) was significantly higher than that found in Yalosidi (15 %) (χ^2-test: $p < 0.01$; Fig. 5).

Discussion

Analyses of the structural attributes of nests and nesting trees indicate asymmetries between (1) availability and choice of nest trees, (2) location and mode of construction of day nests and night nests, (3) nests built by males and females and (4) nests built by members of different populations.

Accordingly, it is concluded that bonobos choose their nesting site selectively and that males and females may show distinct preferences.

The main problem with tracing the precise conditions required for nest building is that each tree may have more than one nest, but contrary, one nest may consist of more than one tree. Since potential nesting sites cannot be identified before a nest has actually been constructed, evaluations of the availability of nest sites can only be based on the physical properties of entire trees.

Nest Trees

In this study, analyses of nest trees were based on three attributes: height, diameter, and leaf size. Usually diameters of trees show a positive correlation with height. However, nests combining more than one tree may involve trees with very small diameters which alone could never support a nest. Consequently, the validity of the attribute diameter seems to be restricted and height of trees remains the crucial indicator for evaluations of potential nesting sites.

The third attribute, leave size, varies independently from the other two. Since the rate of nests built in trees with small or medium sized leaves was higher than expected, this attribute may indeed have affected the choice of nesting sites. The most simple explanation would be that small leaves may make nests more comfortable. In fact, when building nests in trees with big sized leaves, bonobos often covered the basic platform with twigs with smaller leaves. In the current part of the study, it was not possible to closely inspect the different components of material involved in nest construction and therefore the attribute 'leaf size' awaits further investigation.

Nests

Comparison of data from potential and used nest trees suggest that bonobos construct their nests at a preferred height. Factors responsible for this selectivity might be preference for optimal climate (temperature, humidity, protection of wind), material (soft twigs and leafs) or safety reasons.

As mentioned earlier, the construction of nests high above the ground is widely assumed as an adaptation to terrestrial predators (BALDWIN et al. 1981) including humans (KANO 1992). In a recent study BOESCH (1991) reported on 9 documented cases where chimpanzees (*Pan troglodytes*) were attacked by leopards. It is not known whether additional attacks occurred at night when the chimpanzees were resting in their nests, but nests in Tai forest have been the highest compared to other study sites of chimpanzees in Ivory Coast (FRUTH 1990). Although attacks of predators on bonobos have not been reported from Lomako, it seems conceivable that predator pressure sets the lower limit of nesting sites. Nevertheless it is difficult to understand how predator pressure could affect the variability of height existing within the respective study sites (e.g. differences in height between day and night nests in Lomako).

So far, no attempts were made to evaluate elevation-dependent differences in availability of potential nest material. Analyses of the structure and productivity of different forest layers in the primary rain forest habitat of Makokou/Gabon show that the middle layer (10—30 m) contains the majority of flexible branches and twigs with a high proportion of leaves (HLADIK 1978). Extrapolating from that, the preference of bonobos to construct nests in that layer may indeed reflect the choice for optimal nest material. Another aspect not considered in the current study was whether or not nests were covered by vegetation from above. Selection for nest sites protected by higher vegetation could also possibly explain the upper limit of nest trees.

Day nests were considerably higher than night nests. This difference might be related to the fact that day nests were constructed usually after heavy rain in the early morning. At that time bonobos used preferably the uncovered part of the upper canopy to expose the body to the first sun. In addition day nests were often built within a feeding tree, which belongs usually to the larger trees of the forest. The shorter investment of construction may be partly explained by the less sophisticated mode of construction (less trees involved) and the shorter period of use.

Sex Differences

In addition to the general preferences shown by bonobos, the data indicate sex differences concerning the height of nests. Field observations and preliminary analyses indicate that females choose to build their nests not only higher, but also earlier than males (own unpubl. data). If females build nests in the upper part of nesting trees where soft branches provide optimal nest material, males who want to stay close to a female may simply have no better option than building their nest below that of a female. In both *Pan* species males compete consistently for access towards females (GOODALL 1986; DE WAAL 1989; WHITE & BURGMAN 1990). Although mating may happen more frequently during day time, it has also been observed at night (GOODALL 1968). Thus, males building their nests below those of females may do so in order to control females and prevent competing males from approaching them.

Part of the sex differences reported here are in accordance with observations on chimpanzees. At Mahale, male chimpanzees built day nests less frequently than females (HIRAIWA-HASEGAWA 1986) and studies of tool use of chimpanzees at Tai forest have also demonstrated remarkable sex-differences with males concentrating less during nut cracking since yet being notably interested in social events (BOESCH & BOESCH 1984). This leads to another aspect entirely neglected so far: as in other African apes, nest building in bonobos is a social activity, sometimes involving 20 individuals or more. Analyses of the structure of entire nest groups and interactions among members of these groups are still in progress.

As reported above, bonobos use nests not exclusively for rest but also for other activities such as social grooming and play. Juvenile nest owners were joined by peers and engaged in long and exhaustive play bouts often resulting in damage and communal reconstruction of nests. Of particular interest are those cases when bonobos built a nest in obvious response to the approach of another animal.

When approaching their mothers resting in a day nest, immatures do not occupy the nest immediately. Instead, they stop at the fringe and show various gestures of begging and distress, like the "pout face" (DE WAAL 1988), body rocking, baby hooting and self embrace. In these situations it often happens that females leave the nest before establishing physical contact with their young. It is therefore assumed that the reluctance of females to share day nests with older offspring may be a crucial part of the weaning process, encouraging for forcing the offspring to build its own nest. From this point of view, nests may not only facilitate rest but indicate and symbolize a "personal space". The observations reported here indicate that this behavior might not only be restricted to the process of weaning but also practiced among adults. If — as in the case described above — displacements can successfully be avoided by braking a few branches, nests are not only simple roosting sites but function as tools. The high rate of day nest construction observed in bonobos may be partly related to the functional extension of this behavior and could serve as "evidence for symbolic processes". Anthropologists need "to agree that nesting is a manifestation of (bonobo) culture" (TUTTLE 1986, p. 146).

Population Specific Differences

One of the major differences between Lomako and Yalosidi was the mode of construction (integrated vs nonintegrated nests). However, from this and other studies (e.g. GOODALL 1968) it is known that nests consisting of parts from several trees often desintegrate immediately after the nest is abandoned respectively decompose at a faster rate than non-integrated nests. Thus, the higher proportion of integrated nests found in Lomako compared to Yalosidi (Fig. 5) may be related to different sampling techniques. However, the comparatively high location of nests as well as the absence of ground nests at Lomako (Fig. 6) are unlikely to be related to methodological disparities. It certainly deserves further investigation before we will know, whether these differences are due to ecological constraints or document another case of bonobo-cultural peculiarity.

In general, most aspects of nest building behavior of bonobos are very similar to what has been observed in different populations of chimpanzees, and except for the gorilla, nest building seems to follow the same basic scheme in the great apes. The significance of nest building observed during this study documents another facet of tool use in nonhuman primates. Because of its possible link to the process of weaning, it remains to be seen whether or not this behavior is a species-specific trait. In order to regulate social conflicts bonobos seem to have developed a number of unique behavioral patterns (e.g. genito-genital rubbing; KURODA 1980) not known to occur in any of the other ape species. While socio-sexual behavior is thought to reconcile former opponents (DE WAAL 1987, 1989), nest construction may enable an individual to avoid a potential conflict before it occurs. Hence, nest building may be another behavioral element on which the peaceful and cohesive social organization of *Pan paniscus* is based upon.

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