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17 • Nest building behavior in the great apes: the great leap forward?

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INTRODUCTION

Over decades apes have served as either referential or conceptual models in attempts to reconstruct the path of human evolution (Ghiglieri, 1987; Wrangham, 1987). In the search for behavioral traits shared by all members of the great apes, few have turned out to be conservative, that is, common features seen in all extant hominoids, and by inference present in our common ancestor. Of these shared traits, skilled object manipulation has been of great interest in comparative analyses as a basic criterion for hominization. Tool use and tool production, however, vary tremendously not only among the four species but also within a single species. Thus the trait in common is not tool use itself, but the general ability for environmental problem solving (McGrew, 1992). Nest building is part of this ability. It is probably the most pervasive form of material skill in apes. Whether or not this trait should be considered as tool use is much disputed (Goodall, 1968; Alcock, 1972; Beck, 1980; Galdikas, 1982).

Nest building is called 'bed building' by some investigators (Itani, 1979; Hiraiwa-Hasegawa, 1986). It is a daily habit of weaned great apes to build a place in which to rest. The technique employed depends on the site and on the available materials. Orangutans, chimpanzees and bonobos start their arboreal constructions by preparing a foundation of solid sidebranches or forks, bending, breaking and inter-weaving sidebranches crosswise. They complete the structure by bending most of the smaller twigs in a circular pattern over the rim. Detached twigs are added for lining (Davenport, 1967; Goodall, 1968; Horn, 1980). Gorillas, who more often establish terrestrial nests, build similarly. They gather mostly herbaceous materials by pulling, bending and breaking stems to arrange them around and under their bodies. They concentrate on the rim rather than on a foundation (Schaller, 1963). Our knowledge of ape nest building comes from numerous descriptions from early expeditions and dates to the past century (Du Chaillu, 1861). Some of these early descriptions were a misinterpretation of function and use (Garner, 1896), but most studies reported the morphology and use of these constructions for orangutans, gorillas and chimpanzees in accurate descriptions (Hornaday, 1879; Savage & Wyman, 1843). Yerkes & Yerkes (1929, p. 220) summarized the observations on ape nests done by the various explorers of the past century as follows: 'No phase of the mode of life [of the chimpanzee] and no behavior pattern has attracted more attention or produced more useful literature than that of nest construction.'

Beginning with ape-focused field research, nests continued to be an indicator of the subjects' presence, but behavioral descriptions lagged behind. Since apes mostly sleep at night, nest building has been eclipsed by the day-to-day observations on social behavior. With some exceptions (Schaller, 1963; Goodall, 1968; MacKinnon, 1974), nest construction at night and nest leaving in the morning became more the curfew times of behavioral observation than a topic of research itself. Thus, even today, our knowledge of nest building behavior and its social implications is limited. Instead, census methods have been developed that use nests as a way to estimate population density (Ghiglieri, 1984; Tutin & Fernandez, 1984). Height and age of nests, and sometimes species of trees used for nest construction, have often been noted. These have been compared with availability and thus have led to a more comprehensive knowledge of the environmental factors that influence the choice of raw material, nest sites, and locations. One aspect rarely discussed concerns the evolutionary implications of nest building behavior. Yerkes & Yerkes (1929, p. 564) showed great foresight when they noted that:

> The observed range of variation is from almost complete lack of tendency and capacity for construction of nest or bed to their definite presence in the anthropoid apes and their relatively high development in man. This comparison is peculiarly significant because nesting behaviour illustrates the appearance and phylogenetic development of constructivity, and, coincidentally, the transition from complete dependence on self-adjustment to increasing dependence on manipulation or modification of environment as a method of behavioral adaptation.

This paper tries to revive the thinking of more than 65 years ago by considering nest building as one of the crucial steps in hominoid evolution. The chapter's title indicates our attempt to pick up the thread and to pay the attention to this behavioral pattern that it deserves.

We formulate and present a provocative hypothesis: nest building is not only properly placed within the realm of tool use, but it is also the original tool that led to the mental and physical ability to use the tools we see today.

Given space limitation here, a comprehensive review of studies on nest building in apes will be published elsewhere (Fruth, in preparation). This review includes data provided by previous studies as well as unpublished data gathered by a questionnaire distributed in December 1993. Here we present: (a) a summary of the review in detailed tables; (b) a comparison of the results that will attempt to filter the species-specific features and discuss them according to their adaptive or cultural implications; (c) an evolutionary scenario, in which we speculate on how nest building could have been developed and established; and (d) some ideas on the implications nest building may have had for the evolution of apes' mental capacities.

METHODS

The data for interspecific comparison come from previous publications (Tables 17.2–5). To update these publications, responses to the questionnaire (Q) are summarized in Tables 17.6–8. Unless noted, data on bonobos are from our 29-month study at Lomako (1990–94). Interspecific comparison is based on up to 20 variables that include morphological, ecological, metrical and behavioral features. To help assess the data, length of study and type of investigation are indicated. Special terms are defined as follows:

Custom. Special habit within one population or study group, e.g. rain cover.

Nest group. All nests built in close proximity in one night.

Nest site. Place in the home range where the nest group is built. This includes type of habitat, topography and characteristic features, e.g. proximity to water or food resources.

Nest location. Position of the nest in terms of vertical and horizontal distribution, e.g. ground vs. tree, top of the crown vs. bottom of the crown, etc.

Reuse. Abandoned nests used again by the same or another individual on consecutive nights or even later. This term excludes a nest made by an individual, left briefly for defecation and then reoccupied.

RESULTS AND SUMMARY

Table 17.1 gives a detailed description of the abbreviations used in Tables 17.2–17.8. Tables 17.2–5 review published information on great ape nests. Tables 17.6–8 report the results from the questionnaire.

COMPARISON

Table 17.9 summarizes the main results for the four species. Nest building behavior in the four species of great apes appears to be rather uniform throughout all levels of comparison.

Morphology

All four species build both day and night nests. Orangutan and gorilla males may rarely spend the night without a nest. In orangutans, chimpanzees and bonobos, nest sites are not distributed randomly throughout the habitat but are chosen selectively. In gorillas, distribution of nest sites appears to be arbitrary. The degree of selectivity of nest sites seems to depend on the variation in

Table 17.1. *Abbreviations used in (a) Table 17.2–17.5 and (b) Table 17.6–17.8*

(a)	
Type of habitat	F, forest; R, rain; P, primary; S, secondary; E, evergreen; M, montane; L, lowland; G, grassland; W, woodland; SV, savanna; G, gallery; PL, plantation (sometimes combined)
Duration	Duration of the study in months
Direct/indirect observation	+, yes; −, no
Nests	Sample sizes of day nests/night nests; ?, information not quantified; −, no data
Height	Height of nests in meters; numbers indicate the range; bracketed numbers the height of most nests
Choice of material	Opportunistic or selective
No. of species used	?, information not quantified; −, no data
Feeding trees	Feeding trees used for day nests (DN) or night nests (NN) or both
Type of construction	Number indicates the number of construction types distinguished; ?, information not quantified; −, no data
Ontogeny	Information available: +, yes; −, no
Time of construction	In minutes for one nest
Reuse	Number indicates how often reuse has been observed; percentage (%) restricts reuse to either day or night nests (DN/NN); yes, reuse happens but not quantified; −, no data
Activities in nest	See Table 17.9
Nest groups	Sample size of groups in study: +, data available; ?, information not quantified; −, no data
Group size	Numbers indicate range; bracketed numbers the median; +, data not specified
Nearest neighbor	Nearest distances between nests in meters
(b)	
Type	Day nests (DN) or night nests (NN)
Integrated trees	Maximal number of integrated trees per nest; where no trees are used, nests are made of herbaceous vegetation
Percent. int. nests	Percentage of nests that are integrated
Nest group size vs. day-travel party	Size of night nest group (NNGR) versus size of day-travel party (DTP); possible categories: smaller, same, larger

habitat structure: the more variation, the more evident selectivity towards specific site features. Data from Lopé show that western lowland gorillas choose secondary forest more often than expected, while chimpanzees choose primary forest (Tutin *et al.*, 1995). Here, selectivity may be a result of niche differentiation between the sympatric species. Gorillas also differ from the other apes in the location of nests. They mostly sleep on the ground, while the three other species sleep in trees. Analyzing the height of tree nests, gorillas are again the only species to construct nests, on average, below 10 m, while the three other apes usually build between 10 and 20 m. No quantitative data of availability and choice of material were at our disposal for orangutans or for most gorilla and chimpanzee subspecies. By pooling descriptive material with the few data available, however, we conclude that in general, orangutans, chimpanzees and bonobos are highly selective toward specific tree species for nest construction, while gorillas seem to be opportunistic. Feeding trees or plants are used for both day and night nests in all species. The only difference was whether or not feeding trees bearing ripe fruit were used for nest construction. While this behavior is reported for day nests of all species, chimpanzees and bonobos seem to be reluctant to construct night nests within those trees. However, orangutans do so. In all species, proximity to feeding trees is reported to be close. Concerning the type of construction, differences emerge at the species level: with few exceptions, orangutans build nests in single trees, while chimpanzees have been reported to use two trees in 5–10% of all cases. With the exception of Lilungu, bonobos integrate trees in over 30% of all cases. Sometimes they use up to seven trees for a single nest, something never reported for the three other species. For herbaceous ground nests, gorillas integrate stems of different plants in over 50% of all cases. If nests are constructed within trees however, the rate is below 5% and the maximum of integrated trees is three. We

Table 17.2. *Published reports of orangutans*

	Borneo *(Pongo pygmaeus pygmaeus)*						Sumarate *(Pongo pygmaeus abelii)*		
Reference	Schaller, 1961,	Yoshiba, 1964	Davenport, 1967	Rodman, 1979	Galdikas, 1975, 1982	MacKinnon, 1974	Mackinnon, 1974	Rijksen, 1978	Sugardjito, 1983
Study site	Sarawak	NE Sabah	Sepilok, Sabah	E. Kalimantan	Tanjung Puting-NP, Kalimantan	Ulu Segama, Sabah	Ranun River, N. Sumatra	Ketambe, N. Sumatra	Ketambe, N. Sumatra
Country	Indonesia	Malaysia	Malaysia	Indonesia	Indonesia	Malaysia	Indonesia	Indonesia	Indonesia
Type of habitat	PF	PF	PF	PF	PF	PF	PF	PF	PF
Years	1960–61	1963	1964	1970–71	1971–80	1968–70	1971	1971–74	1980–82
Duration	3	2	7	15	108	18	8	38	6
Study's goal	Survey	Survey	Behavior	Ecology, behavior	Behavior	Ecology, behavior	Ecology, behavior	Behavior	Ecology, behavior
Direct observation	+	–	+	+	+	+	+	+	+
Indirect observation	+	+	+	–	–	+	+	+	+
Nest morphology									
Nests	1/228	–/614	?/28	–/?	?/?	?/510	?/?	?/?	?/172
Height	4–40 (15–25)	4–34 (15–30)	–	–	–	4–30 (15–30)	–	13–15	≤30
Choice of material	–	–	–	–	–	selective	–	–	–
No. of species used	–	–	–	–	–	–	–	–	–
Feeding trees	DN/NN	DN/NN	DN/NN	DN/NN	DN/NN	DN/NN	?/?	DN/–	DN/NN
Type of construction	–	?	?	–	–	?	?	?	–
Nest building									
Info. on ontogeny	–	–	–	–	+	+	–	–	–
Time of construction	–	–	6.5 min	–	< 5 min	2–3 min	–	–	–
Reuse	–	–	50% of DN	–	–	8	–	yes	–
Activities within nest	R/I	–	R/E	–	R	R/P/G	R/P/G	R/P/E	–
Nest groups									
Nest groups	–	?	–	?	?	?	–	?	–
Group size	–	3	–	1–5	≤5	1–3	–	1–2	–
Nearest neighbor	–	–	–	–	–	–	–	–	–

Table 17.3. *Published reports of gorillas*

	Mountain (*Gg beringei*)			Eastern lowland (*Gg graueri*)			Western lowland (*Gg gorilla*)			
Reference	Donisthorpe, 1958	Kawai & Mizuhara, 1959	Schaller, 1963	Casimir, 1979	Yamagiwa, 1983	Mwanza *et al.*, 1992	Groves & Sabater Pi, 1985	Remis, 1993	Willisamson, 1988	Tutin *et al.*, 1995
Study site	Kisoro Virungas	Kisoro Virungas	7 diff. areas	Kahuzi Biega	Kahuzi Biega	Itebero		Bai Hokou, Dzanga-S.	Lopé	Lopé
Country	Uganda	Uganda	Uganda, Zaïre	Zaïre	Zaïre	Zaïre	Equ. Guinea	C.A.R.	Gabun	Gabun
Type of habitat	MRF	MRF	MRF	MPF	MPF	PF/SF	PF	PF/SF	PF	PF
Year	1956	1959	1959–61	1979	1978–79	1987–90	1963–69	1990–92	1984–85	1983–94
Duration	8	3	18	15	7	10	18	27	16	48
Study's goal	Pilot study	Ecology behavior	Survey, behavior	Ecology, behavior	Survey, ecology	Survey, ecology	Behavior	Ecology, behavior	Ecology	Survey, ecology
Direct observation	+	+	+	+	+	–	+	–	+	–
Indirect observation	+	+	+	+	+	+	+	+	+	+
Nest morphology										
Nests	?/225	?/365	22/3012	– /964	– /171	– /375	?/448	– /1231	24/748	– /2435
Height	–	0–16	0–15	0–15	–	0–30	0–15	0–30	0–16	0–35
Choice of material	Opportunistic	Opportunistic	Opportunistic	Opportunistic	–	Opportunistic	Selective	Selective	Opportunistic	Selective
No of species used	?	?	?	50	–	–	22	–	38	98
Feeding trees	DN/NN	DN/NN	DN/NN	DN/NN	?/?	?/?	DN/NN	?/?	?/?	DN/NN
Type of construction	3	–	5	2	–	–	4	3	8	7
Nest building										
Ontogeny	–	–	+	–	–	–	–	–	–	–
Time of construction	–	–	5 min	–	–	–	–	–	–	–
Reuse	0	1	–	–	–	–	12	–	0	–
Activities in nest	–	R	R/E	–	–	–	R/E	–	–	–
Nest groups										
Nest groups	–	36	400	63	58	83	49	163	113	373
Group size	3–12	4–15	(16, 9)	(15)	(14, 3)	–	2–16	(8)	1–19	(7)
Nearest neighbor	–	0–50	0–38.5	0–40	–	–	1.5–15	–	–	–

Table 17.4. *Published reports of chimpanzees*

	Eastern *(Pan troglodytes schweinfurthii)*	Central *(Pan troglodytes troglodytes)*		Western *(Pan troglodytes verus)*		
Reference	Goodall, 1968	Baldwin *et al.* 1981	Wrogemann 1992	Baldwin *et al.* 1981	Anderson *et al.*, 1983	Marchesi *et al.*, 1995
Study site	Gombe		Lopé	Mt Assirik	Sapo	Nationwide
Country	Tanzania	Equ. Guinea	Gabon	Senegal	Liberia	Ivory Coast
Type of habitat	GWF	PF/SF	PF	SV/GF	PF	PF/SF/PL
Year	1960–67	1963–69	1988–89	1976–79	1982	1989–90
Duration	?	?	16	40	2	15
Study's goal	Behavior	Behavior, ecology	Behavior, ecology	Ecology	Survey	Survey
Direct observation	+	+	+	—	—	—
Indirect observation	—	+	+	+	+	+
Nest morphology						
Nests	?/384	—/195	—/523	—/252	—/67	?/611
Height	0–25	2–40	2–45	2–44	6–20	—
Choice of material	opportunistic	—	selective	—	—	—
No. of species used	—	—	45	—	—	—
Feeding trees	DN/—	?/?	DN/NN	?/?	?/?	?/?
Type of construction	?	?	?	?	—	—
Nest building						
Info. on ontogeny	+	—	—	—	—	—
Time of construction	1–5 min	—	—	—	—	—
Reuse	20 ×	—	—	—	—	—
Activities within nest	R	—	—	—	—	—
Nest groups						
Nest groups	?	66	68	83	?	182
Group size	1–17 (2–6)	1–12 (2)	1–26 (1)	1–18 (4)	1–10 (1)	1–22 (2–5)
Nearest neighbor	—	4	6	4	4	—

suggest that the higher frequency of integrated nests in bonobos is a response to higher sociality expressed also by larger parties at night (Fruth & Hohmann, 1994). If individuals seek to increase proximity of night nests, then the combination of adjacent trees may compensate for the lack of suitable nest sites. Again, with the exception of the gorilla, customs are reported from all four species. However, variation within a species exceeds variation across species and thus should be considered on the cultural level rather than on that of species-specificity.

Behavior

Ontogeny is similar in all species. Day nest construction by immatures reaches a peak between the first and second year after birth in orangutans and gorillas respectively, and in the third year in chimpanzees. Infants of orangutans and gorillas construct their own night nests slightly earlier (between 3 and 4 years of age) than do chimpanzees and bonobos. Time of construction for a nest varies between 1 and 7 minutes. Time of utilization is similar for all species and is influenced in the same way by season, weather and light conditions. All apes usually rest from dusk to dawn. If light is reduced by rain or clouds, they may leave their nests later in the morning and start to build new ones earlier in the evening. Reuse is reported for all populations but with different frequencies. Orangutans seem to reuse nests most often, followed by chimpanzees in dry habitats, then gorillas and bonobos. Reuse of nests by chimpanzees is mostly a question of habitat and availability of suitable nest material; the drier the habitat the more often reuse

Table 17.5. *Published reports of bonobos*

	Pan paniscus					
Reference	Horn, 1980	Badrian & Badrian, 1977	Fruth & Hohmann, 1993, in prep.	Kano, 1983	Kano, 1992	Sabater Pi & Veá, 1990
Study site	Lake Tumba	Lomako	Lomako	Yalosidi	Wamba	Lilungu
Country	Zaïre	Zaïre	Zaïre	Zaïre	Zaïre	Zaïre
Type of habitat	PF	PF	PF	G/PF	PF	PF
Years	1972–74	1974–75	1990–94	1973–75	1974–86	1988–89
Duration	24	11	31	3.5	*c.* 70	13
Study's goal	Behavior, ecology	Behavior, ecology	Behavior, ecology	Ecology	Behavior, ecology	Ecology
Direct observation	+	+	+	+	+	–
Indirect observation	+	+	+	+	+	+
Nest morphology						
Nests	?/107	–/174	164/1156	19/2380	637/3357	–/611
Height	0–25	5–34	3–50	0–50	0–50	2–36
Choice of material	Opportunistic	–	selective	selective	selective	–
No of species used	–	26	24	103	108	?
Feeding trees	?/?	DN/NN	DN/–	?/?	DN/NN	?/?
Type of construction	–	–	5	5	5	–
Nest building						
Info. on ontogeny	–	–	+	–	–	–
Time of construction	–	–	1–7 min	–	0–7 min	–
Reuse	–	–	0.2% of NN	–	–	yes
Activities within nest	–	–	R/P/G/S/E/T	–	R/G/S/P	–
Nest groups						
Nest groups	–	–	266	–	–	–
Group size	–	–	1–25 (17.5)	–	–	–
Nearest neighbor	–	–	0–86 (9.8)	–	–	–

occurs. (In drier habitats trees are scarcer, semideciduous and show a much lower rate of regeneration than in wetter habitats; nest raw materials are therefore limited.) Although a variety of associated activities occur in the context of nest building as shown in Tables 17.2–17.8, all species use nests for similar purposes. Differences on the species level may refer to the frequency of different activities (Fig. 17.1). Sex differences are reported for all species, mostly involving frequency of nest building. In chimpanzees and bonobos, females construct day nests more often than males. Orangutan and gorilla males build night nests less often. Height of females' nests is on average higher in orangutans, gorillas and bonobos. While orangutan and bonobo females start nest construction at dusk, gorilla females wait until the silverback has chosen the place and has built the first nest. Detailed investigations on further sex differences are available only for bonobos. Thus, interspecific comparison awaits further investigations. Feces are dropped outside the nest by orangutans, chimpanzees and bonobos. Gorillas often defecate in their nests, but there appear to be population differences. Whether or not nests are fouled has been discussed with reference to the fruit content in diet and has its roots at the environmental rather than the species-specific level.

Nest groups

Only recently have primatologists started to consider nest groups, instead of single nests, and to be aware that a nest is not constructed independently from others (Schaller, 1963; Goodall, 1968; Fruth & Hohmann, 1994). The data for nest groups seem to reflect the differences in social organization and are thus a good mirror

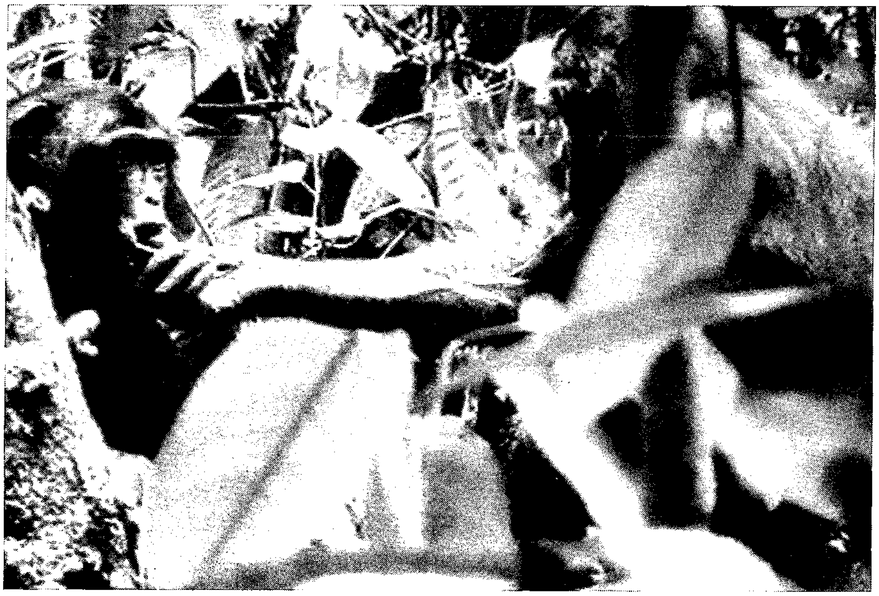

Fig. 17.1. Adolescent female (right) begs for chewed fruit from an adult female bonobo at Lomako. (Photo by G. Hohmann)

of species-specificity. While the semisocial orangutans hardly ever show accumulations of nests, chimpanzees show a wide range, but favor resting in small parties. Gorillas usually stay together as whole groups, while bonobos often congregate to form large overnight parties. Nearest neighbor analyses suggest that interindividual proximity during the day is reflected in night nest association. The more familiar the individuals, the closer the night nests. However, with the exception of gorillas, patterns within the group have not yet been analyzed. In gorillas, nest position is related to age and sex classes. Data on bonobos suggest, however, that not only social organization is reflected (e.g. females built higher than males) but also social structure (e.g. low-ranking individuals nested on the periphery).

Population-specific differences

All species show interpopulational differences in nest building behavior. Orangutans use fruiting trees for night nesting more often on Borneo than on Sumatra; western lowland gorillas build more often in trees than do mountain gorillas; chimpanzees at Gombe and Guinea Bissau build nests in oil palms (*Elaeis guineensis*) but others do not; bonobos at Lilungu do not integrate more than two trees, while others do. Intraspecific differences may indicate the range of ecological adaptation, but considering the variety of ape habitat and differences in social organization and diet, nest building appears to be surprisingly uniform on the interspecific level. Therefore, it is likely that nest building has developed under evolutionary constraints and is thus a long-standing trait for all the great apes.

EVOLUTION OF NEST BUILDING BEHAVIOR: A SCENARIO

Nest building with its basic features is shared by the four species of great apes. Because of this activity's persistence and uniformity among these closely related species, it is improbable that nest building developed independently four times during evolution. When was it invented and why?

Searching for a common ancestor brings us to the great ape stock in the early Miocene (Martin, 1990). At that time eight to ten species of comparatively small apes

Table 17.6. *Gorilla questionnaire*

Questionnaire	*Gorilla gorilla beringei*	*Gorilla gorilla graueri*		*Gorilla gorilla gorilla*		
Reference	Fletcher, unpubl.	Yamagiwa, publ. partly	Williamson, unpubl.	Tutin, publ. partly	McFarland, unpubl.	Williamson, unpubl.
Study site	Virunga NP	Kahuzi Biega NP	Kahuzi Biega outside NP	Lopé NP	Cross River State	Dja Reserve
Country	Rwanda, Zaïre	Zaïre	Zaïre	Gabon	Nigeria	Cameroon
Type of habitat	Hagenia/MF.	MF/PLF	SF/PLF	PF	??	LRF
Year	1989–92	1978–94	1994	1983–94	1993	1994
Direct observation	+	+	—	—	—	—
Indirect observation	+	+	+	+	+	+
Nest morphology						
Type	DN/–	DN/NN	DN/NN	–/NN	–/NN	DN/NN
Location in forest	Undergrowth	Undergrowth	Lower canopy	middle canopy	Lower canopy	Undergrowth
Position in crown	—	Bottom	Middle	—	—	—
Height	< 10	< 10	< 10	< 10	< 10	< 10
Choice of species	—	Opportunistic	—	Opportunistic	—	—
Feeding plants/trees	?/?	DN/NN	?/?	DN/NN	?/?	?/?
Integrated trees	no	3	4 shrubs	3	2	no
Percent. int. nests	> 50%	< 5%	10–30%	< 5%	> 50%	—
Nest building						
Info. on ontogeny	+	+	—	—	—	—
Time of construction	—	1–2 min	—	—	—	—
Reuse	Yes	0	—	Yes	—	—
Activities within nest	R/P/G/E	R/P/E	—	—	—	—
Nest groups						
Nest groups	?	+	+	+	+	+
Group size	—	5–20	5–10	+	2–5	5–10
Nest group size versus day-travel party	Same	Same	Same	Same	Same	Same

inhabited large forested parts of Africa and Arabia. The Miocene shows us the greatest species diversity as well as inferred association patterns of apes. Up to five species inhabited early Miocene forests occupying different strata of the canopy (Andrews, 1987). During the middle Miocene 11 to 13 species were known; they covered a larger geographical area than that of the early Miocene, and some had increased in body size. Their size ranged from that of small Old World monkeys to female gorillas. These apes radiated in size as they adapted to the different strata of the forest. Miocene apes were predominantly frugivorous and differences in body size reduced competition between closely related species (MacKinnon, 1977). Some species became more terrestrial, a pattern that opened up a new ecological niche. Larger body size also may have been favored as a result of selection pressure by terrestrial predators. Thus, some apes also succeeded in interspecific competition with other ground-dwelling mammals.

Monkeys were uncommon during the early Miocene, but expanded by the middle Miocene. From three unspecialized species of cercopithecoids during the early Miocene, monkeys had increased to 14 species by the late Miocene. While the colobines specialized in the abundant food source of leaves, cercopithecines adapted to the frugivorous niche. Both colobines and cercopithecines became better adapted to this diet than did the hominoids by evolving a greater tolerance to plant secondary compounds. The cercopithecoids' capacity to feed on fruits with high tannin or alkaloid content allowed them to consume fruit before it ripened. This adaptation helped during periods of food shortage

Table 17.7. *Chimpanzee questionnaires*

Questionnaire	*Pan troglodytes schweinfurthii*				*Pan troglodytes troglodytes*		*Pan troglodytes verus*					
Reference	Nishida, unpubl.	Moore, unpubl.	Wrangham, publ. partly	Yamagiwa, publ. partly	Wrogemann, unpubl.	Williamson, unpubl.	Sugiyama, publ. partly	McGrew, publ. partly	Boesch, unpbl.	Moore, publ. partly	Alp, unpubl.	Pavy, unpubl.
Study site	Mahale	Ugalla	Kanyawara	Kahuzi-Biega	Lopé	Dja Reserve	Bossou	Mt Assirik	Taï	(south-west)	Tenkere	Bafing area
Country	Tanzania	Tanzania	Uganda	Zaïre	Gabon	Cameroon	Guinea	Senegal	Ivory Coast	Mali	Sierra Leone	Mali
Type of habitat	GWF	W	MRF	MF/PLF	PLRF	LF	SF	SV	PF	G/W	SV/W/F	W/F
Year	1966–94	1985–94	1987–94	1987–94	1988–89	1994	1975–94	1976–79	1979–94	1984	1989–94	1992
Direct observation	+	–	+	–	–	–	+	+	+	–	+	–
Indirect observation	+	+	+	+	+	+	+	+	–	+	+	+
Nest morphology												
Type	DN/NN	DN/NN	DN/NN	DN/NN	DN/NN	DN/NN	DN/NN	DN/NN	DN/ –	DN/NN	– /NN	DN/NN
Location in forest	Middle canopy	Middle canopy and monolayer	–	Lower and middle canopy	Middle canopy	Lower canopy	Middle canopy	Upper canopy	–	Canopy	Middle canopy	Middle canopy
Position in crown	Bottom	No preference	–	Middle and bottom	Middle	Bottom	Top and bottom	Top	–	–	Top	Middle
Height	10–20	10–20	–	10–20	10–20	< 10	10–20	10–20	–	< 10	10–20	10–20
Choice of species	Selective	Selective	–	Opportunistic	Selective	Selective	Selective	Selective	–	–	–	Selective
Feeding trees	DN/NN	DN/NN	?/?	DN/NN	DN/NN	?/?	DN/NN	DN/NN	?/?	?/?	DN/NN	DN/NN
Integrated trees	2	2	–	2	2	3	3	4	–	?	2	–
Percent. int. nests	< 5%	?	–	5–10%	5–10%	30–50%	5–10%	5–10%	–	< 5%	< 5%	–
Nest building												
Ontogeny	+	–	–	–	–	–	+	–	–	–	–	–
Time of construction	–	–	–	> 2 min	–	–	3–5 min	4 min	–	–	3–4 min	–
Reuse	Yes	Yes	0	Yes	Yes	–	Yes	Yes	Yes	–	Yes	Yes
Activities in nest	R/P/G/S/E	–	R/P/G/E	R	R/P	–	R/P/G	–	–	–	R/G/E	–
Nest groups												
Nest groups	?	+	+	+	+	+	+	+	–	+	+	–
Group size	?	2–5	2–10	1–5	1	1	> 10	2–5	–	2–5	5–10	–
Nest group size vs. day-travel party	Smaller	?	Smaller	Smaller	?	?	Same	Same	–	?	?	–

Table 17.8. *Bonobo questionnaires*

Questionnaire	*Pan paniscus*		
Reference	Kano, publ	Sabater Pi, publ.	Fruth, publ. partly
Study site	Wamba	Lilingu	Lomako
Country	Zaïre	Zaïre	Zaïre
Type of habitat	EPF	SF	EPF
Year	1973–94	1988–90	1990–94
Direct observation	+	+	+
Indirect observation	+	+	+
Nest morphology			
Type	DN/NN	DN/NN	DN/NN
Location in forest	Middle canopy	Middle canopy	Middle canopy
Position in crown	Middle	Top	Middle
Height	10–20	10–20	10–20
Choice of species	Selective	Selective	Selective
Feeding trees	DN/ –	?/?	DN/ –
Integrated trees	> 5	2	> 5
Percent. int. nests	30–50%	< 5%	30–50%
Nest building			
Info. on ontogeny	–	–	+
Time of construction	–	–	1–7min
Reuse	Yes	0	Yes
Activities within nest	R/P/G/S/E	R/P	R/P/G/S/E/T
Nest groups			
Nest groups	+	–	+
Group size	> 10	–	1–25
Nest group size vs. day-travel party	Same	–	Larger

(Wrangham, 1980), but also put them in competition with large frugivorous mammals like apes. The increase in monkey species' diversity became directly proportional to the decrease in ape diversity (Andrews, 1987), which may indicate the importance of the adaptation to tolerate plant secondary compounds. Extrapolating the extinction rate during the Miocene, apes 'should' have become extinct 3.2 million years ago (Andrews, 1987, fig. 1). However, some of them have survived. How did they manage to compete successfully against the better adapted monkeys?

One answer to this selection pressure could be the flexibility of ape social organization (Di Fiore & Rendall, 1994). Another answer could be adaptation to new ecological niches. Gorillas may have specialized in superabundant food and chimpanzees may have started nut cracking. A third answer, however, could be the ability to monopolize food resources – not solely by body size, group size and physical power – but by the construction of nests.

Nest construction was not 'invented' all at once in ape evolution. It probably occurred as a byproduct of feeding habits.

Miocene apes came at least occasionally to the ground. With the exception of the orangutan, extant great apes spend at least half of their waking lives on the ground. They feed on fruit that ripens on the ground (e.g. *Parinari, Autranella, Irvingia*; Fig. 17.2). In a party of several individuals they search for ripe fruit, carry as much as they can by hand or mouth, and sit elsewhere, placing all of the fruit in a little heap in front of them. Seated at that one spot, they consume their concentration of 'prey' (see also Hunt, 1994). Perhaps this was the '*proto-nest*?'

Other fruit species ripen in trees. Most fruits and sometimes the most tasty ones are found on the peripheral branches. These distal twigs are often inaccessible for other fruit-eaters. Apes bend and break these branches towards their body, sitting on the more solid, proximal parts toward the trunk (Wrangham, 1975; Rjiksen, 1978; personal observations). Thus their hands are free to reach and to grasp what is wanted. Finally they end up sitting on the end of a limb enhanced by broken branches. This feeding spot may result in a solid platform, a '*feeding nest.*'

Both the 'proto-nest' on the ground and the 'feeding nest' in the tree allow food consumption in a secure and comfortable place and may have been the predecessors of sleeping nests. All modern great apes build such feeding nests. Some apes even remain in feeding trees overnight. In orangutans, nests in feeding trees have been reused. The largest numbers of nests observed in one tree are for day nests within feeding trees. One could argue that the apes who survived were those large enough to bend and break branches to open a niche inaccessible to many others. Additionally, they were able to monopolize and defend food resources against competitors, if necessary, even overnight, by their presence at the resource. Observations of bonobos suggest that the nests built in the feeding context sometimes marked a property for the nest builder and left the 'owner' undisturbed by the approach of other group members (Fruth & Hohmann, 1993). From this scenario onwards

Table 17.9. *Comparison of nest building in the great apes*

Comparison	Orangutan	Gorilla	Chimpanzee	Bonobo
Nest sites				
Distribution	Discontinuous	Arbitrary	Discontinuous	Discontinuous
Choice	Selective	Opportunistic	Selective	Selective
Nests				
Type	DN/NN	DN/NN	DN/NN	DN/NN
Frequency of nest construction	Daily, adult males sometimes not	Daily, sometimes not	Daily, all weaned individuals	Daily, all weaned individuals
Location	In trees only	Predominantly on the ground, in trees also	NN: in trees only DN: sometimes on the ground	NN/ DN: predominantly in trees
Height	10–20 m	< 10 cm	10–20m	10–20m
Choice of material	Selective	Opportunistic (selective)	Selective	Selective
Feeding plants or fruiting trees used for	DN/NN	DN/NN	DN/–	DN/–
Type of construction	Mostly one tree, foundation, rim, lining	Mostly mixed plants, if tree then single, (foundation) rim	Mostly one tree, foundation, rim, lining	Often several trees, foundation, rim, lining
Custom	Roof, raincover	Soil and turf	Oil palm	(Rain) cover
Behavior/Ontogeny				
1st attempts	12 months	8 months	8 months	No analyzed data
DN peak	2 years	1½ years	3 years	
Own NN	3–4 years	3–4 years	4–5 years	
Time to construction	2–3min	1–5min	1–5 min	1–7min
Period of use	Whole night	Whole night	Whole night	Whole night
Reuse	Often	Rarely	Rarely–often	Rarely
Activities	R/P/I/G/O	R/E/P/G	R/E/P/S/G/B/I	R/E/P/S/G/I/T
Sex differences	F: higher F: more often F: before M	F: more often above ground F: after silverback M	F: more DN than M	F: higher, longer, earlier, more elaborate than M
Nest group				
Entity	Party (subgroup)	Group	Party	Party
Nests per group Range (M)	1–5 (1)	1–2 (4–7)	1–26 (2–5)	1–25 (5–13)
Nearest neighbor Range (M)	Same tree	1–10 m	4–6 m	4.5 m
Population				
Differences	Sociality Group size	Feces Selectivity	Reuse Group size	Integration Ground nests

Abbreviations used: DN, day nest; NN, night nest; F, female; M, male; (M), median; m, meter; min, minutes; R, rest; P, play; G, groom; S, sex; I, ill or wounded; T, taboo; B, birth; E, eat; O, other.

we should consider the creation of these restricted zones ('taboo-nests') not as a highly derived evolutionary trait, but as the original use of day nests. Defense of food patches shifted from the level of interspecific or intergroup competition, to the level of interindividual competition.

Most modern great apes construct night nests outside fruit-bearing trees. Rjiksen (1978, p. 151) suggested that this may be to avoid the risk of agonistic encounters with other species, which seems to contradict our hypothesis. However, Rjiksen paid particular attention to man as the threatening species, and he did not discuss nocturnal fruit-eating competitors such as fruit bats (Pteropodidae). Small nocturnal mammals may be successful with or without apes occupying the tree. There-

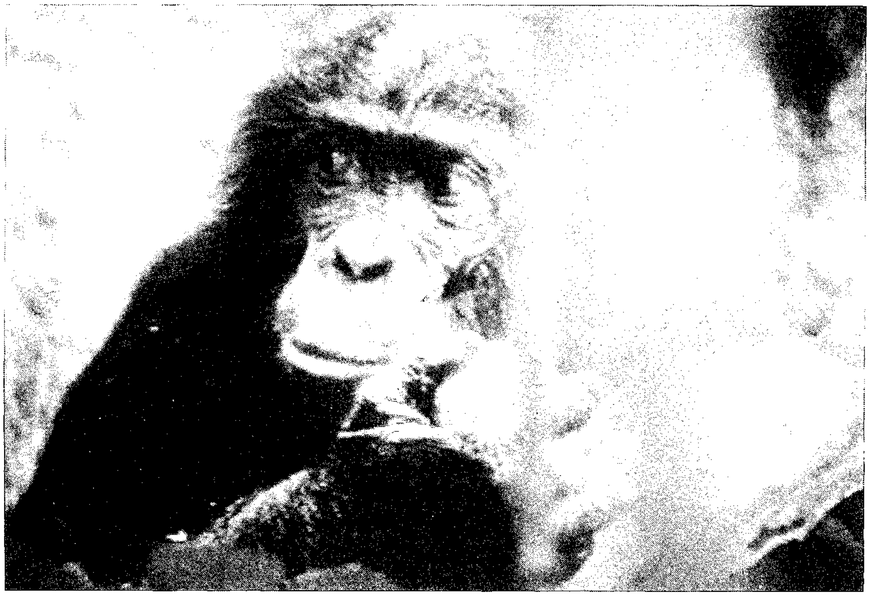

Fig. 17.2. Adolescent male bonobo eats *Irvingia* fruit on the ground at Lomako. (Photo by G. Hohmann)

fore apes may prefer to sleep apart, not to avoid conflicts but to avoid a restless night in the midst of active frugivores. However, apes may stay close enough to reoccupy the tree early in the morning and consequently prevent other competitors such as monkeys from entering the tree. Proximity to feeding trees may thus be a result of the calculation of costs (sleeplessness, loss of food) and benefits (sleep, gain of food). It may change with the quality and interspecific popularity of the resource.

THE GREAT LEAP FORWARD: SPECULATIONS ON THE IMPLICATIONS OF NEST BUILDING FOR HOMINID EVOLUTION

Group living has been discussed either as an adaptation to cooperative defense of food trees (Wrangham, 1980, 1983) or as an adaptation to predator pressure (van Schaik, 1983). At least in *Pan paniscus*, an additional factor may have influenced group size and cohesion. Bonobos who forage in different parts of the home range often gather at night nest sites. The next morning they depart in a specific direction, often in parties of a different composition from that of the day before. We suggest that aggregation at night may facilitate transfer of information on the quality of food patches visited during the day (Hohmann & Fruth, 1994). Accordingly, we consider nest groups as potential 'information-centers' (Ward & Zahavi, 1973).

In addition to the proximate functions of nest building suggested above, we draw attention to a possibly ultimate function: the connection of nest building and sleeping behavior. Is it possible that nests have permitted a different and better quality of sleep and if so, what implications may that kind of sleep have had on the cognitive evolution of the hominoids?

First, nests may have improved sleep by providing better thermoregulation or by the potential for more relaxed and comfortable sleeping postures. Second, apes constructed nests at places less accessible to predators; thus nests may have provided safer sleep. With improved security during sleep, the need for vigilance decreased. Allison & Van Twyver (1970) demonstrated that the proportion of different characteristics of sleep change with the need for vigilance during sleep. 'Secure sleepers' spent more time in REM sleep (rapid eye movement) than 'insecure sleepers'. REM or active sleep is of great importance for maturation of the fetal nervous system. In adults REM sleep seems related to periods of quiet sleep (QS) (QS = SWS + LQS; SWS = slow wave sleep, LQS = light quiet sleep; Meddis, 1975). SWS is associated with metabolic processes such as the release of growth hormones. It accounts for about 25% of adult human sleep. Meddis (1975) contrasts traditional theories on the function of sleep, namely sleep as physiological recuperation, with his theory of 'sleep the immobiliser' (p. 680). Recent investigations on REM and SWS have shown that both phases of sleep combine to establish memory (Wilson & McNaughton, 1994; Karni *et al.*, 1994). Accordingly, REM sleep is thought to repeat practiced tasks, while SWS is responsible for the transfer of information to the cortex resulting in long-term memory. If we apply this to apes' sleep, we may better understand the increase in learning abilities that evolved from monkeys to apes.

Summarizing the previous paragraphs, we conclude: nest building is a phylogenetically conservative behavior that must have evolved in the Miocene. Since we do not have fossil nests from that epoch, the evolutionary scenario mentioned above remains highly speculative. Increase in body size and special patterns of food consumption have been considered as preadaptations for nest building. First, these feeding techniques led to the ability to monopolize food. They presented a tool to compete successfully with other frugivorous animals. Second, nests allowed apes, despite their increased body size, to sleep in places inaccessible to ground predators. Third, nest building had implications for facilitating the evolution of cognitive abilities within hominoids.

Nests were not only the first products of exploratory behavior with twigs and sticks, but also the foundation for all future tool use ability. Nest building may have promoted higher levels of tool use that helped to open up new food resources. Nests may thus have been the cradle for higher cognition, manipulation and technological skills, culminating in human abilities for environmental alteration. Thus, the nest served as the spring board for the great leap forward in hominid evolution.

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