

**NESTS AND NEST GROUPS
IN
WILD BONOBOS (*PAN PANISCUS*):
ECOLOGICAL AND BEHAVIOURAL
CORRELATES**

DISSERTATION

DER FAKULTÄT FÜR BIOLOGIE
DER LUDWIG-MAXIMILIANS-UNIVERSITÄT MÜNCHEN

VORGELEGT VON

BARBARA FRUTH

MÜNCHEN, JULI 1995

Berichte aus der Biologie

Barbara Fruth

Nests and Nest Groups in Wild Bonobos (*Pan paniscus*): Ecological and Behavioural Correlates

1. Gutachter: Prof. Dr. Gerhard Neuweiler

2. Gutachter: Prof. Dr. Irenäus Eibl-Eibesfeldt

Tag der Einreichung der Dissertation: 28. Juli 1995

Tag der mündlichen Prüfung: 25. August 1995

Verlag Shaker
Aachen 1995

Die Deutsche Bibliothek - CIP-Einheitsaufnahme

Fruth, Barbara:

Nests and Nest Groups in Wild Bonobos (*Pan paniscus*): Ecological and Behavioural Correlates / Barbara Fruth. - Als Ms. gedr. -

Aachen : Shaker, 1995

(Berichte aus der Biologie)

Zugl.: München, Univ., Diss., 1995

ISBN 3-8265-1022-4

Copyright Verlag Shaker 1995

Alle Rechte, auch das des auszugsweisen Nachdruckes, der auszugsweisen oder vollständigen Wiedergabe, der Speicherung in Datenverarbeitungsanlagen und der Übersetzung, vorbehalten.

Als Manuskript gedruckt. Printed in Germany.

ISBN 3-8265-1022-4

ISSN 0945-0688

Shaker Verlag GmbH, Hubertusstr. 40, 52064 Aachen

Telefon: 0241 / 406351 - Telefax: 0241 / 406354

CONTENTS

GLOSSARY & DEFINITIONS	I
ZUSAMMENFASSUNG	I
SUMMARY	VI

I. INTRODUCTION

A. NESTS	1
B. NEST BUILDING IN PRIMATES	1
C. NESTBUILDING IN THE GREAT APES	7
D. ORIGIN OF THIS STUDY	22
E. OUTLINE OF THE THESIS	24

II. MATERIAL AND METHODS

<u>A. STUDY AREA: THE LOMAKO FOREST</u>	27
1. GEOGRAPHY	27
2. CLIMATE	28
3. VEGETATION	29
4. FAUNA	30
5. STUDY SITE	31
5.1. History	31
5.2. Location and Infrastructure	32
<u>B. STUDY SUBJECTS & SAMPLING METHODS</u>	33
1. DISTRIBUTION, SOCIAL ORGANISATION, AND SOCIAL STRUCTURE OF THE BONOBOS	33
2. DISCOVERY AND FIELD RESEARCH	35
3. BONOBOS OF LOMAKO	35
4. HABITUATION	37
5. TIME IN THE FIELD	38
6. BEHAVIOURAL DATA & MEASUREMENTS	39
<u>C. DATA COLLECTION</u>	40
1. THE EYENGO COMMUNITY	40
1.1. Demography	40
1.2. Party Size	41
1.3. Party Composition	41
1.4. Travel Patterns	41

CONTENTS

1.5. Home Range	42
2. NEST TREES	43
2.1. Height	43
2.2. Stem Diameter	44
2.3. Height of Crowns	44
2.4. Species	44
2.5. Leaf Size	45
2.6. Selectivity	45
3. NESTS	48
3.1. Physical Correlates	48
3.1.1. Type of construction	48
3.1.2. Height	49
3.1.3. Position within crown	49
3.1.4. Cover	49
3.1.5. Architectural details	49
3.2. Behavioural Correlates	51
3.2.1. Time of construction	51
3.2.2. Duration of construction and use	51
3.2.3. Activities in day nests	52
4. NEST GROUPS	52
4.1. Distribution and Size	53
4.1.1. Distribution within the home range	53
4.1.2. Group size	53
4.2. Physical Correlates	55
4.2.1. Horizontal dispersion	57
4.2.2. Vertical dispersion	57
4.2.3. Distances between nests	57
4.2.4. Nearest neighbour distances	58
4.3. Behavioural Correlates	58
4.3.1. Time of construction	58
4.3.2. Duration of construction	58
4.3.3. Initiator of construction	59
4.3.4. Nearest neighbour and sex of the nest owner	59
<u>D. DATA ANALYSES</u>	59

CONTENTS

III. RESULTS

1. THE EYENGO COMMUNITY	61
1.1. Demography	61
1.2. Party Size	62
1.2.1. Seasonal distribution	63
1.2.2. Diurnal distribution	64
1.3. Party Composition	66
1.3.1. Monthly distribution	67
1.3.2. Diurnal distribution	68
1.4. Travel Patterns	69
1.5. Home Range	72
2. NEST TREES: AVAILABILITY & CHOICE	74
2.1. Height	74
2.2. Stem Diameter	75
2.3. Height of Crowns	76
2.4. Species	77
2.5. Leaf size	79
3. NESTS	81
3.1. Physical Correlates	81
3.1.1. Type of construction	82
3.1.2. Height	84
3.1.3. Position within the crown	85
3.1.4. Cover	86
3.1.5. Architectural details	86
3.2. Behavioural Correlates	88
3.2.1. Time of construction	90
3.2.2. Duration of construction and time of use	91
3.2.3. Sex differences	92
3.2.3.1. Night nests	93
3.2.3.2. Day nests	96
3.2.4. Age differences	97
3.2.4.1. Duration of construction and use	98
3.2.4.2. Number of individuals	100
3.2.4.3. Activities	101

CONTENTS

4. NEST GROUPS	103
4.1. Distribution and Size	104
4.1.1. Distribution within the home range	106
4.1.2. Group size	108
4.1.2.1. Group size and location in the home range	108
4.1.2.2. Group size over seasons	110
4.1.2.3. Group size by day and night	111
4.1.2.4. Intensity of group fusion	112
4.2. Physical Correlates	113
4.2.1. Horizontal dispersion	113
4.2.2. Vertical dispersion	113
4.2.3. Distance between nests	115
4.2.3.1. Mean internest distances and group size	115
4.2.3.2. Mean internest distances and tree density	116
4.2.4. Nearest neighbour distances	117
4.3. Behavioural Correlates	119
4.3.1. Time of construction	119
4.3.2. Duration of construction	120
4.3.3. Initiator of nest construction	121
4.3.4. Nearest neighbour and sex of the nest owner	121

IV. DISCUSSION

1. THE EYENGO COMMUNITY	123
1.1. Demography	123
1.2. Party Size	128
1.3. Party Composition	131
1.4. Travel Patterns	132
1.5. Home Range	133
2. NEST TREES: AVAILABILITY & CHOICE	135
2.1. & 2.2. Height and Stem Diameter	135
2.3. Height of Crown	135
2.4. Species	137
2.5. Leaf Size	138
3. NESTS	140
3.1. Physical Correlates	140
3.1.1. Type of construction	140
3.1.2. Height	142

CONTENTS

3.1.3. Position within the crown	144
3.1.4. Cover	144
3.1.5. Architectural details	145
3.2. Behavioural Correlates	146
3.2.1. Duration of construction and time of use	146
3.2.3. Sex differences	147
3.2.4. Age differences	148
4. NEST GROUPS	153
4.1. Distribution and Size	154
4.2. Physical Correlates	159
4.2.1. & 4.2.2. Horizontal and vertical dispersion	159
4.2.3. Distance between nests	160
4.2.4. Nearest neighbour distances	161
4.3. Behavioural Correlates	162
4.3.1. & 4.3.2. Time and duration of construction	162
4.3.3. Initiator of construction	163
4.3.4. Nearest neighbour and sex of the nest-owner	164
V. ACKNOWLEDGEMENTS	168
VI. REFERENCES	171
VII. APPENDIX: TREE SPECIES	183
VIII. CURRICULUM VITAE	185

GLOSSARY & DEFINITIONS

accumulation: nests found independent of direct observation, at one nest site.

community: unit of bonobos who share a common range, maintain affiliative relationships, and defend it against others of the same species.

group size: number of nests per group

home range: Area that members of one community cover in all their activities from year-to-year.

M: median

nest: construction of branches, twigs and leaves manipulated (bent, broken, transferred) in order to establish a resting site in a tree. Nest materials are typically oriented and arranged from the periphery to the centre toward the nest builder.

nest group: nests of 2 or more individuals built simultaneously (during same session) in close proximity. Nests in close proximity would be visible to the observer if the trees were leafless.

nest site: area of the home range in which a nest group is sited. It includes e.g. type of habitat, topography, and features like proximity to water.

n.s.: not significant ($p > 0.05$)

party: sub-grouping of individuals of one community seen together at a specific time and place.

re-use: Nests built on previous day or earlier that are re-occupied by maker or another. This term excludes nest constructed by an individual, left for defecation and re-occupied afterwards.

SD: standard deviation

socionomic sex ratio: sum adult and adolescent females divided by sum of adult and adolescent individuals in a community or party.

ZUSAMMENFASSUNG

Bonobos (*Pan paniscus*) bauen, wie die anderen Menschenaffen auch, Nester. Diese dienen in erster Linie der Ruhe und werden für jede Nacht, bzw. jede Nutzung, neu angefertigt. Weibchen bauen für sich und ihren abhängigen Nachwuchs ein gemeinsames Nest, ansonsten baut und beansprucht jedes Individuum sein eigenes. Bei Bonobos ist Nestbau ein soziales Ereignis. Zahlreiche Individuen einer Kommune finden sich am Abend zusammen, gehen in benachbarte Bäume und bauen aus Ästen und Zweigen Plattformen. Das Ergebnis ist eine Nestgruppe. Die vorliegende Arbeit entwickelte sich aus der Frage, ob die Anordnung der Nester innerhalb einer Gruppe bestimmten Mustern folgt und, wenn ja, ob sie einen Spiegel der Sozialstruktur darstellt.

Zur Beantwortung dieser Frage wurden ökologische und ethologische Aspekte von Einzelnestern und Nestgruppen freilebender Bonobos untersucht. Die Datenaufnahme erfolgte über 22 Monate zwischen 1990 und 1994 in Lomako, Provinz Equateur, Republik Zaïre. Voraussetzung für diese Untersuchung war Habituation und Identifikation einer Bonobokommune (Eyengo Kommune). Die Kommune bestand aus 34 Mitgliedern, einschließlich des abhängigen Nachwuchses. Etwa zwei Drittel der erwachsenen Kommunenmitglieder waren Weibchen. Nie wurden alle 34 Individuen am gleichen Ort gesehen, sondern auf kleinere Gruppen (*parties*) verteilt, deren Größe und Zusammensetzung variierte. Im Mittel bildeten sechs Individuen eine solche Gruppe, ein Durchschnittswert, der sich sowohl von Monat zu Monat als auch während des Tages änderte. Eine Gruppe war morgens groß, spaltete sich während des Tages auf und fand sich gegen Abend wieder zusammen. Meist waren Individuen beider Geschlechter vertreten, ein Drittel aller Gruppen waren entweder Männchen oder Weibchen. Männchen wurden häufiger allein angetroffen als Weibchen. Die Tagesroute einer Gruppe betrug ca. 3 km. Die Individuen

foragierten, wanderten und schliefen in einem Aktionsgebiet (*home-range*) von 15 km². Zwei Drittel des Gebiets waren von Primärwald bedeckt, ein Drittel war Sumpf.

Die Wahl der Nestbäume erfolgte selektiv. Die meisten Bäume, die zum Nestbau verwendet wurden, waren ca. 20 m hoch und hatten Stammdurchmesser von ca. 15 cm Dicke. Die niedrigsten Äste waren ungefähr 10 m über dem Erdboden. Von 54 an Nestplätzen vorkommenden Baumarten, wurden lediglich 26 zum Bau von Nachtnestern verwendet. Zehn davon fanden sich in 85% aller Nester. Bäume mit kleinen Blättern wurden häufiger gewählt als erwartet.

Tag und Nachtnester zeigten markante Unterschiede. *Tagnester* waren höher als Nachtnester. Sie wurden schneller fertiggestellt und kürzer genutzt. In den meisten Fällen (96%) wurde nur Material eines Baumes für den Bau eines Nestes genutzt. *Tagnester* dienten nicht nur der Ruhe sondern auch dem Essen, der sozialen Fellpflege, dem Spiel, dem Sex und konnten die Privatsphäre eines Individuums markieren. Manchmal teilten sich zwei oder mehr erwachsene Individuen eine Nest. *Nachtnester* hatten eine komplexere Struktur. 35% aller Nester kombinierten Material mehrerer Bäume. Wenn Nester auf ihre Einzelbestandteile untersucht wurden zeigte sich, daß sie in der Regel auf drei tragenden Seitenästen gebaut wurden und zahlreiche gebrochene und gebogene Äste und Zweige einbezogen. Stets wurden gänzlich vom Baum gelöste Zweige als Polstermaterial verwendet. Die meisten Nachtnester befanden sich in der mittleren Baumschicht des Waldes (*canopy*). Mehr als die Hälfte von ihnen war zum Himmel zu offen, ein Prozentsatz, der während der Regenzeit anstieg.

Weitere Unterschiede im Nestbau waren *geschlechtsabhängig*. Weibchen bauten höher als Männchen, verwendeten mehr Zeit auf die Konstruktion ihrer Nester und bauten häufiger *Tagnester* als Männchen. Meist waren es ihre *Tagnester*, die in sozialem Kontext genutzt wurden. Bei der Analyse verschiedener *Altersklassen* wurde deutlich, daß, unabhängig

vom Geschlecht, jüngere Individuen länger zur Vervollständigung eines Tagnestes brauchten und dieses in der Regel deutlich kürzer nutzten als Erwachsene.

Nachtnestgruppen wurden lediglich im Primärwald gebaut und traten an manchen Orten gehäuft auf. Im Mittel bestand eine Nestgruppe aus zehn Nestern und war damit stets größer als eine Gruppe während des Tages. Sowohl die Nestgruppengröße als auch die Differenz zwischen Tag- und Nachtgruppengröße (*Intensity of fusion*) waren von Monat zu Monat verschieden, korrelierten aber nicht mit Saisonalität. Es bestand kein signifikanter Zusammenhang zwischen Nestgruppengröße und dem Ort innerhalb des Aktionsgebietes, obwohl große Gruppen (20 Nester oder mehr) näher am Zentrum des Gebietes waren als an dessen Peripherie. Je größer die Anzahl der Nester pro Gruppe, desto größer war die Ausdehnung der Gruppe sowohl horizontal als auch vertikal. Je größer die Dichte geeigneter Nestbäume, desto kleiner war der mittlere Nestabstand. Er blieb unbeeinflusst von der Anzahl der Nester pro Gruppe. Die Distanz nächst benachbarter Nester betrug im Mittel 8 m und korrelierte negativ mit der Anzahl der Nester pro Gruppe. Der Bau von Nestgruppen begann je nach Wetter entweder am Nachmittag oder am Abend. Wenn es regnete wurde früher mit dem Nestbau begonnen und die Zeit, die zwischen dem Bau eines jeden Nestes der Gruppe verstrich, war größer als an trockenen Tagen. Weibchen initiierten in der Regel den Bau einer Nachtnestgruppe. Sie bauten ihre Nester am nächsten zu denen anderer Weibchen, gefolgt von Männchen, die etwas weiter weg bauten. Am größten war der Abstand zwischen den Nestern von Männchen.

All die gezeigten Differenzen bezüglich der Höhe, Distanzen und nächsten Nachbarn von Nestern sowie die geschlechtsspezifischen Gepflogenheiten in der Nestplatzwahl und beim Nestbau weisen darauf hin, daß Nestgruppenformation kein Ergebnis des Zufalls ist, sondern Mustern folgt, die Beziehungen innerhalb der Bonobosozietät widerspiegeln: Weibchen zeigen ein hohes Maß an Assoziation, koalieren miteinander und

dominieren die Gesellschaft. Erst der Vergleich zu Nestgruppen anderer Menschenaffen kann jedoch Aufschluß darüber geben, ob die gefundenen Muster tatsächlich die artspezifische Gesellschaftsformen widerspiegeln oder einem übergeordneten Muster folgen.

SUMMARY

As do the other great apes bonobos (*Pan paniscus*) build nests. These are used mostly for rest and are freshly made each night or for each other use. Females construct nests for themselves and for their dependent offspring, but otherwise each individual builds and uses its own nest. In bonobos, nest building is a social event. Many members of a community converge at dusk, climb neighbouring trees and undertake nest construction, thus forming a nest group. The present study is based on the question of whether or not nests within a group are arranged in specific patterns and if so, whether or not these reflect the social structure of the society.

Aspects of both the ecology and ethology of nest building in wild bonobos were studied during 22 months over 4 years in the Lomako forest, Republic of Zaïre. One bonobo community (**Eyengo-community**) was habituated to human observers. It had 34 members, including dependent offspring, all of whom were identified. The socionomic sex ratio was skewed toward females, with about twice as many females as males (SSR = 0.67). All members of the Eyengo community were never seen together, but instead ranged in parties that changed regularly in number and composition. *Party size* on average was 6 weaned individuals. It fluctuated from month-to-month and during the day. Parties were large in the morning, split up later, and increased again in the late afternoon. Most parties were made up of both sexes, but nearly a third of all parties contained one sex only. Males were seen alone more often than females. The typical *daily range* of a party was about 3 km. They foraged, travelled, and slept within a *home range* of 15 km², comprising about 2/3 primary forest and 1/3 swamp.

Bonobos were highly selective in their choice of **nest trees**: Most nested-in trees were of 20 m height, had about 15 cm stem diameter, and their lowest branches were about 10 m above the ground. Of 54 species of

trees occurring at nest sites, only 26 were used for overnight nest construction. Ten of these species made up for 85% of all nests. Small-leaved species were chosen more often than expected by chance.

Day and night nests differed significantly. *Day nests* were higher than night nests, needed less time for construction, were used more briefly than night nests and almost always (96%) involved only a single tree. They were used not only for rest but also for other activities such as eat, groom, play, sex and as zone of privacy. Day nests were sometimes shared by two or more mature individuals. *Night nests* were more sophisticated in structure: 35% incorporated material from more than 1 tree. Architectural deconstruction revealed that nests were built of up to 3 supporting branches, included many bent and broken twigs, and always had some detached twigs for lining. Most night nests were made in the middle layer of the forest, and, referring to the height of the crown of a tree, in its middle part. More than half the night nests were not overhung by vegetation, and this proportion increased during the rainy season.

The data revealed several *sex differences*. Females built nests higher, needed longer to construct them, and built day nests more often. In most cases, it was females' nests that were used for social purposes. When *age classes* were compared it was evident that, regardless of sex, younger individuals needed longer to make nests, and used them much shorter than did adults.

Night nest groups were found only in primary forest and were clumped at certain spots. The average number of nests per group was close to 9, and thus was always larger than travel groups by day. Both group size and the intensity of group fusion changed from month-to-month but did not correlate with seasonality. No correlation was found between nest group size and position within the home range, but largest groups (of 20 or more nests) tended to be close to the centre. Horizontal and vertical dispersion of groups increased with group size. Mean inter-nest distances

decreased with increasing density of suitable nesting trees but did not change with group size. Nearest neighbour distances between nests averaged 8 m, and this distance correlated negatively with group size. Two peaks of onset of construction were seen: One in the afternoon, one in the evening. Onset of construction was earlier on rainy days, and the time from onset-to-onset across all nests in a group was less synchronous. Females usually built the first nest of a group. They nested closest to each other, followed by males nesting less close to females, and males nesting least close to other males of the same night party.

Differences in height, distances, or nearest neighbours of nests, as well as sex differences in nest site choice and construction, suggest that nest group formation in bonobos is not random, but follows patterns that reflect individual relationships within bonobo society: Females show a high degree of association, form coalitions, and dominate the society. Only by comparison to nest groups of the other great apes, will we be able to ascertain if the patterns found here are species-specific, rather than a result of environmental determinants or influencing factors.

I. INTRODUCTION

A. NESTS

The term *nest* immediately reminds us of birds with their elaborate constructions: woven, excavated, chesseled, or masonry, some with elaborate decoration. We think of their mating displays, brooding, and rearing of youngsters. For these nests, HEDIGER (1977) gave the following definition: "A *nest* as a rather loose construction of plant material, as it is used by most birds and some of the lowest primates, never serves as a goal of flight, very rarely as sleeping place but mainly as a support for the offspring." (p. 170). Also, we think of the collected contents of dry and snug refuges of many mammals, also termed nests. These are often built in tree hollows, or underneath the earth. HEDIGER (1977) clearly separated these from the "bird, or leaf nest" and defined them as the most important fix-point within an animal's territory, as a "*home*": According to him, this is a " ... place of maximal security, goal of flight, shelter ... sleeping place and sometimes breeding place." (p.174).

B. NEST BUILDING IN PRIMATES

In primates, again we have to deal with the term nest. There are 4 great branches in the radiation of the Order *Primates*: At the base of the primate phylogenetic tree are the prosimians (*Prosimii*: *Daubentonioidea*, *Lemuroidea*), followed by the New World monkeys (*Ceboidea*), the Old World monkeys (*Cercopithecoidea*) and the apes (*Hominoidea*). Nest building only occurs in 2 branches, once in the prosimians, and again in the great apes. Since prosimians diverged in the early Eocene, nest-building

was absent in monkeys and lesser apes, only to emerge again in the great apes, so it must have evolved twice in the Order *Primates*.

Most *prosimians* are nocturnal primates that typically use shelters in dense vegetation or tree hollows to hide during the day. Some of them construct leaf-nests either within or outwith tree hollows, which are used as breeding nests and as fix-points in the home range. MARTIN (1975) stated that nest construction in prosimians coincides with the habit of mouth carriage of offspring and with predator avoidance. Infants who cannot actively grip their mothers' fur are obliged to be left behind while the mother forages. To camouflage efficiently themselves and their offspring, shelters made of vegetation or tree hollows are needed. Another connection which can be made is litter size. Multiple offspring are harder to carry around than singletons even if they could hold on to the carrier's fur.

Table 1 shows the occurrence of nest building in the primate clade, along with litter size and method of transportation: In Madagascar, the aye-aye (*Daubentonia madagascariensis*, the only living member of the monotypic *Daubentoniidae*) regularly builds nests made of leaves and grass, about 60 cm in diameter, mostly in hollow tree-trunks. They have only one offspring per litter. Among the lemurs (*Lemuroidea*), mouse and dwarf lemur (*Microcebus* spp., *Cheirogaleus* spp.), and the variegated lemur (*Varecia variegata*) use nests. Short before birth, the *Varecia* female buffers her nest, made of leaves, with her fur plucked from her flanks. The youngsters are carried in the mouth. Indris (*Indriidae*) do not build nests. The baby usually hangs ventrally sideways in the mother's fur during transport (FIEDLER *et al.* 1968, MARTIN 1973). Within the lorises, nests occur in neither the African nor the Asian lorises (*Lorisinae*). They usually have one offspring that actively grips the fur of the mother during transport. They are also "parked" (but not in tree hollows or nests) somewhere in thick vegetation.

	Infra - order	Super-family	Family	Sub-family	Litter Size	Transport of Litter	Nests	Species
Madagascar	Lemuriformes	Daubentoniidae	Daubentoniidae		1	mouth	+	aye-aye
		Lemuroidea	Lemuridae	Cheirogaleinae	1-4	mouth	+	mouse lemur dwarf lemur
				Lemurinae	1-4	mouth	+	variegated lemur
				Lepilemurinae	1	fur	-	
Africa	Loriformes	Lorisidae	Galaginae	1-3	mouth	+	bush babies (3 species)	
			Lorisinae	1	fur	-		
Asia	Tarsiiformes		Tarsiidae		1	fur	-	

Table 1: Occurrence of nest building in the *Prosimii*. + = present, - = absent. For scientific name of species see text.

In contrast, within the subfamily *Galaginae*, which occurs only in Africa, 3 species of bushbabies (*Galago demidovii*, *G. senegalensis*, *G. crassicaudatus*) build nests. (FIEDLER *et al.* 1968, CHARLES-DOMINIQUE 1977, BEARDER 1987). *Galago* spp. females and juveniles congregate at nest sites, while adult males sleep alone. Nests are made of leaves, and are either spherical or flat. They are used when the weather is cold or even more often when there are dependent offspring (VINCENT 1968, CHARLES-DOMINIQUE 1977). Tarsiers (*Tarsiidae*), again from the Asian continent, do

not use nests. Prosimian nests are important because the dependent offspring cannot grip the fur of the mother during transportation, so infants are carried in the caretaker's mouth. But this is incompatible with eating, so nests or tree hollows serve as "parking lots" where parents cache their offspring during foraging (BEARDER 1987). Detailed field research on nest building is underway in Madagascar (KAPPELER *pers. comm.*, RADESPIEL *pers. comm.*) and should provide new information on the nest-building of at least the Lemuridae.

In contrast to the prosimians, New and Old World monkeys (*Ceboidea*, *Cercopithecoidea*) are almost all diurnal and sleep mostly at night. They choose sleeping sites above the ground, usually in vegetation (e.g. *Cercocebus* spp., *Cercopithecus* spp., *Macaca* spp., *Colobus* spp.), or on promontories or cliff-faces (e.g. *Papio anubis*, KUMMER 1968), or in caves (*Trachypithecus f. delacouri*, ADLER 1991). In contrast to the nest-building prosimians, infants of these genera actively grip the fur of their mothers' during transportation or sleep, so they do not fall. None of the 138 species of the New and Old world monkeys is known to build a nest or a nest-like construction.

Amongst the *Hominoidea*, gibbons (*Hylobates* spp.) and siamangs (*Symphalangus syndactylus*) do not build nests. All the great apes, however, orang utans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), do so. Members of both sexes and all ages (except dependent infants) build nests every night and sometimes during the day for the purpose of resting. These nests have nothing to do with the breeding nests of prosimians, but instead are "only sleeping nests" (HEDIGER 1977). This kind of "nest building" is therefore called "bed-building" by some investigators (ITANI 1979, HIRAIWA-HASEGAWA 1989). Others term it "sleeping platform" (McGrew 1992). The term nest is somewhat confusing since ape nests neither share the often artistic structure of birds' nests, nor do they correspond in functional

respects. My continuing to use the term nest to refer to the sleeping structures of apes is in deference to tradition or precedent.

The technique of nest construction depends on the site and on the available materials. Orang utans, chimpanzees, and bonobos start their arboreal constructions by preparing a foundation that uses solid sidebranches or forks, bending, breaking and inter-weaving sidebranches crossways. They complete the structure by bending most of the smaller twigs over the rim, resulting in a circular disc, which is roughly radially symmetrical in the horizontal plane and bilaterally symmetrical in the vertical plane. Detached leafy twigs are added for lining (DAVENPORT 1967, GOODALL 1968, HORN 1980, MCGREW 1992).

Gorillas typically use similar techniques to build nests on the ground. They gather different, mostly herbaceous material and pull, bend and break saplings to arrange these around and under their bodies. Mostly they concentrate on the rim rather than on a foundation (SCHALLER 1963).

Early descriptions of apes' nests date to the 18th century and were based on various anthropomorphic interpretations of function and use, such as chimpanzee fathers building huts at night to provide shelter for their family (e.g. MATTHEWS 1788, cited in YERKES & YERKES 1929). Even 100 years ago there were doubts about the existence of nests. GARNER (1896), who went to Gabon in 1882 wrote: "As to his [chimpanzee's] building huts or nests in trees or elsewhere, I am not prepared to believe that he ever does so. I hunted in vain, for months, and made diligent inquiry in several tribes, but failed to find a specimen of any kind of shelter built by an ape ..." (p. 49). Most early studies, however, gave the form and use of these constructions for orang utans, gorillas and chimpanzees in useful descriptions (HORNADAY 1879; SAVAGE & WYMAN 1843). In 1929 the YERKES wrote: "No phase of the mode of life [of the chimpanzee] and no behaviour pattern has attracted more attention or produced more useful literature than that of nest construction." (p.220)

Nevertheless, the scientific literature mostly provided descriptions based on indirect evidence, that is, on nests as the products (artefacts) of behaviour, rather than on the behaviour itself. Only in the 1960s, when GOODALL (1962, 1968) began her studies on wild chimpanzees at Gombe, Tanzania, did the first detailed behavioural descriptions appear. Supplementary, captive studies tackled the question of whether or not these behavioural patterns were innate or learned (BERNSTEIN 1962, 1967; LETHMATE 1977). According to BERNSTEIN (1967), captive-born chimpanzees failed to construct nests even when suitable raw materials were provided and when nest-making cage-mates were present. Only wild-born chimpanzees were able to make nests and actually they did so whenever material was available. BERNSTEIN (1967) suggested that nest building was learned by the age of 2, but that the disposition to manipulate objects was innate. Probably it is not the difference of wild versus captive-born that determines whether or not a young ape will voluntarily build nests, but its exposure to nest building individuals, either the mother or cage-mates.

Nest building is one of the few behavioural traits shared by all members of the great apes. It reflects the general ability for environmental problem solving (MCGREW 1992). Whether or not nest building should be considered as tool use is much disputed (GOODALL 1968, ALCOCK 1972, BECK 1980, GALDIKAS 1982), however, it is probably the most pervasive form of material skill in apes.

C. NEST BUILDING IN THE GREAT APES

Tables 2 - 5 summarise the most detailed field observations of nest building in the 4 species of great apes done in recent decades.

For *orang utans*, studies on nests were done on both subspecies, the Bornean and the Sumatran orang utan (*Pongo p. pygmaeus* and *Pongo p. abelii*). Orang utans do not live in social groups or communities but are largely solitary. The ranges of solitary males comprise several female ranges which may overlap. Males join females only for mating and sometimes during periods of food abundance, when individuals of each sex may gather at feeding sites. (MACKINNON 1974, RIJKSEN 1978, GALDIKAS 1979, VAN SCHAİK & VAN HOOFF *in press*). The most comprehensive studies contributing to the knowledge of orang utan nest building are summarised in Table 2, which includes both direct observations and surveys of habituated and non-habituated subjects.

Ecology & form: With few exceptions restricted to adult males, who stayed overnight in a fork of a tree without a *nest*, nest building occurs nightly (DAVENPORT 1967, RODMAN 1979). Orang utans are reported to use some types of their forest more than others. Primary forest is generally considered as the main *habitat* for nest construction (SCHALLER 1961), in which nests occur in clumps (MACKINNON 1974). Measurements were published only for nests as artefacts divorced from the behaviour of making them, and thus, no analysis distinguishing day and night nests is available. Nests are made in trees, at estimated *heights* ranging from 4 - 40 m, with most nests built between 15 and 30 m (SCHALLER 1961, YOSHIBA 1964, MACKINNON 1974). Only GALDIKAS (1975) mentions 4 rudimentary ground nests, not knowing whether they were used by day or at night. Although orang utans are said to be selective in their *choice of materials*, using soft leaves and specific *tree species*, no investigations on availability and

choice have been done (MACKINNON 1974). *Feeding trees* are said to be used for day and night nests. Depending on the age and sex of the nest maker, Bornean orang utans are reported to nest close by or within feeding trees (SUGARDJITO 1983). Sumatra orang utans, in contrast, are said to avoid feeding trees for night nest construction (RIJKSEN 1978, VAN SCHAIK & VAN HOOFF *in press*). As to the *type of construction*, most nests involve only single trees, and parts of a second tree are integrated only if branches overlap naturally.

Behaviour: Detailed descriptions of the behaviour of nest building in the wild are scarce, but as summed up in the various anecdotes, typical nest building emerges as follows: In *ontogeny*, the first signs of nest construction begin during the day at the age of 2 yr. First night nest construction is seen in "juveniles" of 3 years of age (MACKINNON 1974). Weaned juveniles may try to join the mother in the nest (HORR 1972). **Duration of construction:** A nest is built before dusk in 2 - 7 min on average, and is left the next morning (DAVENPORT 1967, MACKINNON 1974). Females, who occupy small ranges, often use the same nest site to build nests on consecutive nights. On these occasions, nests of the previous night are sometimes *re-used* (MACKINNON 1974, RIJKSEN 1978). Females share their nest with the dependent offspring, and sometimes are accompanied by an elder offspring who builds its nest close by. Male construction of lower nests than females is reported as a *sex difference* by SUGARDJITO (1983). Given the species' prominent sexual dimorphism, this is not surprising. The lower the branches of a given tree, the stronger they are, and males as heavy as 90 kg need solid boughs for support. According to RODMAN (1979), females construct nests more often than males, who sometimes sleep without making them. HARRISSON (1969) found that one female usually built earlier and used her nests longer than did one male, but her subjects were 2 released juveniles of different ages, so the data were few. **Activities:** Day nests are common. As a specific habit, orang utans sometimes build over these nests raincovers that are termed "roofs"

or "umbrellas". Here, detached leafy twigs are piled over horizontal branches above the nest. These overhead devices also were seen to be used as parasols, for camouflage and in play (DAVENPORT 1967, MACKINNON 1974, GALDIKAS 1975, RIJKSEN 1978). Nests are also used to rest, eat, groom, take refuge, or hide.

Nest groups are not explicitly mentioned, although some studies referred to accumulations of more than one nest (YOSHIBA 1964, HARRISSON 1969, RIJKSEN 1978, MACKINNON 1974). **Group size:** Whether or not these accumulations were caused by one or more individuals on consecutive nights or by several individuals over one night remained unclear (for a definition of nest accumulation versus nest group see p. 1). GALDIKAS (1975) mentioned 5 individuals building a nest group overnight once and splitting up the next morning. Investigations on the distances between nests are apparently not done and thus nothing more is known on *nearest neighbour* distances except that sometimes, during consortship, males nest close to females, often in the same tree beneath her.

REFERENCE	Borneo (<i>Pongo pygmaeus pygmaeus</i>)						Sumatra (<i>Pongo pygmaeus abelii</i>)					
	Schaller 1961	Yoshiha 1964	Davenport 1967	Rodman 1979	Gaidikas 1975, 1982	MackKinnon 1974	MackKinnon 1974	Rijkse 1978	MackKinnon 1974	Rijkse 1978	Sugardjito 1983	
Study Site	Sarawak Indonesia	North-East Sabah Malaysia	Sepilok Sabah Malaysia	East Kalimantan Indonesia	Tanjung Puting-NP Kalimantan Indonesia	Ulu Segama Sabah Malaysia	Ranun River N Sumatra Indonesia	Ketambe N Sumatra Indonesia	Ranun River N Sumatra Indonesia	Ketambe N Sumatra Indonesia	Ketambe N Sumatra Indonesia	
Country	Indonesia	Malaysia	Malaysia	Indonesia	Indonesia	Malaysia	Indonesia	Indonesia	Indonesia	Indonesia	Indonesia	
Type of Habitat	PF	PF	PF	PF	PF	PF	PF	PF	PF	PF	PF	
Years	1960-1961	1963	1964	1970-1971	1971-1980	1968-1970	1971	1971-74	1971-74	1971-74	1980-82	
Duration	3	2	7	15	108	18	8	38	8	38	6	
Study's goal	survey	survey	behaviour	ecology behaviour	behaviour	ecology ethology	ecology behaviour	behaviour	ecology behaviour	behaviour	ecology behaviour	
Direct Observation	+	-	+	+	+	+	+	+	+	+	+	
Indirect Observation	+	+	+	-	-	+	+	+	+	+	+	
ECOLOGICAL & FORM												
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/NN	DN/NN	DN/NN	DN/NN	DN/NN	
Sex Differences	-	-	-	+	-	-	-	-	-	-	-	
Type of Construction	-	?	?	-	-	?	?	?	?	?	?	
BEHAVIOUR												
Info. on Ontogeny	-	-	-	-	+	+	-	-	-	-	-	
Duration of Construction	-	-	6.5 min	-	< 5 min	2 - 3 min	-	-	-	-	-	
Re-use	-	-	50% of DN	-	-	8 x	-	-	-	yes	-	
Activities within Nest	R/I	-	R/E	-	R	R/P/G	R/P/G	R/P/G	R/P/G	R/P/E	-	
GROUPS												
Nest Groups	-	?	-	?	?	?	-	-	-	?	-	
Group Size	-	3	-	1-5	≤ 5	1-3	-	-	-	1-2	-	
Nearest Neighbour	-	-	-	-	-	-	-	-	-	-	-	

Table 2

For *gorillas*, studies of nest building have been done on all 3 subspecies. In the 1950s and 1960s, these were mostly of mountain gorillas (*Gorilla g. beringei*) (DONISTHORPE 1958, KAWAI & MIZUHARA 1959, SCHALLER 1963; FOSSEY 1974), then beginning in the 1970s eastern lowland gorillas (*Gorilla g. graueri*) (CASIMIR 1975, 1979, YAMAGIWA 1983, MWANZA *et al.* 1992), and finally, except for a pioneering study in the late 1960s (JONES & SABATER PI 1971), in the 1980s the western lowland gorillas (*Gorilla g. gorilla*) (TUTIN & FERNANDEZ 1983, 1984; GROVES & SABATER PI 1985, WILLIAMSON 1988, TUTIN *et al.* 1995). These studies are summarised in Table 3.

Gorillas usually live in harem groups dominated and led by a single silverback male. He indicates not only the direction of travel but determines the night nest site and initiates nest construction (SCHALLER 1963, FOSSEY 1974). Despite many studies in the Virunga Volcanoes using direct observation, most analyses refer to nests only as artefacts.

Ecology & Form: *Nests* are used as indicators of presence, density, habitat use, home range, and core area. In contrast to the other great apes, gorillas sometimes recline on the ground without nests, but they usually build nests of mostly herbaceous material. For all 3 subspecies, most nests are below 10 m in *height* (cf. Table 3.). In most studies gorillas are said to use their habitat opportunistically. Reports on selectivity in the *choice* of nesting site are exceptional, and are restricted to the western lowland gorilla who nest in areas of secondary growth rather than in primary forest (MWANZA *et al.* 1992, TUTIN *et al.* 1995). TUTIN *et al.* 1995 reported the maximal *number of species used* for any gorilla site: At Lopé, Gabon, they identified 98 different plant and 85 different woody species used for nest construction. Avoidance of *food plants* for nest construction is reported from mountain gorillas (FOSSEY & HARCOURT 1977, WINA 1989), but almost all other references (cf. Table 2) mention the use of food material for day and night nests. *Types of construction* of both ground

and tree nests are described, distinguishing several types according to quantity and to quality of the material involved. They include: rudimentary depressions on the forest floor but without plant material, shifted turf or soil, crushed plants on the ground, and elaborate tree nests. The proportion of tree nests varies considerably depending on habitat and season: Western lowland gorillas more often use trees for nest construction than do eastern or mountain gorillas, and in the rainy season more nests are built in trees than in the dry season (REMIS 1993, TUTIN *et al.* 1995). When trees are involved, the most making up a nest is 3 (YAMAGIWA *pers comm.*, TUTIN *pers. comm.*).

Behaviour: Ontogeny: First attempts of nest building start at about 8 months of age. Fairly effective nests are made by about 12 months and a real nest by 18 months. Nest construction for overnight use starts at about 3-4 years of age. **Duration of construction:** Adults build nests in 1-5 min, prior to dusk, and a nest group is completed within 14 min (GROVES & SABATER PI 1985). **Re-use** of nests rarely occurs. **Sex differences** were reported concerning the size of nests with male nests being much larger, presumably reflecting sexual dimorphism. Silverback males build only on the ground, while juveniles and subadults tend to nest higher (SCHALLER 1963, GROVES & SABATER PI 1985). **Activities:** Nest are mainly used to rest and eat. FOSSEY (1974) reported another use of nests: lone males when separating from their natal group and establishing their own range, overuse a certain area with many nest constructions. They defend this area against neighbouring groups and establish thus their own core area.

Table 3 (p. 13): Nest building in gorillas. Legend see p. 21 ▶

REFERENCE	Mountain (<i>G.g. beringei</i>)			Eastern Lowland (<i>G.g. graueri</i>)			Western Lowland (<i>G.g. gorilla</i>)				
	Study Site	Country	Type of Habitat	Year	Duration	Study's Goal	Direct Observation	Indirect Observation	Year		
Donis- Thorpe 1958	Kisoro Virungas Uganda	Uganda	MRF	1956	8	pilot study	+	+	1958		
Kawai & Mizuhara 1959	Kisoro Virungas Uganda	Uganda	MRF	1959	3	ecology behaviour	+	+	1959		
Schaller 1963	7 diff. areas	Zaire	MRF	1959-1961	18	survey behaviour	+	+	1963		
Casimir 1979	Kahuzi Biega Zaire	Zaire	MRF	1979	15	ecology behaviour	+	+	1979		
Yamagiwa et al. 1983	Kahuzi Biega Zaire	Zaire	MPF	1978-1979	7	survey ecology	+	+	1983		
Mwanza et al. 1992	Hebero	Zaire	PF/SF	1987-1990	10	survey ecology	-	-	1992		
Jones & Sabater PI 1971	Equ. Guinea	Guinea	PF/SF	1967-1968	18	ecology behaviour	+	+	1971		
Groves & Sabater PI 1985	Equ. Guinea	Guinea	PF	1963-1969	18	behaviour	+	+	1985		
Remis 1993	Bai Hokou Dzanga-S.	CAR	PF/SF	1990-1992	27	ecology behaviour	-	-	1993		
William- son 1988	Lopé	Gabun	PF	1984-1985	16	ecology	+	+	1988		
Tutin <i>et al.</i> 1995	Lopé	Gabun	PF	1983-1994	48	survey ecology	-	-	1995		
ECOLOGY & FORM											
Nests	7/225	7/365	22/3012	-/964	-/171	-/375	7/410	7/448	-/1231	24/748	-/2435
Height	-	0-16	0-15	0-15	-	0-30	0-8	0-15	0-30	0-16	0-35
Choice of Material	opport.	opport.	opport.	opport.	-	opport.	?	selective	selective	opport.	selective
No. of Species Used	?	?	?	50	-	-	9	22	-	> 38	98
Feeding Trees	D/N/N	D/N/N	D/N/N	D/N/N	?	?	?	D/N/N	?	?	D/N/N
Type of Construction	3	-	5	2	-	-	?	4	3	8	7
BEHAVIOUR											
Info. on Ontogeny	-	-	+	-	-	-	-	-	-	-	-
Duration of Construction	-	-	5 min	-	-	-	-	-	-	-	-
Re-use	0	1x	-	-	-	-	-	12x	-	0	-
Sex Differences	-	-	+	-	-	-	-	+	-	-	-
Activities within Nest	-	R	R/E	-	-	-	-	R/E	-	-	-
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	(9)	1-19	(7)
Nearest Neighbour	-	0-50	0-38.5	0-40	-	-	0-6.4	1.5-15	-	-	-

Table 3

Groups: Since usually all members of a group nest in close proximity, attempts to consider whole *nest groups* have been made: **Group size** consists of 4 - 21 individuals. **Nearest neighbour** investigations from SCHALLER (1963) and JONES and SABATER PI (1971) reveal inter-nest distances of 0 - 38 m. By investigating age classes according to nest and dung size, both sets of authors found some regularities within a group: Juveniles slept closest to adolescents, followed by juveniles sleeping close to juveniles and adolescents to silverbacks. Distances between silverbacks' nests were reported to be the largest. ELLIOTT (1976) reported silverbacks nesting peripherally to the neighbouring groups, when members of the neighbouring group were within hearing. CASIMIR (1979), seeking to find indications within a nest group that reflected the central position of the group's leader, measured the relative positions of each nest within a group. He reported mean inter-nest distances of 8 - 10 m, but found no consistent pattern. Recent studies on western lowland gorillas show inter-subspecific variation in gorilla nesting habits: Western lowland gorilla groups comprising 2 silverback and several blackback males, were not only seen occasionally to split up during the day, but also sometimes to build nests at different sites within the home range, at least a kilometre apart (MITANI 1992, REMIS 1993).

Of the African apes, *chimpanzees* have the broadest distribution, covering the largest area in terms of geographical and ecological variability and thus inhabiting the widest range of habitats (cf. Figure 3). Intensive, long-term studies with detailed investigations on nest building started in the early 1960s on *Pan t. schweinfurthii* in western Tanzania (GOODALL 1962, 1968, SUZUKI 1969), in the late 1960s and 1970s in Uganda (REYNOLDS & REYNOLDS 1965, GHIGLIERI 1984). For the central subspecies *Pan t. troglodytes*, the first investigations took place at Equatorial Guinea (Rio Muni) in the late 1960s (JONES & SABATER PI 1971). Most investigations on

this subspecies, however, have been done in the past 10 years (TUTIN & FERNANDEZ 1984, 1985; WROGEMANN 1992). With the exception of Guinea (NISSEN 1931, DE BOURNONVILLE 1967), it was in the 1970s when detailed investigations on nest building started for the western subspecies *Pan t. verus* (BALDWIN *et al.* 1981, 1982; TUTIN *et al.* 1983).

Chimpanzees live in large communities composed of both sexes and dependant offspring. Their social organisation is characterised by a fission-fusion pattern in which the community disperses into subgroups or parties of varying number and composition. The chimpanzee society is male dominated: each healthy adult male can dominate all females of his community independent of rank and age (GHIGLIERI 1984, GOODALL 1986, NISHIDA 1990). FRUTH & HOHMANN (1994a) presented a detailed review on chimpanzee nests: Most of the studies cited were based on indirect evidence of nests or on methods developed by GHIGLIERI (1979) and by TUTIN and FERNANDEZ (1983), for the purpose of population density estimations (ANDERSON *et al.* 1983, GHIGLIERI 1984, TUTIN & FERNANDEZ 1984, FRUTH 1990, HOPPE-DOMINIK 1991, MARCHESI *et al.* in press.). **Table 4** shows data from studies with only the most comprehensive investigations.

Ecology & Form: Chimpanzees build an arboreal *nest* each night. Only for Tai forest, Côte d'Ivoire, did BOESCH (1995) mention day nests which sometimes are located on the ground. **Height** ranges from 2 - 45 m, with most nests between 10-20 m. Chimpanzees are selective in the **choice** of their nesting site, according to specific habitat features: Nests accumulate at specific areas depending on type of forest, slopes, valleys, and proximity to water or food resources (BALDWIN *et al.* 1982, GROVES & SABATER PI 1985, SEPT 1992, KORTLANDT 1992). Recently, SEPT (1992) used such accumulations of nests of different ages to devise a new scenario of the possible formation of early archaeological sites, searching for ecological structures that influence the spatial patchiness of chimpanzee

nesting sites. With respect to the *material* for nest construction, GOODALL (1968) said that "almost any type of tree may be used for nesting" (p.194), but she did not compare availability and choice of nest material. WROGEMANN (1992) studied chimpanzee nests at Lopé, Gabon, and provided the first findings on availability and choice of nest material: Lopé chimpanzees are selective for height. They use 56 *species for nest construction*. Proximity to feeding trees is close (GOODALL 1968, WRANGHAM 1975, ITANI 1979), and chimpanzees avoid construction of night nests within them. Day nests, in contrast, are often constructed within feeding trees. Detailed descriptions on the technique and *types of nest construction* are given by BOLWIG (1959) and GOODALL (1962, 1968). Nests range from very rough and superficial structures (usually day nests), to careful built nests, representing all parts described above (p.5). Chimpanzees do not hesitate to integrate trees when these interface, but they usually use only one tree for a nest. The maximal number of trees integrated in a single nest is 4 at Mt. Assirik, Senegal (MCGREW *pers comm.*). The largest number of nests found in a single tree is 10 (GOODALL 1962).

Behaviour: Ontogeny: Chimpanzees start at the age of 8-12 months to show their first nest building attempts (GOODALL 1968, HIRAIWA-HASEGAWA 1989). Quality and quantity of day nest construction increases with age and reaches a peak at the age of 3 years. At about 4-5 years, infants start to sleep independently from their mother and in their own night nest. The *duration of nest construction* varies from 1 - 5 min. In the fine weather of the dry season, when several individuals are present, nest construction begins later in the afternoon, but when it rains, it begins earlier. **Re-use**, although little has been published, is more often the drier the given habitat is. It is interpreted as a consequence of nest places as limited resource (SUGIYAMA *pers comm.* YAMAGIWA *pers comm.*). **Sex differences:** HIRAIWA-HASEGAWA (1989) reported that males less often construct day nests than do females. The extent to which the data shown in Table 3 refer

to day nests is unknown, but day nests are used for many *activities*, such as to eat, groom, play, rest (during illness), or give birth (GOODALL 1968, GOODALL & ATHUMANI 1980).

Groups: In 1968 GOODALL wrote about *nest groups*: At Gombe, Tanzania, they were made up by 2-6 nests on average but never exceeded 17. GOODALL, however, never investigated the quantitative relationships between nests. WROGEMANN (1992), found *group sizes* of 2 - 26 individuals. JONES & SABATER PI (1971) describe the *nearest neighbour* distances of chimpanzees' nests with 50% of the nests being only 3 - 4 m apart. These results, however, are based partly on estimates and height is not taken into account when inter-nest distances are determined. TUTIN & FERNANDEZ (1983, 1984) did a nation-wide census of Gabon that included detailed ecological data on nests. They did not, however, discriminate groups built on the same day from groups built over 2 or more days. BALDWIN *et al.* (1981) analysed inter-nest distances in nest groups, but these nests were not seen to be made and the definition was crude, based on the estimated age of nests and maximal distance from one nest to another. WROGEMANN (1992) investigated 213 nest groups of various ages, of which she singled out 31 groups that were less than a week old from the day of construction and thus fresh. The nest-to-nest data provide for the first time some data on intra-group relationships, although WROGEMANN (1992), due to the lack of habituation, solely relied on indirect rather than observational data. Thus, nothing can be said about differences between day and night, sex or age related characteristics of nests, context of nest construction, or other behavioural features.

	Eastern (<i>Pan t. schweinfurthii</i>)	Central (<i>Pan t. troglodytes</i>)	Western (<i>Pan t. verus</i>)
REFERENCE	Goodall 1968	Jones & Sabater Pi 1971	Baldwin et al. 1981
Study Site	Gombe	Okorobiko	Wroge-mann 1992
Country	Tanzania	Equ. Guinea	Lopé Gabon
Type of Habitat	GWF	PF/SF	SV/GF
Year	1960-1967	1967-1968	1976-1979
Duration	?	18	40
Study's goal	behaviour	ecology behaviour	ecology survey
Direct Observation	+	+	+
Indirect Observation	-	+	+
ECOLOGICAL & FORM			
Nests	? / 384	/ 82	- / 252
Height	0-25	3-20	- / 523
Choice of Material	opport.	selective	2-45
No. of Species Used	-	-	-
Feeding Trees	DN / --	?	45
Type of Construction	?	?	DN / NN
BEHAVIOUR			
Info. on Ontogeny	+	-	-
Duration of Construction	1-5 min	-	-
Re-use	20 x	-	-
Sex Differences	-	-	-
Activities within Nest	R	-	-
GROUPS			
Nest Groups	?	?	68
Group Size	1-17 (2-6)	?	1-26 (1)
Nearest Neighbour	-	3-4	4
			1-10 (1)
			4
			182
			1-22 (2-5)
			-

Table 4: Nest building in chimpanzees. Legend see p. 21.

For the *bonobo* or pygmy chimpanzee, *Pan paniscus* (for a more detailed description of the species see p. 33), investigations in the wild started in the 1970s (see also p. 35), and nests were first mentioned by NISHIDA (1972). Later, short investigations took place at Lomako (BADRIAN & BADRIAN 1977), Lake Tumba (HORN 1980), and Ikela (SABATER PI & VEA 1990). The first detailed report was published by KANO (1983) from Yalosidi including structural and ecological aspects of nests. Long term investigations of over 3000 nests were carried out at Wamba (KANO 1980, 1992). These studies are summarised in Table 5:

Ecology & Form: Bonobos build arboreal *nests* each night. Ground nests exist at Yalosidi and much less often at Wamba. Whether or not they are used for day nests only or also during the night is unknown (KANO 1982a, 1992). Ground nests were never reported for Lomako (BADRIAN & BADRIAN 1977). Nests vary between 0 - 50 m in *height*. KANO (1982a, 1992) reported on some differences between day and night nests; e.g. day nests are higher than night nests. Investigations on availability and *choice* at Wamba reveal a high selectivity towards certain *tree species* (KANO 1992). KANO reports 108 species used, of which only 10 make up 72% of the total. Feeding trees are among the species used, and they are used for both day and night nests (BADRIAN & BADRIAN 1977, KANO 1992). KANO (1983, 1992) distinguishes 5 *types of construction* according to the position within the tree and the number of trees involved. At Yalosidi, 15% of nests are integrated versus 45% at Wamba. Most nests are located on side branches. Similar to what was reported for orang utans, KANO (1982b) reported the use of leafy twigs as rain cover.

Behaviour: Nothing is known on the *ontogeny* of nest building. **Duration of construction:** At Wamba nests are built in 0 - 7 min, and day nests are used on average for 17 min (KANO 1992). **Re-use** is mentioned by SABATER PI and VEA (1990), however it is considered as rare and insignificant. No data on *sex differences* are published. **Activities:** Nests

are used for rest, groom, sex and play. At Wamba, KURODA (1980) saw several day and night nests shared by 2 mature individuals.

Groups: *Nest groups* were not investigated, and thus no data on *group size* or inter-nest relationships are available. KURODA (1979) gives one example of a nest group, mentioning that young males tend to rest on the periphery. The sample size of such observations, is not given, however.

At Lomako, detailed investigations started with the present study. Data provided by other than the present study are given in Table 5.

	<i>Pan paniscus</i>				
REFERENCE	Horn 1980 ^a	Badrian & Badrian 1977	Kano 1992	Kano 1983	Sabater Pi & Veá 1990
Study Site	Lake Tumba	Lomako	Wamba	Yalosidi	Ikela
Country	Zaire	Zaire	Zaire	Zaire	Zaire
Type of Habitat	PF	PF	PF	G/PF	SF
Year	1972-1974	1974-1975	1974-1986	1973-1975	1988-1989
Duration	24	11	ca. 70	3.5	13
Study's goal	ecology behaviour	ecology behaviour	ecology behaviour	ecology	ecology
Direct Observation	+	+	+	+	-
Indirect Observation	+	+	+	+	+
ECOLOGY & FORM					
Nests	? / 107	- / 174	637 / 3357	19 / 2380	- / 611
Height	0 - 25	5 - 34	0 - 50	0 - 50	2 - 36
Choice of Material	opport.	-	selective	selective	-
No. of Species Used	-	26	108	103	?
Feeding Trees	? / ?	DN/NN	DN/NN	? / ?	? / ?
Type of Construction	-	-	5	5	-
BEHAVIOUR					
Info. on Ontogeny	-	-	-	-	-
Duration of Construction	-	-	0-7 min	-	-
Re-use	-	-	-	-	yes
Sex Differences	-	-	-	-	-
Activities within Nest	-	-	R/G/S/P	-	-
GROUPS					
Nest Groups	-	-	-	-	-
Group Size	-	-	-	-	-
Nearest Neighbour	-	-	-	-	-

Table 5: Nest building in bonobos. Study sites are arranged from west to east. Legend see p. 21.

Legend for Tables 2 - 5:

	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
ECOLOGY & FORM	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 are used for day nests (DN) or night nests (NN) or both
	Sex Differences	+ = data available; ? = information not quantified; - = no data
BEHAVIOUR	Type of Construction	Number indicates the number of construction types distinguished; ? = information not quantified; - = no data
	Info. on Ontogeny	Information available: + = yes; - = no
	Duration of Construction	In minutes for one nest
	Re-use	Number indicates how often re-use has been observed; Percentage (%) restricts re-use to either day- or night nests (DN/NN); yes= re-use happens but not quantified; - = no data
	Activities within Nest	R = Rest; P = Play; G = Groom; S = Sex; I = Ill or Wounded; T = Taboo; B = Birth; E = Eat; O = Other
	GROUPS	Nest Groups
Group Size		Numbers indicate range; bracketed numbers the median; + = data not specified
Nearest Neighbour		Nearest distances between nests in meters

Given so many studies of nest building, it is necessary to justify adding another. Examination of published knowledge, however, reveals the following: (a) Most investigations on nests seek to produce density estimations and thus are based on abandoned artefacts of differing ages found on arbitrary transects or by chance. Nests decompose, and many of their characteristics change with time; (b) Little is known of the behaviour of nest building, e.g. sex of the maker, timing or means of construction; (c) Almost always only single nests are considered, but nest building is mainly a social event involving several individuals building their nests at a common site. (d) When nest groups are addressed in published studies, they comprise accumulations termed groups based on the age or spatial proximity of nests, but these may be confusing accumulations of nests made on different nights and by different parties.

Despite the large number of studies dealing with apes' nests, few *behavioural* patterns in the great apes have drawn so little attention as the ethology of nest building. Nest building is eclipsed by the day-to-day observation of social behaviour. Great apes spend at least half their lives in nests, and so it is highly likely that the choices they make about nest sites and the company in which they build their nests are of major importance.

D. ORIGIN OF THIS STUDY

This study derives from an idea born when I did research at Taï forest, Côte d'Ivoire, where a long-term study of chimpanzees has continued since 1979 (BOESCH & BOESCH 1981, 1983, 1989). In November 1988, my study recorded nests found on standardised transects in the range of the habituated chimpanzee community, in order to have a base for future comparison with other sites in Côte d'Ivoire (FRUTH 1990, BOESCH *et*

al. 1994). After searching each day for abandoned nests, I wanted to see them being built. On November 30, 1988, I got the opportunity: Together with GRÉGOIRE NOHON, an Ivorian field assistant, I followed chimpanzees the whole day. An older juvenile male had already built a nest, when suddenly, the star hunter of the community captured a red colobus monkey. Food sharing was in full swing, and the atmosphere was tense. The party was large, sticks and broken bones were thrown, quarrels between party members were frequent. All party members gave high-pitched vocalisations and many tried to approach the meat owner. Not all members of the party got a share, despite begging and attendance, and even the dominant male of the community waited in vain. He left the party "visibly purple" from anger. Shortly before sunset, the remaining party quickly moved 100 m from this place to start nest construction. They had been in a dry part of a periodically inundated forest and then moved on to a place of higher elevation. Within a couple of minutes, everybody had climbed trees, and about 15 min later it was silent. Everyone was in their nests. With the last rays of light I identified 2 females and a male. The next day we returned to measure the entire group; 8 trees were used for 15 nests. I was impressed by the long distances between the nests, which were about 15 - 50 m apart. The lowest nest was at 10 m height and was built by the male closest to the observers. He was central and the others who had built at 10 - 40 m away, were much higher, between 20 and 40 m. The nest of the female was hard to recognise from below. She had built at 20 m and was alone in a tree. But there were 3 trees, each containing 3 nests very close to each other. I asked myself to what extent the food sharing session the day before had influenced the composition of this nest group. I found it hard to imagine that the angry alpha male would nest beside the owner of the prey which he had refused to share. Such ideas, however, led to general goals for future investigations:

I hypothesised that the pattern of nests within a given group likely reflects the social relationships of the individuals involved. In a more general sense, a nest group should mirror the social structure of the individuals involved. The published literature about nest building showed that "several investigators have attempted to read organisation into the placement of individual nests" within a group (SCHALLER 1963, p.182). Most of them worked with mountain gorillas: Nests were thought to be in a position so that their owners could keep each other in view (BLOWER 1956, OSBORN 1957, LEQUIME 1959 cited in SCHALLER 1963). GROVES & SABATER PI (1985) looked for the silverback males' nest to be in a "special position". KAWAI & MIZUHARA (1959) described blackback males nesting 150 m away from the rest of the group, and a group splitting up at night sleeping more than 100 m apart. Their interpretation was "The above examples are not cases of combination and division between troops, but rather suggest changes in membership and *social relations within one troop*" (p.19). CASIMIR (1979) wrote: "...it has not yet been clarified whether any correlation exists between nest building and environmental factors; nor have patterns been sought which might *reflect social factors in the group*."(p. 291). Except the regular habit of young males resting in the periphery, none of the studies mentioned above actually found any special arrangements of nests depending of age and sex classes.

E. OUTLINE OF THE THESIS

In 1990 I got the opportunity to study wild bonobos. Keeping the above hypothesis in mind, I had to start on a much more basic level: The community was not habituated to human observers, individuals had to be identified, and the general patterns of group life were unknown. Therefore, the present study begins with baseline information on bonobo nest building, showing that nests are more than just a simple reflection of habitat

availability or of seasonality: Bonobos determine the place, shape, size, and pattern of the nests they make, and they pay attention to their neighbours, among whom they take up their nest positions. On the base of this information, future investigations may extend consideration of the original hypothesis.

Here are brief descriptions of the chapters in the thesis, indicating their relevance to current research on bonobos and nest building:

In **Chapter 1, THE EYENGO COMMUNITY**, I give information on the study group upon whom all later calculations are based. Data are given on the number, composition and sex ratio of the community under study. This is the first time that an unprovisioned community has become completely known. The findings are contrasted with other bonobo study sites (Wamba, Yalosidi) in terms of number of individuals and sex ratio within a community or party. Data on party sizes and on diurnal and monthly dynamics indicate that bonobos at Lomako split up and fuse regularly not only from month-to-month but also during the day. Results obtained in this chapter are used later (Chapter 4) for comparisons with night nest groups. As a consequence the bonobo fission-fusion society is reconsidered and gives rise to speculations concerning their informational network.

In **Chapter 2, NEST TREES: AVAILABILITY & CHOICE**, I address the question of whether or not bonobos are selective in their choice of trees used for nest construction. I focus on key features describing the physical characteristics of trees and compare the proportions of characteristics selected by bonobos with the availability of these features in the forest. The chapter shows clearly that bonobos are highly selective. The results are discussed later in comparison with those of other bonobo and chimpanzee study sites. The degree to which selectivity differs between the *Pan* species

is discussed in the context of trees as a limited resource and of inter-specific competition over nest trees.

In Chapter 3, NESTS: PHYSICAL AND BEHAVIOURAL CORRELATES, I focus on single nests and their physical properties, and on the behaviour of nest construction. Nests made for overnight resting purposes are compared with those built during the day. Depending on the time of day, the time and effort invested in construction differs. As a result, day versus night nests differ in their type of construction, and in the number of trees involved. While the physical parameters agree with other studies (KANO 1992), sex and age related differences in the construction and use of nests, and the related activities, are given here for the first time. In the discussion I seek to explain the pronounced sex differences and to give an interpretation for the differences emerging from comparisons with other study sites.

In Chapter 4, NEST GROUPS: DISTRIBUTION, PHYSICAL & BEHAVIOURAL CORRELATES, I examine nest groups as social assemblages. After a general evaluation of the choice of nesting sites within the home range, I quantitatively describe groups in terms of their dispersion in space. Nests are seen as a system of mutual relations and are characterised accordingly. I pick out behavioural characteristics that relate to the social aspect, such as time of construction, initiating individuals and inter-individual distances. Nest groups are compared with what is known from party associations during the day. This synthesis tries to bring together results from Chapters 1 and 4, and suggests that the bonobo fission-fusion system is much more dynamic than previously thought. Finally, I discuss inter-individual distances in the context of bonobo social structure. This chapter provides the first characteristic features of real nest groups.

II. MATERIAL AND METHODS

A. STUDY AREA: THE LOMAKO FOREST

1. GEOGRAPHY

About 100 km north of Boende, a remote area entirely covered by tropical lowland forest extends between the Lomako and the Yekokora Rivers (20°40' - 21°40'E, 00°39' - 01°12'N). The Lomako is one of the many tributaries of the Maringa River that finally empties into the Zaïre River. The forest adjacent to the Lomako River spreads over more than 3700 km², and the study site within it, covering about 35 km² (21°05'E, 00°50'N), is named accordingly. The study sites' part of the forest is administered by Tshuapa District, Equateur Province, Republic of Zaïre. At least part of this forest is included in timber concessions held by SIFORZAL (Karl Danzer Furnier-Werk/ Rheutlingen/ Germany), but only the western part was exploited until 1986, while the eastern part was never used because of commercial unviability (DE RIDDER *pers. comm.*). Today this area is proposed to become a bonobo reserve (THOMPSON-HANDLER *et al.* 1995).

The region described here is characteristic of the Central Equatorial Basin. It is flat, with the altitude averaging 400 m above sea level; it shows little variation in physical geographical terms (WIESE 1982). Soils are of sedimentary origin (limestone, clay, sand, gravel) which is little consolidated. The landscape is broken up by a network of many water courses, and the greatest differences in relief within the study area are only up to 40 m, being the ravines of small streams (e.g. Eyengo, Yirte). Distinct coniform hills of up to 10 m height are common and are said to be former termite mounds.

2. CLIMATE

Annually, temperature averages 25°C ($\pm 1-2$ °C, range 18°C - 30°C). Changes within 24 hours exceed by about 10 °C the differences in the mean monthly temperatures measured over the year (WIESE 1980).

With a mean annual rainfall of above 2000 mm, this region is part of the most humid zone in Zaïre. On average, there are 10 wet months (above 50mm rainfall per month on average), and more than 120 days per year with rainfall above 10 mm. At the study site *rainfall* was recorded daily; the amount was noted in mm using a graduated cylinder in a rain gauge. Monthly totals ranged from 61 mm in February 1990 to 393 mm in April 1993. Since there were no completely dry months, a calendar month was classed as dry if rain occurred on less than 11 days (34%). Accordingly this wet-dry classification was used as for *monthly seasonality correlations*.

Figure 1 shows the quantity of rainfall for each month of observation.

When the influence of rain on nest building was tested more specifically (e.g. dripping water from overhanging vegetation was thought to influence the variable of nest cover, c.f. chapter III; 3.1.4.) neither the amount of rain nor the crude seasonal classification was precise enough. Instead it was important to distinguish *when* it rained during the day (= *daily weather correlates*). Each day was split into four phases: morning (05:00 - 10:00 hr), midday (10:00 - 14:00 hr), afternoon (14:00 - 18:00 hr), and night (18:00 - 05:00 hr). The night phase was chosen because overnight nests were already built by that time, and thus rain occurring afterwards was unlikely to influence nest site choice. The phases during the day were arbitrarily chosen. For each phase it was noted whether or not rain occurred. Vegetation dampened by a cloud-burst in the morning was dry by the time of night nest construction. Therefore, if it rained only during the morning, the day was classed as dry. When it rained at midday or in the afternoon, the day was classed as rainy.

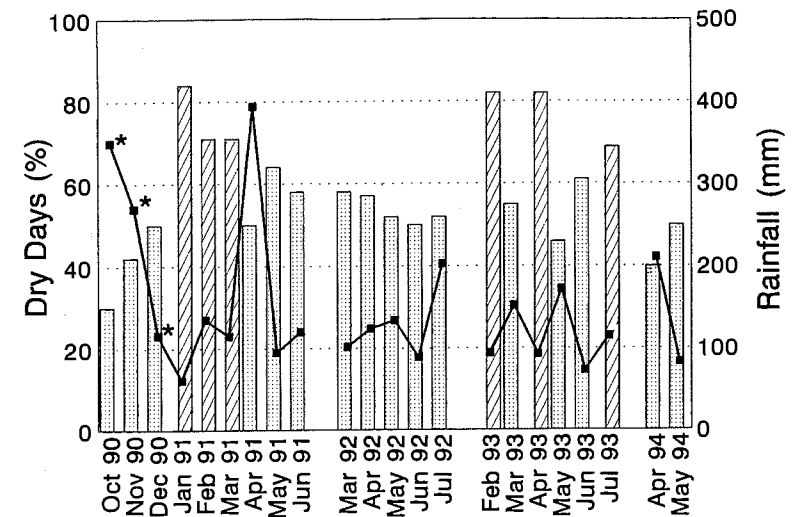


Figure 1: Points connected by bold lines indicate rainfall for each month of observation (mm). Hatched bars indicate wet months, dotted bars are dry months. Length of bar represents percentage of dry days within month. Points marked with an asterisk were extrapolated from proportion of days sampled within month, as daily records were incomplete.

3. VEGETATION

The Lomako forest is part of the largest contiguous block of rainforest on the African continent, covering about 108 million ha. of the central Congo Basin. It is rich in species diversity, depending on the heterogeneity of the forest. Overall, 119 families with 2593 different species of spermatophytes have been recorded for the central Basin (EVRARD 1968). In the primary forest of most heterogeneous structure, the leading species is *Scorodophloeus zenkeri*. Up to 542 species are recorded for that forest type (KNAPP 1973). In other parts the structure may be more homogeneous.

Here characteristic species are: *Gilbertiodendron dewevrei*, *Brachystegia laurentii*, *Diogoia zenkeri*, *Diospyros* spp. (WIESE 1980). The region between the Lomako and Yekokora Rivers has 60% swamp and periodically inundated forest and the rest is evergreen lowland and degraded semi deciduous mesophile forests (EVRARD 1968). The following levels can be distinguished: Emergents with trees between 40 and 50 m high. These stand out, with their crowns towering above the next lower stratum, the canopy. Canopy trees range in height between 10 and 30 m, and their crowns usually touch each other and form a continuous layer. One lower stratum between 2 and 10 m lies below.

4. FAUNA

Elephants (*Loxodonta africana*) at Lomako were shot out in the late 1960s. Their trail system persists and is used by many other species, including bonobos. The forest supports a rich mammalian fauna including common animals like forest duikers (*Cephalophus* spp.), red forest hogs (*Potamochoerus porcus*), porcupines (*Atherurus* spp.), civets (*Viverra* spp.) and pangolins (*Manis* spp.). The primate fauna is diverse. In addition to bonobos, there are 4 species of monkeys that often form large mixed groups (*Colobus angolensis*, *Cercocebus aterrimus*, *Cercopithecus wolfi*, *C. ascanius*). There are at least 2 species of nocturnal prosimians, *Galago demidovii* and *Perodicticus potto*. For more detailed descriptions of the fauna see BADRIAN & BADRIAN (1977, 1981), SUSMAN (1984), and MALENKY & STILES (1991).

The forest is also inhabited and used by *Homo sapiens* belonging to the Mongo (Bantu) tribe. They live from horticulture and forest products, fish and bushmeat. Trees are cut for making dug-out canoes (pirogues) and for collection of honey. Wire snares, bows and arrows, spears and rarely guns are used to capture or to kill prey; these are mainly monkeys and small

ungulates for local consumption. The overall impact of the local people on the forest is very low. In addition to *Homo sapiens*, *Panthera pardus* is considered potentially to prey on bonobos. Leopards' presence was confirmed indirectly in 1985 by WHITE (1992a), but neither vocalizations nor footprints were recognized during the present study. Frugivorous birds and mammals are present, of which monkeys are considered to be the most important competitors.

5. STUDY SITE

5.1. History

The Lomako study site was founded by ALISON and NOËL BADRIAN in 1974 (BADRIAN & BADRIAN 1977, 1978). After a pilot study in 1979, "The Lomako Forest Pygmy Chimpanzee Project" (LFPCP) was established under the direction of DR. RANDALL SUSMAN, State University of New York (SUNY) at Stony Brook (for a synopsis, see SUSMAN 1984). From 1980 - 1985, several doctoral students from SUNY collected data on bonobos at Lomako, focussing on sexual behaviour (THOMPSON-HANDLER 1990), ecology (MALENKY 1990), behavioural ecology (WHITE 1986), and locomotion (DORAN 1989). In 1989 DR. GOTTFRIED HOHMANN made a prospecting visit to Zaïre and visited Lomako. At that time, the study site was abandoned, and according to local people no research had been done for 4 years. In 1990 HOHMANN and I began "PROJET PAN", under the auspices of the Max-Planck-Society, which continues to the present. At the end of 1990, members of the LFPCP returned to the study site, but they had to stop research in 1991 when political problems escalated in Zaïre and the American government withdrew all funding for studies in Zaïre.

5.2. Location and Infrastructure

The Lomako study site covers about 35 km². Most of the forest is: (1) primary, climax, evergreen, polyspecific forest, but there is also (2) swamp, (3) slope forest (*Gilbertiodendron drewerei* forest, which separates the higher polyspecific forests from the swamp forests) and small areas of (4) secondary forest (WHITE 1992b). In 1990 we established a basecamp about 2 km from the nearest village, Ndele. A natural clearing of about 25 m diameter was enhanced and three huts made of local materials were built. The furthest point of the range of the study subjects was reached in 90 minutes' walk, and the closest point in less than 10 min. Following a published map (BADRIAN & BADRIAN 1984) and with the help of local guides, the original trail system was reopened in October 1990 (Figure 2 a).

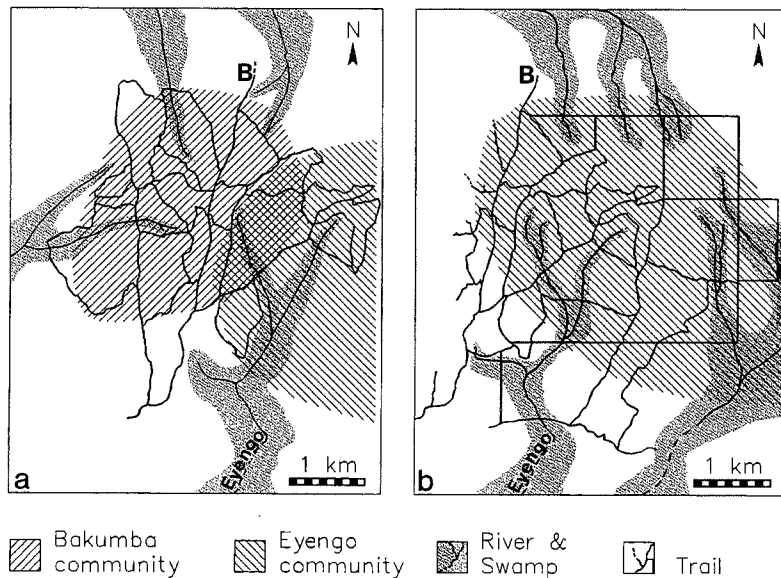


Figure 2:(a) Lomako study area published by BADRIAN & BADRIAN 1984 (from SUSMAN 1984, p. 327) indicating home ranges for Bakumba and Eyengo community. (b) Study area during this study shifted to the East (for line of reference see Eyengo) with enlarged trail system indicating home range for Eyengo community only (cf. III; 1.5.).

These trails were based on former elephant trails. Whenever the study subjects moved to another area of the forest, the system was enlarged by adding trails. Standardised transects for the calculation of habitat structure and other ecological parameters also were cut. Both types of trails were marked every 50 m. In 1994 the total length of the regularly used trail system was about 40 km, and it covered an area of about 20 km² (Figure 2 b).

B. STUDY SUBJECTS & SAMPLING METHODS

1. DISTRIBUTION, SOCIAL ORGANISATION, AND SOCIAL STRUCTURE OF THE BONOBO

In contrast to chimpanzees who show a vast *distribution* throughout west, central and east Africa, bonobos are restricted to the evergreen lowland rainforest of central Zaïre (Figure 3), the "cuvette centrale" or central Congo Basin south of the Zaïre river. They do not occur sympatrically with chimpanzees or gorillas. All bonobos sharing a common range, maintaining affiliate relationships, and defending it against other individuals of the same species, were said to belong to one community (following GOODALL 1973). This community splits up into several parties or subgroups which may use diverse parts of the home range independently from each other for extended periods. They may join or leave associations of differing number and composition. Individuals of either sex have almost complete freedom to come and go as they wish (GOODALL 1986). As in chimpanzees, this pattern is called *fission-fusion social organisation*. Females typically emigrate from their natal community (female dispersal) while males stay within it (male philopatry) (KANO 1982a). As a

consequence of this pattern of sex-differentiated migration, the *social structure* of chimpanzees and bonobos should be the same, but bonobos are a female dominated society. Females cooperate while males compete. Even an adolescent female may dominate a male, although this does not mean that every adolescent female dominates every male of the community. Hierarchy is a complex interwoven system dependent on sex, age, character, and individual social competence.

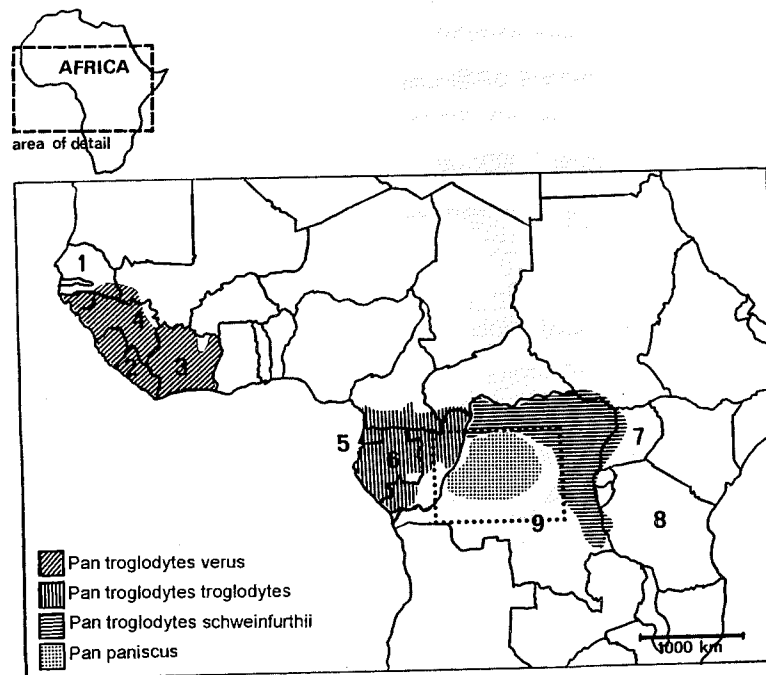


Figure 3: Distribution of chimpanzees and bonobos throughout Africa. 1 = Senegal, 2 = Liberia, 3 = Côte d'Ivoire, 4 = Guinea, 5 = Equatorial Guinea, 6 = Gabon, 7 = Uganda, 8 = Tanzania, 9 = Zaïre, dotted square = area of Zaïre in detail see Figure 4.

2. DISCOVERY AND FIELD RESEARCH

The bonobo was scientifically discovered in the Tervuren Museum, Belgium in 1929. SCHWARZ (1929) attributed to a new subspecies of chimpanzee the skulls that had previously been interpreted as being juvenile chimpanzees. The taxon became a full species in 1931 (COOLIDGE 1933). Bonobos were distinguished from chimpanzees by their slender frame, long hind limbs, short clavicle, and small molars (JOHNSON 1981). They have however a comparable weight to what is known from chimpanzees, with the exception from Gombe chimpanzees (*Pan troglodytes schweinfurthii*) who weigh less (JUNGERS & SUSMAN 1984, MORBECK & ZIHLMAN 1989). No sexual dimorphism was found (CRAMER & ZIHLMAN 1978). Recently, however, PARISH (*in press*) confirmed that like chimpanzees, bonobos show sexual dimorphism with males being larger than females. Field research on bonobos in Zaïre began in 1972 (NISHIDA 1972, HORN 1980) and has continued intermittently. Location and duration of these studies are indicated in Figure 4. Four short term sites and 2 long term sites have been established. Today the 2 long term sites are at Wamba, conducted by members of Kyoto University since 1975 (KANO 1992), and at Lomako.

3. BONOBOS OF LOMAKO

Several bonobo communities live in the Lomako forest. Three were described by members of the SUNY-Project: the Hedon (= Bakumba) community, the Rangers (= Eyengo) community, and an apparent splinter group, the Blobs (BADRIAN & BADRIAN, 1984; THOMPSON-HANDLER *et al.* 1984; WHITE 1988; WHITE & BURGMAN 1990). We adopted group names according to the main streams in the community's range, i.e. Bakumba in

us to follow them on the ground and did not hesitate to build their night nests nearby to us. During the first year, most adult members of the Eyengo community were identified. This was extended to most adolescents and juveniles in 1992. By 1993 the whole community was known (for more details see chapter III; 1), and the distance tolerated between observer and bonobo was 3 - 10 m, depending on the individual confidence of the subjects and on visibility in the forest. During periods of rest, individuals regularly approached us while we sat on the ground. Although the degree of habituation was not as great as that in Taï forest (BOESCH & BOESCH 1989) or Gombe (GOODALL 1986), follows on the ground were possible on average every other day.

5. TIME IN THE FIELD

This study was done in 29 months spread over 4 years. Table 6 gives an overview of the time spent in the country, at the study site, and in the forest. Logistical demands were responsible for the difference between time spent in the country and time spent in the field. Because it was easier to travel into the study area when it was dry, field time was biased toward the drier first half of the year.

6. BEHAVIOURAL DATA & MEASUREMENTS

Behavioural data presented here come from 1030 hr of direct observation (Table 6). Whenever possible, members of the Eyengo community were followed from the nest site in the morning until the nest site in the evening. In reality we often lost them and then found them again by using direct and indirect evidence such as vocalizations, feeding remains, odour, or other signs. Data on nests were sampled on the basis of

all-occurrences. All other observations were recorded ad libitum (ALTMANN 1974). Data were taken in a notebook or dictated onto cassette tape in a Dictaphone (GRUNDIG Stenorette 2070). In the evenings or at weekends, data were transcribed into a field diary. We took no data at night.

	1990/91	1992	1993	1994	Total
Months in Zaïre	11	7	8	3 (8)	29 (34)
Months at Lomako	9	5	6	2 (5)	22 (25)
Field Hours	1350	1073	1084	284 (894)	3791 (4401)
Observation Hours	306	204	456	64 (278)	1030 (1244)

Table 6: Time spent and hours of direct observation during 4 field seasons. Numbers in brackets are total time spent at study site, with difference being time HOHMANN spent in forest in 1994. Data on nest groups for June - August 1994 derive from total hours of observation.

Detailed measurements of nests and nest groups were part of the 3791 hours spent in the field. These were focused on as a consequence of behavioural observations. The majority of nests measured were seen to be constructed. The sample size of some data presented here was increased by findings of other researchers: Party size: Whenever HOHMANN (GH) and I followed different parties, both data sets were joined for the calculation until 1993; Nest groups: GH and I split up in the afternoon whenever the group was lost, in order to increase the possibility of finding at least one

nesting group for the next morning. GH also collected data on nest groups during my absence in 1994 (see Table 6). Two Zairois field assistants, B. LOKULI & B. BOLESA, alternately searched for additional nest groups. Measurements of nests were always taken with the help of one other person, usually GH. The field assistants aided in investigations, transects, and plots, and the village elders helped in plant identification.

Unless specified otherwise, all measurements were done with the following low-tech equipment: Vertical dimensions with an altimeter (SILVA, range 0 - 65 m, precision: below 30 m: ± 50 cm, above 30 m: ± 1 m); horizontal dimensions with a tape measure, range 1 - 30 m, precision: ± 5 cm; directions (with degrees adjusted to magnetic north) with a Recta DP-10 compass using the prism (precision: $\pm 0.5^\circ$). Binoculars (10x42, Leica) were used for observation.

C. DATA COLLECTION

1. THE EYENGO COMMUNITY

1.1. Demography

Each member of the community was identified and assigned to one of 4 different age classes (FURUICHI 1987): adult (≥ 15 years old), adolescent (9 - 14 years old), juvenile (5 - 8 years old) and infant (birth - 4 years old). Age classes were assessed on physical criteria such as body size, development of external genitalia, cycling (in females), condition of teeth, and mode of locomotion or transport (in immatures). The number of individuals increased by birth or immigration and decreased by disappearance, from either emigration or death.

1.2. Party Size

All bonobos visible to the observer were considered to be in one party. This included individuals known to be present but briefly out of sight, for example behind a tree trunk or termite mound. If individual identification was not possible, the age and sex of an individual was noted. Individuals were identified and scanned when visibility was good enough actually to see the entire party. Time, location and position (in a tree or on the ground) were noted. For the influence of rain on party size, the monthly seasonality correlates were used (cf. II B; 2.). If not specified otherwise, the term party size refers to all individuals except dependent offspring.

1.3. Party Composition

The *socionomic sex-ratio* (SSR) of a party was calculated by dividing the number of adult and adolescent females by the number of adult and adolescent individuals.

1.4. Travel patterns

Travel patterns of whole parties were analysed. Direction of travel, landmarks (e.g. watercourses, marked feeding trees, known termite mounds), and marks (50 m tags) of crossed trails were noted whenever possible. After observation the route of the day was traced onto the map of the study area resulting in a "spaghetti". The length of each "spaghetti" was measured with a ruler and calculated in respect to the scale. Zig zags, ups and downs in trees, movements within spots, of temporary rest-stops were disregarded in these calculations.

1.5. Home range

A grid of 100 m x 100 m was superimposed on the same map (following WRANGHAM 1975). All quadrats entered by parties of the Eyengo community were considered to be part of their home range. All 100 m² quadrats entered over the 4 study periods were summed. The extreme comers were connected by drawing a line resulting in an outside concave polygon. All quadrats partly or entirely enclosed by the frame of the polygon were summed, and the resulting calculated area was considered to be the home range of the Eyengo community.

For an estimation of the distribution and scope of *habitat types*, various data were recorded every 100 m on transects cut along compass directions to enlarge the trail system to the east. These standardised transects totalled 16.6 km. The criteria were taken from FRUTH (1990) and adapted to the Lomako forest. Later the map was divided into squares, each representing 100 m x 100 m (1 ha). Quadrats were classed as either primary forest, slope forest, secondary forest, or swamp. In addition to typical indicator species, the structure of vegetation was used for classification (see Table 7). The classification was used throughout the home range whenever a new area was explored. Because of the homogeneity of the habitat, blank squares were extrapolated according to the surrounding squares. To calculate proportions of the different types of habitat, all squares of each habitat type were summed and taken as a fraction of the total area of the home range.

	Emergents	Canopy	5-10m Stratum	Understory/ Lianas
Primary Forest (PF)	frequent = more than one tree visible	frequent = tree tops may touch each other	rare = isolated trees	absent - rare = lianas thick and ground
Slope Forest (RF)	frequent = more than one tree visible	rare = isolated trees	absent	absent - rare = lianas thick and above ground
Secondary Forest (SF)	absent	frequent = tree tops may touch each other	abundant = tree tops overlap	abundant = lianas thin and tangled thick
Swamp	absent	rare = isolated trees	rare = isolated trees	rare = isolated lianas

Table 7: Four major habitat types into which the study site was differentiated. Categories of abundance refer to the vegetation indicated in the column heading: emergents: trees (height) > 40 m; canopy: trees (height) 10-30 m; 5-10m stratum: trees (height) 5-10m; undergrowth/lianas: shrubs or lianas.

2. NEST TREES

2.1. Height

Height was measured from the ground to the top of the tree. The sample of measured trees was split into 12 size classes, with heights ranging from up to 5 m to up to 60 m. Size classes were chosen according to measurements taken from trees used for nesting by bonobos.

2.2. Stem Diameter

Circumference (= girth) was measured at breast height (= 1.5 m) for each tree (CBH). The stem diameter (DBH) was calculated thereafter by using the formula $2\pi r = C$ where C is the circumference of the tree measured. The sample was divided into a matrix of 12 size classes ranging from a DBH of 2 cm to a DBH of more than 55 cm. Size classes were chosen according to measurements taken from used nest trees.

2.3. Height of Crown

Height of the crown was calculated by subtracting the height of the lowest branch from the height of the tree.

2.4. Species

Species was determined by the morphological features of trunk, bark, sap, leaves and fruit (LETOUZEY 1982, VIVIEN & FAURE 1985). All species not identified by this procedure were determined by local people using indigenous names. For these trees, the scientific name was sought on a list available from former researchers of the C.R.S.N. (Centre de Recherches en Sciences Naturelles) at Lwiro and cross-checked with the above-cited literature. All species of plants used for nest construction and those determined in plots (see 2.7.) are listed in the Appendix.

2.5. Leaf Size

Four classes of leaves were distinguished according to their relative size (width x length): 'small' = < 5.0 cm², 'medium' = 5.0 - 24.9 cm², 'large' = 25.0 - 64.9 cm², and 'extra large' = > 65 cm². In the case of leaves composed of several leaflets (eg. *Pancovia laurentii*) the size of a single leaflet, and not the whole compound leaf, was considered. After once measuring various leaves from different species, their classes were assigned.

2.6. Selectivity

The selectivity of bonobos in choosing trees for nesting was assessed by the relation between availability of nest trees (potential nest trees) and choice by the bonobos (used nest trees): Systematic analyses on the *availability of trees* and their specific characteristics were derived from 48 forest plots of equal size (20 m x 20 m). The side length was always measured and adjusted to be aligned north. Plots were investigated either at nesting sites or at random. Table 8 shows the categories and the numbers of plots, with the parameters for each category.

3. NESTS

3.1. Physical Correlates

Nests were located by (a) following and directly observing individual behaviour, (b) searching at prospective nesting sites, and (c) incidental discovery. Only fresh nests (those constructed the previous night) were included. They were identified by observation or by fresh signs of defecation and urination underneath and were marked with date and number. Marks were applied either just after the bonobos had left the nest site or later in the day. Details were recorded as follows:

3.1.1. Type of construction

Nests were assigned to 5 categories according to their type of construction. The terminology used is a slightly modified version of that introduced by KANO (1983). The types distinguished were characterised by the number of trees involved and by the position of the nest within the tree (Figure 6).

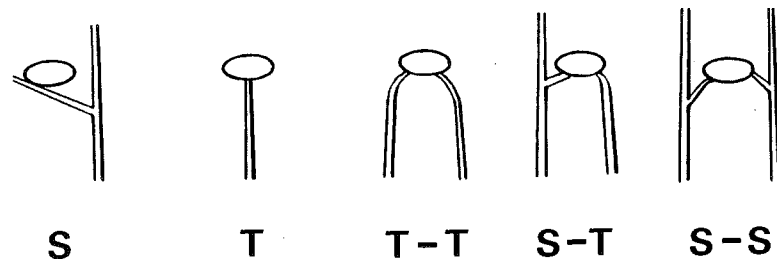


Figure 6: Five types of nest construction depending on the part and number of trees involved: S = side branch, T = tree top, T-T = two or more tree tops combined, S-T = two or more side branches and tree tops combined, S-S = two or more side branches combined (after KANO 1983).

3.1.2. Height

Absolute height was measured from the ground to the middle of the nest. (For calculation of the *relative height*, see p. 56).

3.1.3. Position within crown

Position within the crown was calculated by dividing the distance between the nest and the lowest branch of a given crown by the entire height of the crown. The result was a quotient between 0 (lowest branch) and 1 (top of the tree). The quotient yielded 3 categories indicating the nest's position within thirds of the crown: bottom third: 0.0 - 0.33; middle third: 0.34 - 0.66; upper third: 0.67 - 1.00.

3.1.4. Cover

A nest was considered to be covered, when the sky above the nest was hidden by overhanging vegetation. It was open, when there was no vegetation between nest and sky. For the influence of rain on nest cover, monthly and daily seasonality correlates were used (cf. II B; 2).

3.1.5. Architectural details

Nests were selected according to their accessibility and were analysed in detail by climbing into the tree and taking them to pieces. Nests were reached by using ladders (HACA-Steckleiter 7.30 m, STRUBA Steckstrickleiter 7 m.) or speleologic climbing gear (PETZL) and ropes

(EDELRID superstatic 10 mm). Figure 7 indicates the characteristics that were measured. Diameters for broken and bent branches were measured at the broken end or point of return, respectively. Diameter of detached twigs was measured at the proximal end.

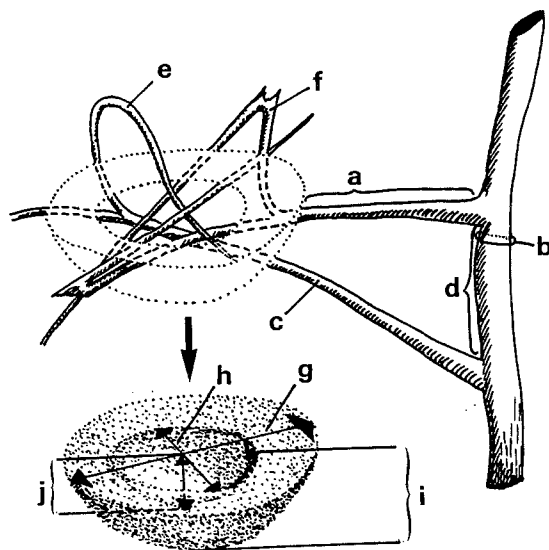


Figure 7: Schematic depiction of nest on a side branch. a = distance to stem, b = diameter of stem, c = supporting branch, d = vertical distance between branches, e = twig bent, f = twig broken, g = diameter of nest outside, h = diameter of nest inside, i = depth of nest outside, j = depth of nest inside.

3.2. Behavioural Correlates

Whenever possible nest construction was recorded and the nest builder identified. If identification was not possible, sex and age of the constructing individual was noted. Whenever possible, behaviour before nest construction, within the nest, and after leaving the nest was recorded.

3.2.1. Time of construction

Nest construction began when the nest building individual bent or broke the first branch that became part of the nest. This point of onset was used to investigate diurnal distribution of nest construction. All nests built and left in the same day were considered to be *day nests*. Only nests that were used overnight were considered to be *night nests*.

3.2.2. Duration of construction and use

Duration of construction was measured in units of whole minutes, from the onset of nest construction until the individual lay down in it. Interruptions of more than 1 min within the nest or temporarily leaving the nest (e.g. to take part in social interactions) were subtracted from the time of construction. *Duration of use* lasted from the end of nest construction until the individual left the nest.

3.2.3. Activities in day nests

Five patterns of activity were used to classify the context of nest use: *Rest*: Individual reclines without movement. *Groom* (social): Individual grooms with another mature individual. *Play* (solitary & social): Individual moves acrobatically or tussles or otherwise interacts with others. The faces of all participants usually show the typical open mouth play face and the actions are accompanied by the typical laugh-gagging. *Eat*: Individual eats food detached from a feeding tree and brought into the nest or food within reach of the nest. *Privacy*: Individual builds and occupies a nest in response to another approaching, usually with obvious competitive or agonistic intentions. After such building, no interaction occurs.

4. NEST GROUPS

A nest group was defined as 2 or more nests constructed and used in close proximity in one night. All nests in close proximity would be visible to the observer if the trees were leafless. If a party was followed directly and nest construction was seen, then all nests making up that group were discovered easily. Frequent vocalisations often accompanied nest construction. While the focal group vocalised in concert, distant individuals vocalised in alternation to the chorus. This also helped to identify all the nests of the simultaneously vocalising group as being a cluster belonging together, and sometimes helped to localise the distant group. If a group was discovered the morning after construction, the entire site was systematically scanned for both fresh nests and fresh signs of urine or feces underneath. The periphery of each nest was combed for more nests in a 20 m radius. All nests found were marked and counted the day that they were abandoned by the bonobos.

4.1. Distribution and size

Each nest group was visited either in the evening of construction or the next morning. With identification of the members, the group was attributed either to the Eyengo community or to other communities. The *position* of each nest group in relation to the nearest trail was calculated by measuring the distance from the nesting tree closest to the trail and recording the resulting angle to the trail. The position and the community of the nest building individuals was noted later on a calibrated computer map drawn in AutoCAD (ACAD11). Distances between groups built on the same night refer to the bee-line between the midpoints of each nest group, and were measured from the computer maps.

4.1.1. Distribution within the home range

A grid of 200 m x 200 m was superimposed on the map and the number of nest groups for each community were counted. The pattern of distribution was calculated by comparing the number of nest groups in each square of primary forest with a Poisson distribution.

4.1.2. Group size

Group size was defined as the number of nests per group and thus as equivalent to party size (cf. II C; 1.2.). On 3 occasions an individual was seen to abandon a nest during construction and then to build another. That happened so rarely that it was considered not to influence group size. Moreover, such nests were not marked by fresh urine or feces underneath and thus were not included in the number of nests per group. Group size was analysed as a *function of seasonality* using the monthly correlates

(c.f. Figure 1). It was analysed as a *function of day and night* by comparing the size of parties during the day (cf. II C; 1.2.) with the number of nests per group. The number of nests per group was considered to be the most reliable measure of party size for the night. This also included solitary nests. To investigate the *intensity of group fusion*, the mean size of all night nest groups in one month was subtracted from the mean size of all day travel parties in the same month (party size = number of weaned individuals). Party size was equal between day and night when the result was 0, parties fissioned for the night when it was less than 0, and they fused when it was above 0. The absolute difference from 0 thus was considered to be a measure of the strength of fission or fusion. To investigate the *function of position within the home range* on group size, all nest groups of the Eyengo community were noted in relation to the *centre of the home range*. This was defined as the 200 m x 200 m square in which most nest groups were found. The midpoint of the centre became the origin of a 2 dimensional coordinate system (0,0) and all groups were determined according to their x and y value in respect to this point. The direct distance from each group to the centre was calculated by applying the Pythagorean theorem (so that distance equals hypotenuse of the triangle) using a program written in CLIPPER 5.0. Since members of neighbouring communities were seen to nest in the north-western and south-western parts of the Eyengos' range, their range was divided into 4 sections by drawing straight WE and NS lines through the midpoint of the centre (Figure 32). Separately for each section, the number of nests per group was calculated as a function of distance from the centre.

4.2. Physical Correlates

The metrical relationships between all nests of a given group were done in 3 steps: a) measurement in the field, b) entering the data into a 3 dimensional graphics program of software (ACAD11), and c) calculation of within-group characteristics by applying a purpose-written program.

a) **Measurements in the field:** Two persons (A and B) and the above mentioned instruments (tape measure, compass, altimeter cf. II B; 4.2.2.) were needed for the following procedure: Within a nest group, a tree in central position was chosen as point of reference. (A) stood with the back to the trunk looking in the direction of a nest holding one end of the tape measure. (B) walked with the other end of the tape measure from (A) directly to the spot the nest would cast a shadow if the sun were in its zenith. (A) noted the *distance* from the trunk of reference to (B), and the *angle* of the nest relative to north. This was achieved by bringing the fine vertical line of the compass prism into line with the sagittal midline of B. In addition the *relative height* of the nest was measured. Figure 8 shows the difference of absolute height used for single nests (c.f. II C; 3.1.2.) and relative height used for the nests in a group. For relative height, the level at the base of most of the trees at the nest site was considered to be the "zero level". Nest positions showing a vertical deviation from the zero level were adjusted to this reference height by adding or subtracting the resulting differences.

If the nest was not visible from the original point of reference, the point was changed and the relation between the first and second point of reference was measured. The same was done for all trees involved. All diameters of trees used for nest construction or as point of reference were noted. The distance from the outer part of the tree trunk to the physical centre of the tree stem was calculated later and added to the distance.

b) **Three dimensional graphics:** These data were introduced into a commercial graphic program AutoCAD (ACAD11) resulting in a 3D reproduction of the nest group. From these computer representations of the nest groups the distance from nest to nest was taken.

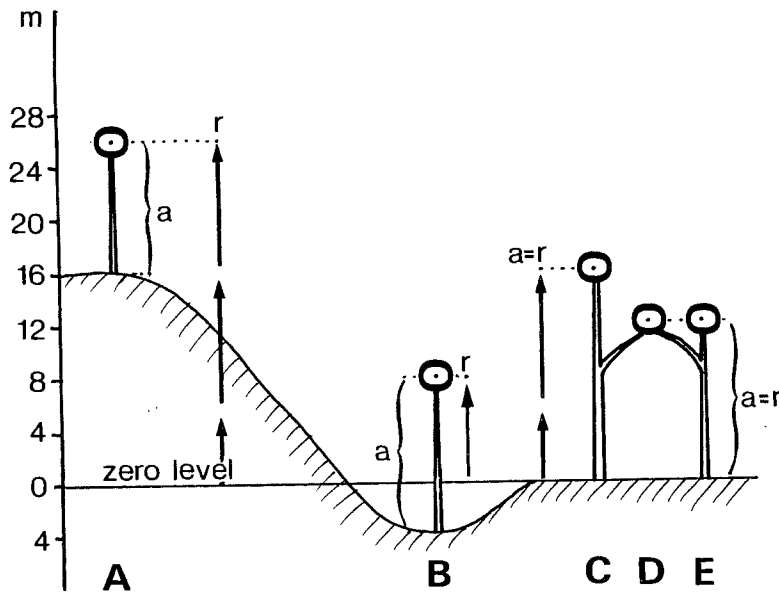


Figure 8: Arched brackets indicate absolute (a) height, vertical arrows relative (r) height of nests within a nest group on uneven landscape. Absolute height : Nests (A: 10m ; B: 12m; C: 16m; D: 12m; E: 12m); relative height: Nests (A: 26m; B: 8m; C: 16m; D: 12m; E: 12m).

c) **Calculation of within group characteristics:** Metrical dimensions were calculated by a program written by DIETER LEIPPERT in CLIPPER 5.0. (copyright: LEIPPERT & FRUTH 1994). They show the following:

4.2.1. Horizontal dispersion

All distances among nests of a group were measured to the nearest 5 cm. The largest horizontal distance between 2 nests was considered to represent the horizontal group dispersion.

4.2.2. Vertical dispersion

Vertical relative distances among each nest of a group were measured to the nearest meter. The difference between the lowest nest and the highest nest of a group was considered to represent the vertical group dispersion.

4.2.3. Distances between nests

The mean distance between the nests of a group was calculated. Since with increasing group size, overall inter-nest distances also increased, the nest with the smallest summed distance to all other nests of the group was chosen as the central nest. The sum of the distances of all other nests to this nest was divided by the number of distances (number of nests - 1) so that each distance to this central nest only entered the calculation once. The result was defined as the *mean inter-nest distance*. It

was set in relation to group size and tree density. Calculation of the general *tree density* derived from 35 nest sites plots of 400 m² (cf. II C; 2.6.). Calculation of the density of the 5 tree species most often used for nests (Top Five) was derived from 18 of the 35 plots (since species were not identified for the other 17).

4.2.4. Nearest neighbour distance

For nest "A" of a group, distances to all other nests of this group were compared. The nest with the smallest distance to "A" was considered to be the nearest neighbour to "A". Both the mean nearest neighbour distances for each group and the mean nearest neighbour distances for all groups of one size were set in relation to the number of nests per group.

4.3. Behavioural Correlates

4.3.1. Time of construction

Onset of building the first nest in each nest group was considered to mark the beginning of the group's construction. The start of each nest group was set in relation to the weather on the day of construction (cf. II A; 2.).

4.3.2. Duration of construction

The moment the last individual lay down was considered to be the end of nest group construction. When nest building extended into the dark, construction was considered to end when the typical noises of nest building

ceased. The duration of construction of a group divided by the number of nests per group was considered to describe the interval between each nest construction within the group. The closer the result was to the average time of a single nest construction, the more simultaneous the nests of a group were built. The duration of construction of every nest group was set in relation to the weather of each day (cf. II A; 2.).

4.3.3. Initiator of nest construction

Whenever possible the individual who started nest construction in the evening was identified. She or he was considered to be the initiator of nest construction for that particular group.

4.3.4. Nearest neighbour and sex of the nest owner

For a definition see chapter II; 4.2.4. Here only distances between identified nest occupiers were analysed, if all potential neighbours were known.

D. DATA ANALYSES

All data measured in the field were introduced into a data base (dBase IV) or in a graphics program of software (ACAD11) (c.f. chapter 4.2.). Extended results were calculated either by application of programs written in dBaseIV or in Clipper 5.0. For statistical analyses, the final results were introduced into the statistical package SPSS 6.0 for Windows. For regression analyses concerning, e.g. metrical dimensions as a function of group size, tests of second and third order were investigated. First, all dimensions averaged for each group were plotted against group size (one

point = one group), and second, all mean dimensions were averaged for all groups of one size (each point = all groups of one size). This decreased the sample size but strengthened the result, because values were closer to the mean and degrees of freedom were reduced.

SPSS provided for most tests a 2-tailed value of probability to 4 decimal places. Whenever possible the exact value of probability is given. However when SPSS gave a value of $p = 0.0000$, it was changed to $p < 0.0001$, since a probability value of 0 does not exist. For tests calculated by hand the resulting probability value was taken from standard statistical tables (ROHLF & SOKAL 1981). Probability values above 0.05 were considered to be not statistically significantly different from chance (n.s.). The following statistical guides were used: HAGGET *et al.* (1977), CLIFF & ORD (1981), SOKAL & ROHLF (1981), ZÖFEL (1988), BROSIUS & BROSIUS (1995).

III. RESULTS

1. THE EYENGO COMMUNITY

1.1. Demography

Table 9 shows the *number of individuals* in the Eyengo community distinguished by age and sex for the 4 field seasons. Between 1992 and 1994, the community's size increased from 32 to 34 individuals. Five infants were born: 3 females and 2 males. In the same period 3 adults disappeared: 2 females and 1 male. There were about twice as many females as males in the combined class of adults and adolescents. Thus, apart from infants and juveniles, the number of females outnumbered the number of males as indicated by the *socionomic sex ratio*, which ranged from 0.65 to 0.68. In contrast to the adult sex ratio, the ratio in infants was shifted towards males. In addition to this shift in sex ratio, there was a striking decrease from infants to juveniles and adolescents.

	Adults		Adolescents		Juveniles		Infants		Total	SSR
	M	F	M	F	M	F	M	F		
1990/91	6	13	1	2	1	2	5	2	32	0.68
1992	7	13	1	2	-	2	5	2	32	0.65
1993	6	14	1	2	1	2	5	3	34	0.65
1994	6	12	1	3	1	1	6	4	34	0.68
Losses & Gains	-1	-2	0	±1	0	0	+2	+3	+2	

Table 9: Eyengo community by age and sex classes for 4 seasons of research. Individuals changed age classes. Losses & Gains refer only to immigrants and missing individuals. SSR = socionomic sex ratio; M = males; F = females. For age sex classes see p. 40.

1.2. Party Size

15.05.1992

04:30 - It is pitch-dark as usual - we leave our base camp to walk to the nest group found the previous evening (EC 1100m E). The vegetation is wet from a brief night's rain. 05:20 - The sky becomes grey by the time we arrive at the nest site. It is misty and the Guerezas forgot to roar this morning. We wait for the bonobos to get up. All individuals seem sound asleep. Their nests are motionless, not the smallest bit of black fur is visible. They are completely hidden in their leafy bowls. There is not a single trace of faeces or urine, so the typical deep humming of the dung-beetles' invasion is missing ... Finally, one nest starts shaking. An infant appears at the rim and disappears again - it plays. 06:16 - A high frequency hoot from about 100m N brings life to the silent site. Individuals literally leap from their nests. They urinate, defecate, and descend to the ground. Within 5 minutes they travel in the direction of the loud call. I follow 2 males on the ground while Gottfried stays at the nest site to get a faecal sample from Gina and to mark the nests. There are more in the party than just the 2 males, but any count is impossible, as the understory is too thick. The party I am following forages on the ground, eats *Haumania* piths and Gambeya fruits. An hour later they are about 200 m NW of the nest site. Gina & Lolo, Viola & Vasco, Lolema, Lorle and an adolescent female, Max and Blas enter an emergent tree that I have never seen before. Its leaves and fruit remind me of mistletoe and I take some to try to identify later. Here they eat voraciously and start to groom about one hour later. I contact Gottfried via walkie talkie. He has marked 11 fresh nests and stays with Senufo and her son Ufo. Both left their nest 50 min after most of the individuals had left the site. They did not follow the larger party, but spent the day near the nest site, eating *Eremospatha* and *Safou*. The party I am with leaves the tree at 09:00 hr, and walks widely spread out on the ground to the East. They convene again at 09:30 in a large Gambeya tree. Thabita & Tagore, Seka and Planck have joined the party somewhere on the way, but I can not see Max and Lolema - have they chosen another route? The individuals I am with eat for about an hour before they again come to the ground and go on. 10:30 - A few minutes further East they stop for a Siesta. Some groom, others play, most rest - about an hour later they continue their travel

Even the first 4 hours of a routine morning description shows the fission-fusion character of bonobo society. Whether or not there is a pattern in both number and composition of parties is one focus of the following sections.

A total of 611 scans on party size during the day (05:00 - 18:00 hr) were done over 1990 - 1994. Of these, 108 parties were scanned at night nesting sites. The remaining 503 were scanned independently from nesting sites (For a detailed analysis of parties at night and the relation to day travel parties see III: 4.1.2.3.). Most (83%) of the 503 counts collected during the day took place when bonobos were in trees, and the remainder (17%) when they were on the ground. There was no difference in size between parties in trees versus on the ground: tree: $M = 5$, mean = 5.8, $SD = 3.35$, $n = 418$, vs. ground: $M = 5$, mean = 5.4, $SD = 3.27$, $n = 85$; Mann-Whitney U-test, $z = -1.1498$, $p = 0.25$, n.s. Overall, the mean party size of weaned individuals was 5.77 ($M = 5$, $SD = 3.34$, range 1 - 17, $n = 503$). On average, parties consisted of 7.12 individuals, when dependent offspring were also included ($M = 6$, $SD = 4.03$, range 1 - 22, $n = 502$). This represents about 1/5 of the community's membership.

1.2.1. Seasonal distribution

Figure 9 shows the median size of parties by day independently from night nest sites ($n = 503$) in different months of observation. Party size varied significantly from month to month (Kruskal-Wallis Median Test; $\chi^2 = 39.982$, $df = 21$, $p = 0.0075$). The average party size in the rainy season tended to be smaller ($M = 5$, mean = 5.60, $SD = 3.34$, $n = 324$) than in the dry season ($M = 6$, mean = 6.03, $SD = 3.33$, $n = 179$), but this

difference was not statistically significant (Mann-Whitney U-test: $z = -1.6991$, $p = 0.089$, n.s.).

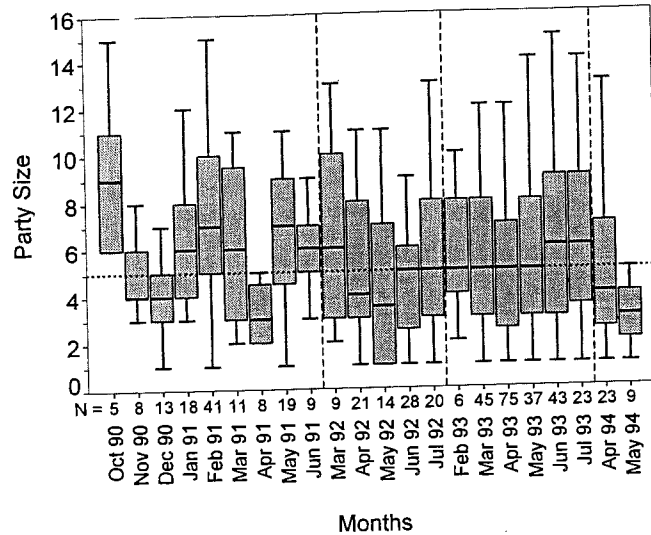


Figure 9: Median party size for each month of observation. Horizontal bar in boxes indicates median, length of box corresponds to interquartile range, limited by 75th percentile above and 25th percentile below. Bars outside boxes indicate range for observed values (excluding outliers). Horizontal dotted line indicates overall median party size ($n = 503$). Vertical dashed lines indicate gaps in observation between different years of study. N gives sample size by months.

1.2.2. Diurnal distribution

Party size fluctuated with the time of day. Figure 10 shows the mean party size with 95% confidence interval at each hour during the day. To complete the picture, 108 scans of parties at night nest sites were added to

the 503 scans investigated during the day, independently from night nest sites. The reference line indicates the average party size at day. Throughout the day parties joined and separated and thus size changed from hour to hour. There was a clear decrease in party size in the early morning until 07:00 hr and a clear increase at from 17:00 - 18:00 hr when they gathered to larger sleeping groups at night (Kruskal-Wallis 1-Way ANOVA; $\chi^2 = 49.756$, $df = 12$, $p < 0.0001$). This phenomenon is analysed in more detail in chapter III: 4.1.2.3). During the rest of the day, party size fluctuated without showing a regular pattern.

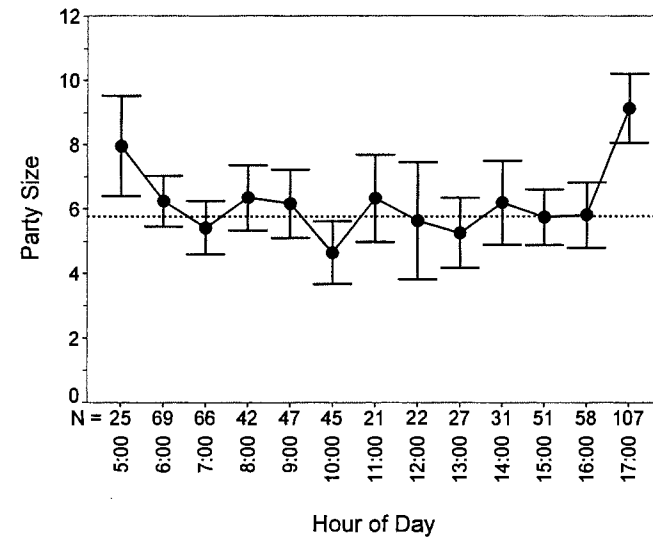


Figure 10: Mean party size for hour of day, with parties collected independently from nest sites ($n=503$) and at nest sites ($n=108$). Each point represents mean for all scans of party size for one hour of day. Bars indicate 95% confidence interval for mean. Dotted line represents overall party size independently from night nest sites ($n = 503$). Hour on abscissa represents begin of hour (5.00 = 5.00-5.59, 6.00 = 6.00-6.59, etc.). N gives sample size by hour.

1.3. Party Composition

A party during the day on average consisted of 1.6 males ($M = 1$, $SD = 1.295$, range 0 - 6) and 3.5 females ($M = 3$, $SD = 2.123$, range 0 - 11, $n = 485$). The maximum number of males per female was 3. The maximum number of females per male was 8. The overall socionomic sex ratio was 0.69 ($M = 0.67$, $SD = 0.23$, range 0 - 1). This result did not differ from the sex ratio of the community, overall. In 118 of 485 cases, the party consisted of one sex only: 17% were all-male and 83% were all-female. Most ($n = 367$) were mixed-sex parties. Expected frequencies of all-male parties and all-female parties, respectively, were calculated from the adult sex ratio in the community. Accordingly, females travelled more often without males than did males without females ($\chi^2 = 13.83$, $df = 1$, $p < 0.001$). All-male parties had an average group size of only 1.05, while all-female parties had an average group size of 2.48. This indicates that males travelled alone far more often than females did. Socionomic sex ratio did not depend on party size. Figure 11 shows the mean socionomic sex ratio for each party size class, which was almost always close to the overall socionomic sex ratio (dotted line). Only when individuals travelled alone, did males do so more often than expected by the socionomic sex ratio ($\chi^2 = 18.452$, $df = 1$, $p < 0.001$).

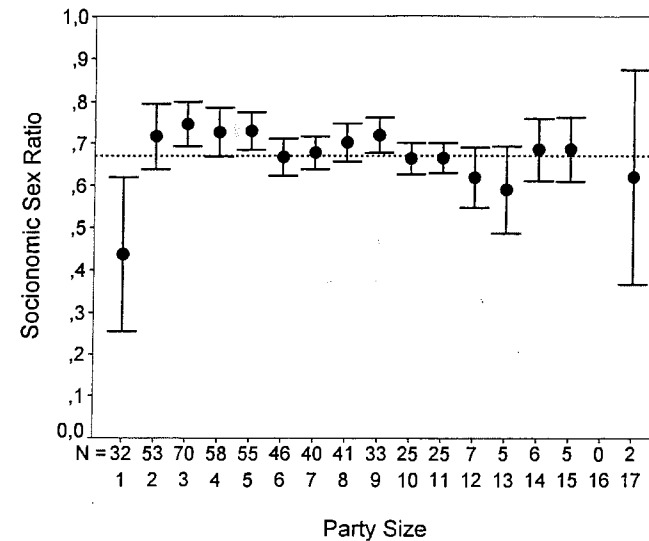


Figure 11: Mean socionomic sex ratio related to size of parties collected independently from nest sites ($n=503$). Each point represents mean for all scans of one party size. Bars indicate 95% confidence interval for mean. Dotted line represents overall socionomic sex ratio. N gives sample size by party size.

1.3.1. Monthly distribution

Figure 12 shows the median socionomic sex ratio for each month of observation. It differed significantly from month to month, mostly in favour of females (Kruskal-Wallis 1-Way ANOVA; $\chi^2 = 44.291$, $df = 21$, $p = 0.002$).

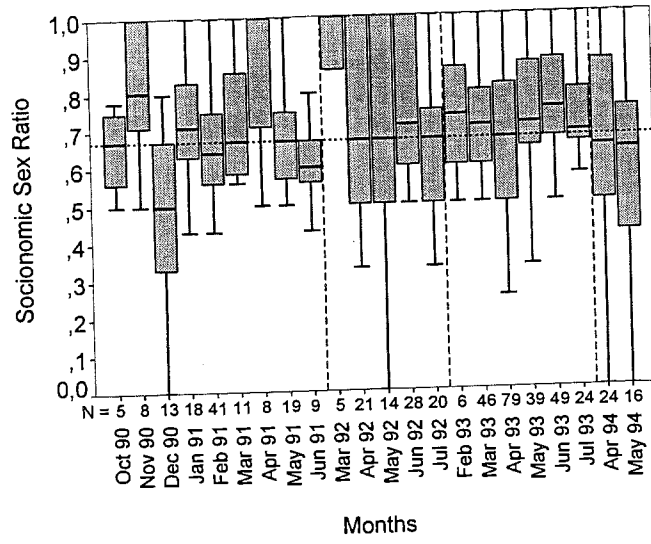


Figure 12: Median socioeconomic sex ratio for each month of observation. Horizontal bar in boxes indicates median, length of box corresponds to interquartile range, limited by 75th percentile above and 25th percentile below. Bars outside boxes indicate range for observed values (excluding outliers). Horizontal dotted line indicates overall median socioeconomic sex ratio for $n = 503$ parties. Vertical dashed lines indicate gaps in observation between different years of study.

1.3.2. Diurnal distribution

The ratio of males to females in a party did not change over the day. There appeared to be a slightly higher proportion of females than males at the end of the day, but, as a comparison of the mean socioeconomic sex ratio for each hour of the day indicates (Figure 13), the deviation was not significantly different from the overall mean (Kruskal-Wallis 1-Way ANOVA; $\text{Chi}^2 = 10.257$, $\text{df} = 12$, $p = 0.59$, n.s.).

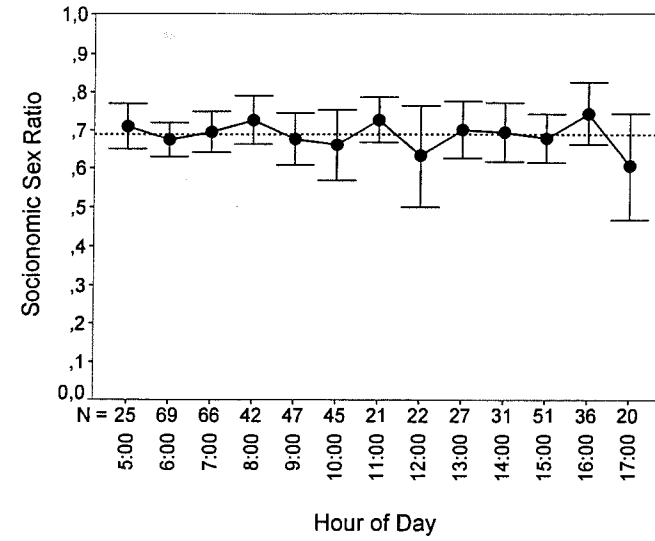


Figure 13: Mean socioeconomic sex ratio for each hour of day. Each point represents mean for all scans of one hour. Bars indicate 95% confidence interval for mean. Dotted line represents overall socioeconomic sex ratio for parties during day ($n = 503$). Hour on abscissa represents begin of hour (5.00 = 5.00-5.59, 6.00 = 6.00-6.59, etc.). N gives sample size by hours.

1.4. Travel Patterns

06.05.1993

05:00 - We leave camp shortly before dawn. It was a clear night with full moon, everything is dry and we expect them to start travelling early. Indeed, we are just in time upon reaching their nest site at 05:39. Some of the 16 individuals leave their nests 6 min later and travel East. 05:52 They enter several feeding trees, *Polyalthia* and a *Ficus*. Individuals in the trees separated by about 10 - 50 m keep acoustical contact.

07:54 - Max, the alpha male, briefly chases Pink - a late adolescent underdog - male,

before they continue to travel further east - without Pink! Another *Polyalthia* is entered at 08:15. Seven minutes later Lolema starts nest construction. They have an early siesta. Seven of 9 individuals build nests. 08:57 - A black mangabey's loud-call makes them jump out of their nests and vocalise. Or was there another vocalisation too far away for us to identify ?? 09:04 - The first individuals are back on the ground and head south. We follow. A small, sandy streambed, almost dry, directs their path. They go for sprouts, shoots, then dig in the mud and scratch in the sand - eating unidentifiable particles. They walk slowly, still tending to the south, south east. The sandy streambed changes into a small creek, and they strain the water through their fingers to trap shrimp and other delicacies. 10:31 About one kilometre further south they leave the streambed and enter the slope forest: Only *Gilbertiodendron dreweri* as far as the eye can see. The ground is covered by many layers of old red leaves each of them twice as big as my foot. Walking here at this time of the year is as noisy as in late October at home. They systematically overturn the leaves, exposing the bare earth underneath to daylight. Sometimes they suddenly start to dig and eat pieces so small that again I cannot identify them. Are they eating larvae? Eggs? Mushrooms? - Holes I check when they have left are empty - of course - and I have no time to mimic their digging since I have to keep up with them. They continue walking between forest and swamp, shifting between digging and palm heart consumption. At 11:10 we cross the X trail at 2850 m, close to its end - they continue east. We leave the familiar range and enter completely new (to me!) parts of the forest, walking through muddy basins with unfamiliar vegetation, with only the swamp palms to give a familiar picture, and the systematic, loud cracking that gives proof of the bonobos consuming leaf marrow. 11:20 - We again reach a river. Volker, an adolescent male close to us, seems to have lost contact to the party. He vocalises and gets many answers, reflecting a widespread group ranging from Volker ahead of us to much further south. We join most of the individuals at 11:57 again in a *Gilbertiodendron* forest. They are still digging, but then suddenly form a line - the usual sign for faster travel. We keep up and at 12:09 reach the Yirte river. Compared to the watercourses we are used to in the familiar home range, this is a large stream: about 10m wide and hip-deep, amber coloured but crystal clear and fast running. There is a tree which is fallen partly and touches the trunk of a tree on the opposite bank. We see Lolema, Max, Gina, Blas, Kamba & Mongo and Volker climb this stem. We enter the river and wade across, but fail to spot a metre-long wasps' nest hanging from a sidebranch directly across the river, at about 1.50 m above the water surface. When we emerge from heavy attacks by the wasps, the bonobos are gone. We decide to find our

way back to familiar terrain, in case of unforeseen reactions to the many stings. That evening, about 3 km north of that spot, Medoz, the field assistant, finds a night nest group. The next morning brings not only 13 new nests, but also half of the individuals who left us behind, when we got waylaid by the wasps at the river.

Extended travels through the basins are a regular pattern during the dry months, when fresh, succulent fruit is scarce in the primary forest. However, there are other days, mostly days of heavy rain, when bonobos hardly move, build one nest after the other, eat little and sleep much. The following chapter tries to calculate the average travel distances for nearly complete all-day follows.

Table 10 indicates the mean daily travel distances of parties in terms of the completeness of the observation. The first category, T1, represents travel distances from parties followed all-day, from leaving the nest in the morning to building a new nest in the evening. This 100% nest-to-nest distance was 3077 m per day on average. For the second category, T2, we followed individuals for 9 - 11 hours a day (so, 99% - 85% of the nest-to-nest distance was recorded). These averaged 2681 m per day. Extrapolated to the comparable length for an all-day follow, the bonobos travelled 2916 m per day. In the third category, T3, the mean number of observation hours was 8 - 9 hours (or 84% - 75% of daily activity), and the mean distance individuals travelled during that time was 2490 m. Extrapolated to the extent of an all-day follow, it was 3113 m per day. Shorter periods of observation have been excluded from analyses, as being too incomplete. The sum of the nest-to-nest follows mentioned above (n = 86) provide a known underestimate of the daily travel distance, being on average 2793 m per day. Summing up the more accurate results obtained by extrapolation, the more realistic average travel distance for bonobos at Lomako was 3035 m.

	Mean	SD	Min	Max	n
T1	3077	181	800	5200	34
T2	2681 (2914)	230	600	7800	32
T3	2490 (3113)	246	400	5500	20
Total	2793 (3035)	1174	400	7800	86

Table 10: Travel distances (m) according to 3 levels of completeness (T1-T3). Proportion of nest-to-nest observation: T1 = 100%, T2 = 85% - 99%, T3 = 75% - 84%. Numbers in brackets indicate comparable length to all-day follows (T1) obtained by extrapolation.

1.5. Home Range

Figure 14 shows the home range of the Eyengo community. All 100 m² quadrats of the grid superimposed on the map and entered by the community resulted in the polygon marked by shaded squares. This total surface area was 13.2 km², and is the most conservative calculation of the home range of the community. The range was increased to a surface area of 14.7 km² by smoothing the polygon's sides (bold perimeter line). The resulting increase adds 11.5% to the obtained range. The larger area has been used for density calculations and ecological samples.

Most (64%) of the home range was primary forest. It consisted of the polyspecific evergreen forest (44%) and a lesser proportion of slope forest (*Gilbertiodendron dewevrei*, 20 %). Most of the slope forest was concentrated in the eastern part of the range. Swamp made up 32% of the home range, also concentrated in the eastern part of the area. Only about 5% of the range was secondary forest. The same proportions emerged when habitat types were investigated along standardised transects.

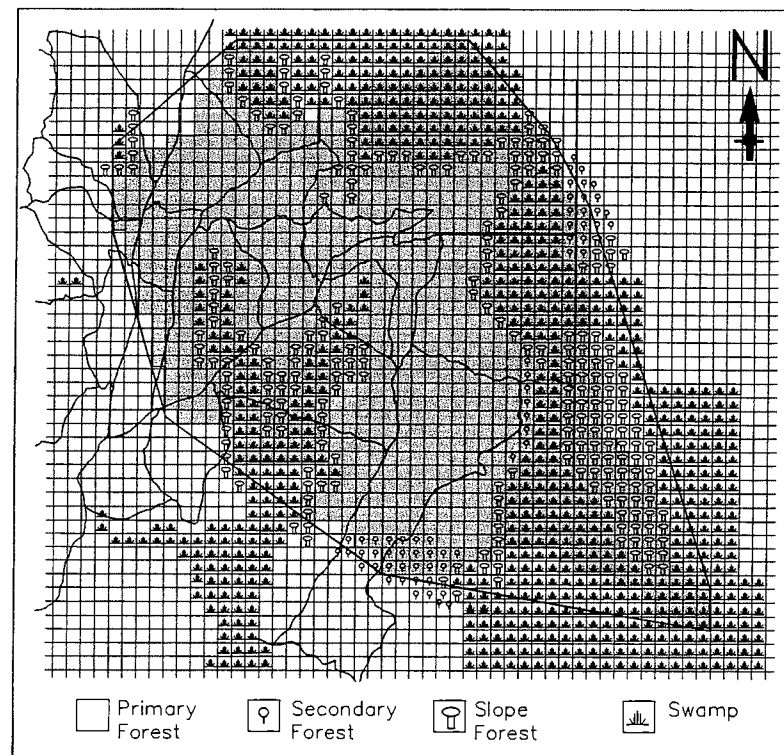


Figure 14: Home range of Eyengo community and habitats. Shaded squares indicate all quadrats entered by community members = most conservative calculation (13.2 km²). Bold perimeter line indicates extrapolation of the conservative range (14.7 km²). Lines represent trail system. Each square is 100 m x 100 m.

2. NEST TREES: AVAILABILITY & CHOICE

The aim of this part of the study was to determine the physical properties and abundance of nesting trees. A total of 1753 trees used for nest construction were analysed, and compared with potential nest trees recorded in the forest plots. The sample sizes of the respective forest plots are given accordingly in each analysis.

2.1. Height

Figure 15 shows the frequency distribution of heights of potential versus nested-in trees. The 1753 trees used for nest construction had an average height of 21.1 m ($M = 20$, $SD = 8.17$, range 3 - 60). Taking into account all trees with a minimum height of 3 m, data from 10 forest plots taken in 1991 (see methods) showed that potential nest trees had an average height of 7 m ($M = 5$, $SD = 6.12$, range = 3 - 52, $n = 1641$). Bonobos clearly selected taller trees (Mann-Whitney U-test: $z = -44.2935$, $p < 0.0001$). To avoid the potential bias of having many trees below 5 m (60%) within the plot sample, a more conservative analysis was restricted to the range in which most of the trees used for nest construction were found. The majority of nested-in trees (82%) belonged to the middle layer of the forest (range 11 - 30 m high). Only 12% of the plot sample consisted of this layer. Focussing on this layer only, the difference between potential and used nest trees by height was again significant. The nested-in trees ($n = 1436$) had a median height of 20 m, which was higher than the potential trees ($n = 201$) with a median height of 15 m (Mann-Whitney U-test: $z = -8.5308$, $p < 0.0001$). Bonobos were highly selective for trees of medium height in which to nest.

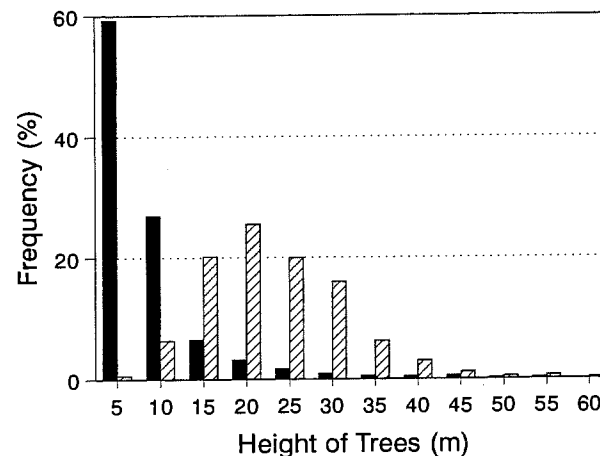


Figure 15: Height of potential nesting trees (black bars; $n = 1641$) and used nesting trees (hatched bars; $n = 1753$). Each class of height (m) represents upper limit of class (5 = 1-5; 10 = 6-10 etc.)

2.2. Stem Diameter

Figure 16 shows the frequency distribution of diameters (DBH) of 1753 trees used for nest construction. These ranged from 2 to 296 cm with a median of 19 cm. The frequency histogram shows that 99% of trees chosen for nest construction had a diameter of more than 5 cm. In contrast, most (77%) of the potential nest trees had diameters between 2 and 5 cm ($M = 3$, range 2 - 137, $n = 1673$). Thus the diameter of the nested-in trees was significantly greater than that of potential ones (Mann-Whitney U-test: $z = -44.7396$, $p < 0.0001$). Bonobos were selective in the diameter of the trees chosen for nest construction. Since diameter correlated positively with tree height (linear regression; $r = 0.71$, $F_{1,1751} = 1796.30$, $p < 0.0001$;

$R^2 = 0.51$) it can be concluded that bonobos favoured larger trees more than smaller ones.

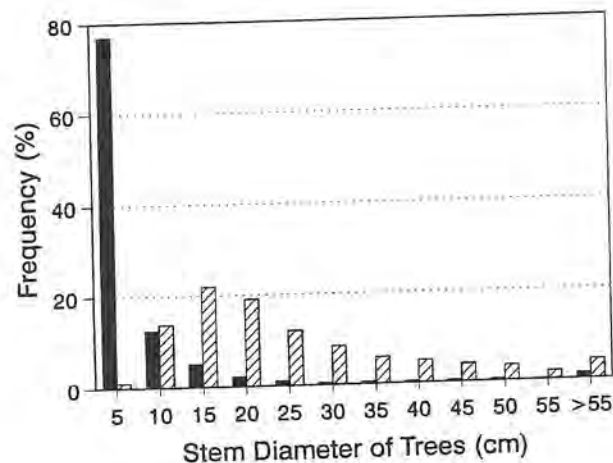


Figure 16: Stem diameter of potential nesting trees (black bars; $n = 1641$) and used nesting trees (hatched bars; $n = 1753$). Each class of diameter (cm) represents upper limit of class (5 = 1-5; 10 = 6-10 etc.)

2.3. Height of Crown

The height of the lowest branch and the vertical dimension of crowns used for nest construction were investigated. Crowns chosen for nest construction started on average 10.7 m above the ground ($M = 10$, $SD = 4.129$, range 2 - 31 m; $n = 513$). The vertical extent from the lowest branch to the top of the crown ranged from 1 m to 33 m ($M = 11$, mean = 11.8 m, $SD = 6.005$; $n = 512$). Both the height of the lowest branch and the vertical extent of the crown correlated positively with tree height. (linear regression; lowest branch: $r = 0.54$, $F_{1,510} = 214.04$, $p < 0.0001$,

$R^2 = 0.30$; length: $r = 0.83$; $F_{1,510} = 1094.05$, $p < 0.0001$, $R^2 = 0.68$). No data were taken on the availability of tree top sizes, but choice for bigger tree tops reflects the choice for taller trees.

2.4. Species

To test for selectivity in species of nesting tree, 16 plots along standardised transects and 17 plots containing nesting sites were investigated. These 33 plots contained 1052 trees of more than 5 cm diameter. Most of these trees (91%) were identified as 80 species; the rest (9%) remained unidentified. A comparison of the randomly chosen plots with those where nests were constructed showed the bonobos' selectivity in their choices of nest sites. The plots used for nesting sites had different species compositions from the randomly selected plots. While in the randomly selected plots 64 species were identified, there were only 52 species in the plots with nesting sites. Only 36 species were the same in both plot types. In addition many of them occurred at much different frequencies ($\text{Chi}^2 = 110.568$, $df = 13$, $p < 0.0001$). About one third of the randomly chosen plots occurred in swamp. However, not a single nest group was seen in that type of habitat (for habitat choice see III; 4.1.).

To get a more conservative idea of bonobos' species selectivity, the randomly chosen plots were excluded from further analyses. This left 17 forest plots with 554 potential nesting trees. Most of this sample (89%) was classified into 52 species and was compared to the proportion of identified species (92%) of 634 trees used for nest construction. Only 26 species of the 52 potentially available species were used for nesting. Figure 17 shows the frequency for the 10 most often used tree species and the availability of these species. As can be seen from the 10 tree species most frequently chosen at Lomako, 6 (DZ, SZ, PS, AM, CS, SG) were used with higher

frequencies than expected by chance, 2 (CG & D_(a)) with lower frequencies and 2 (GP, D_(b)) fitted the expectations ($\chi^2 = 532.90$, $df = 9$, $p < 0.001$). Trees bearing ripe fruit were never used for nest construction at night, although the fruits of the most often used tree species were part of the bonobos' diet. However, trees used during the day for nest construction often bore ripe fruit. Bonobos therefore were not only selective concerning their nest sites, but also they showed high selectivity toward certain tree species and considered the phenological state of the trees chosen for nest construction.

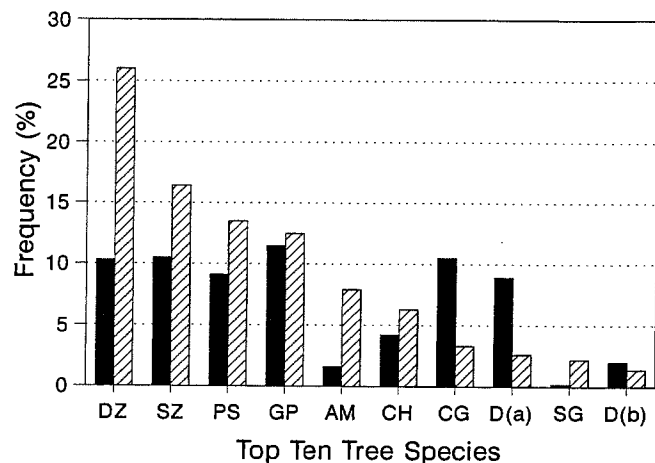


Figure 17: Ten most often used tree species (hatched bars; $n = 634$ trees) and their percentage of availability (black bars; $n = 554$ trees). DZ = *Diogoia zenkeri*, SZ = *Scorodophloeus zenkeri*, PS = *Polyalthia suaveolans*, GP = *Garcinia punctata*, AM = *Anonidium mannii*, CH = *Crudia harmsiana*, CG = *Cola griseiflora*, D(a) = *Diospyros* sp. a, SG = *Strombosia grandifolia*, D(b) = *Diospyros* sp. b.

2.5. Leaf size

Figure 18 compares the representation of the different classes of leaf size in potential nest ($n = 1641$) and nested-in trees ($n = 1694$). Small and medium sized leaves were chosen more frequently than expected. In the class 'large', availability and choice were more or less balanced, while the class 'extra large' was chosen less frequently than expected ($\chi^2 = 73.536$, $df = 3$, $p < 0.0001$).

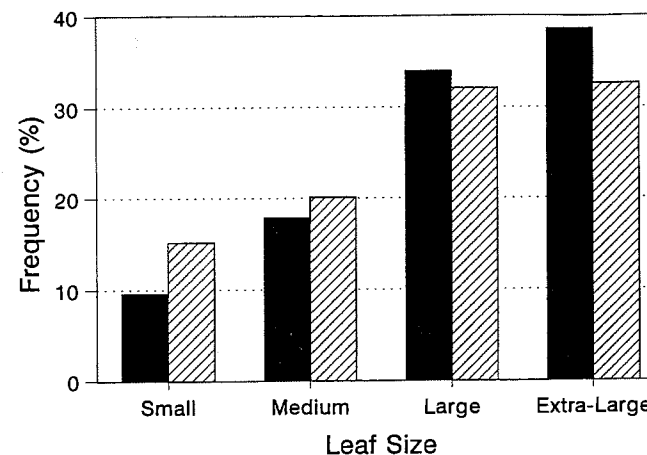


Figure 18: Class of leaf size collected from potential nest trees (black bars; $n = 1641$ trees) and trees used for nest construction (hatched bars; $n = 1694$ trees).

Table 11 shows the variation of leaf size for the 10 most often used tree species. For any species the leaf size usually covered 2 classes. Despite the fact that leaf size was species specific, it was calculated to what extent leaf size could be considered as a function of tree size. The

mean DBH of the tree stem was calculated for each class of leaf size for each of 7 species where there was both variation in leaf size and sufficient sample size (*Diogoa zenkeri*, *Polyalthia suaveolans*, *Garcinia punctata*, *Anonidium mannii*, *Crudia hamsiana*, *Cola griseiflora*, and *Diospyros* sp. a). The diameter was always larger in the larger class of leaf size (t-Test, $t = -3.27$, $df = 10$, $p = 0.008$). Leaf size therefore is a function of tree size.

Species n (trees)	DZ	SZ	PS	GP	AM	CH	CG	D(a)	SG	D(b)
123	83	53	48	33	31	16	14	3	4	
Leaf Size (cm ²)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
< 5.0	0	100	0	0	0	0	0	0	0	0
5.0-24.9	0	0	19	63	0	90	0	0	0	75
25.0-64.9	10	0	81	37	9	10	25	71	33	25
> 65.0	90	0	0	0	91	0	75	29	67	0

Table 11: Class of leaf size for 10 most often nested-in tree species. DZ = *Diogoa zenkeri*, SZ = *Scorodophloeus zenkeri*, PS = *Polyalthia suaveolans*, GP = *Garcinia punctata*, AM = *Anonidium mannii*, CH = *Crudia hamsiana*, CG = *Cola griseiflora*, D(a) = *Diospyros* sp. a, SG = *Strombosia grandifolia*, D(b) = *Diospyros* sp. b.

3. NESTS

3.1. Physical Correlates

05.03.1993

07:58 - After heavy and long overnight rains (10.5 mm), we join the party not far from their night nest site. They eat in *Dialium* emergents between 50 and 60 m above the ground. Two nests are visible but I cannot identify any individual. - The nests may be from a previous visit. 08:13 - Blas breaks three branches, lies down on them and continues to eat. This platform took him only a few seconds to make. 08:15 - Gina starts nest construction close by 2 minutes later. She also takes less than a minute and continues to eat, adding each stripped twig to her nest. She is joined later by Bhagmati and another female with dependent offspring. They groom extensively.

29.04.1993

Not a single sunbeam has penetrated the thick layer of grey clouds for the entire day. The party I was with had travelled only about 400 m, a ridiculously short distance by bonobo standards. They spent hours in day nests, seemingly still tired and ready for an early nap. 17:11 - EC 250 S. A few metres from the last *Irvingia* feeding site, Thabita, Zora, Gina, Viola and the others enter trees. Their repeated distance calls promise night nest construction soon. 17:13 - Focus on Zora and her about 3-year-old son, Zulu: Will she use the tree she is now in for nest construction? No. Instead, she climbs into the upper part of the crown and then crosses over to the next tree. She bridges several trees in the same way, using adjacent or overlapping side branches. Then she moves onto a projecting branch of an Efombo tree. Walking on it towards the end, the branch bends under her weight and touches a side branch from the neighbouring Efombo tree. This time she does not cross but rather grasps a side twig of the neighbouring branch and breaks it into her direction. It is 17:27. She continues breaking additional twigs, pauses for about 15 sec, looks around, steps on the now integrated branch from the neighbouring tree and breaks twigs from her original branch. She continues until 17:31. The nest is about 25 m high, properly circular and neatly fixed to the branches deriving

from the 2 different trees. Zulu is hanging from a side branch, dangling playfully around his own axis. Zora lies in her nest, moving about as if to test its shape, and indeed, 2 minutes later she completely detaches several twigs from outside the nest and adds them to the nest cavity. Half a minute later she lies down, and Zulu immediately joins her.

Day and night - 2 situations, 2 types of nests. The following sections deal with the structural differences of both types of nests, focussing on type of construction, and on height. Since day nests will be more intensively treated in the second part of this chapter, the emphasis in this part is on night nests. Position, weather-dependent changes in the choice of placement, and structural details are shown.

Detailed, quantitative analyses were done on 1373 nests: 91% were built for overnight sleeping, 9% for resting during the day. Since previous analyses (FRUTH & HOHMANN 1993) revealed differences between day and night nests, these will be treated separately in the following analyses.

3.1.1. Type of construction

Integration of woody vines or lianas entangled in the tree of choice occurred regularly in day and night nests. These, however, were not considered to be actively integrated and thus were not analysed. Therefore, the data presented here refer to trees only.

Analyses of the number of trees contributing to a single nest involved 1240 night nests and 120 day nests. Figure 19 shows that for night nests, non-integrated (i.e. single-tree) nests accounted for about 3/5 of all nests.

The rest (40%) belonged to the class of integrated nests, combining up to 6 trees. In contrast, 115 of 120 day nests (96%) were built with material of only one tree. The other 5 day nests integrated parts of 2 trees. Hence the numbers of trees contributing to day nests vs. night nests were significantly different ($\chi^2 = 133.7$, $df = 4$, $p < 0.001$).

Figure 20 shows the classification of 1217 night nests and 120 day nests into 5 different types of construction. Night nests were constructed most often on a side branch (37%), but most nests were of other types. Day nests were built almost always on a side branch (92%), but never on 2 or more side branches combined. The distributions of types over day and night nests clearly differed.

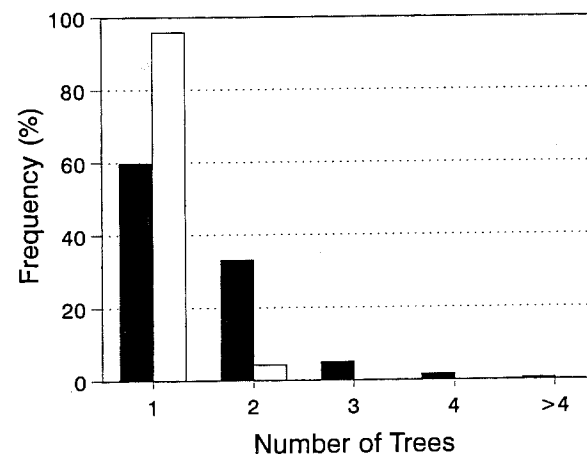


Figure 19: Number of trees involved in night nests (black bars, $n = 1240$) and day nests (white bars, $n = 120$).

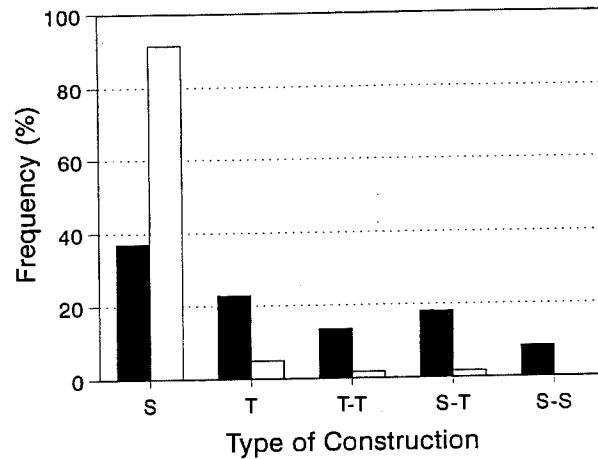


Figure 20: Different types of construction for night nests (black bars, $n = 1217$) and day nest (white bars, $n = 120$). S = side branch, T = tree top, T-T = 2 or more tree tops combined, S-T = 2 or more side branches or tree tops combined, S-S = 2 or more side branches combined.

3.1.2. Height

Figure 21 shows frequency distributions for night ($n = 1081$) and day nests ($n = 112$) with regard to absolute height. Most of the night (86%) and day nests (79%) were sited in the middle layer of the canopy, but the percentage of nests built above 30 m was greater in day nests (9%) than in night nests (1%). While no night nest was constructed above 37 m, day nests were as high as 50 m above the ground. The mean heights of the 2 kinds of nests differed significantly: Night nests were much lower ($M = 16$, mean = 16.1 m, SD = 5.093, range 3 - 37 m) than day nests ($M = 20$, mean = 20.4 m, SD = 8.307, range 5 - 50 m) (Mann-Whitney U-test: $z = -5.5257$, $p < 0.0001$). No evidence for construction of nests on the

ground was found during this study. However, when resting on the ground, individuals sometimes chose logs to lie on, and rarely they bent an nearby twig for use as a cushion.

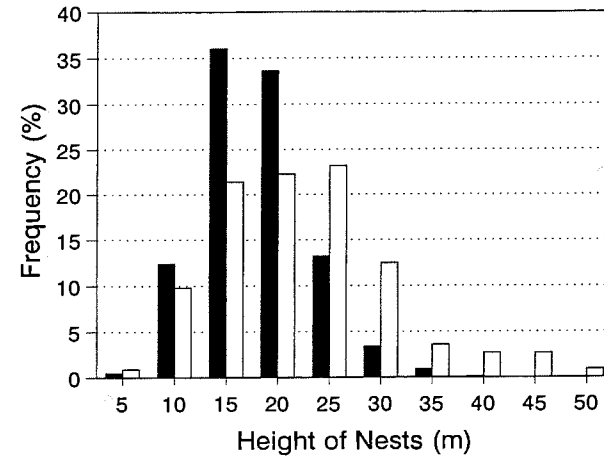


Figure 21: Height of night nests (black bars, $n = 1081$) and day nests (white bars, $n = 112$). Each number on abscissa represents upper limit of a class (5 = 1 - 5 m, 10 = 6 - 10 m, etc.).

3.1.3. Position within the crown

The position within the crown was calculated for 613 trees used for night nest construction. For these trees both measures, length of the stem and height of the lowest branch were available. The average position was 0.52 (SD = 0.22, range 0.07 - 0.94), that is almost exactly in the middle of the crown. Most nests (45%) were located in the middle third of the crown, fewer were located in the upper third (31%), and least in the lower third (24%).

3.1.4. Cover

For 658 nests built for sleeping overnight, it was recorded whether or not nests were sheltered by an overhanging layer of vegetation. Fiftyfive percent of these nests were directly exposed to the sky, while 45% were covered by vegetation overhead. To estimate the influence of seasonality on the presence or absence of cover, I used monthly seasonality correlations (c.f. methods B.2.). Only 44% of nests built during the wet season ($n = 594$), versus 55% of nests in the dry season ($n = 64$) were covered by overhanging vegetation. This difference between seasons was not statistically significant ($\text{Chi}^2 = 2.61$, $df = 1$, $p > 0.05$, n.s.). To refine the above analysis, the occurrence of rain at midday or afternoon was noted for each date: On rainy days, 58% of the nests were open to the sky while 42% were closed. On dry days, however, the result was no different: 54% were open while 46% were overhung.

3.1.5. Architectural details

For detailed scrutiny of a nest, it was necessary to be close to it. Since only limbs close to a tree trunk supported my weight, only those nests were examined in detail. For preliminary investigation, 24 fresh nests were examined. Table 12 shows detailed measurements for nest dimensions, supporting branches, bent, broken, and single twigs. For visual depiction of the points of measurement, see Figure 7.

Parameter		mean	M	SD	min	max	Nests n	
Distance to Stem	cm	101.3	85	124.80	1	400	10	
Diameter of Stem	cm	28.5	25	10.80	10	50	12	
Branches Used	n	3.9	3	2.021	2	9	22	
Supporting Branches	n	1.6	2	0.656	1	3	23	
Vertical Distance Between Branches	cm	127	110	73.659	35	230	9	
Diameter of	cm	92.1	90	17.339	65	130	19	
Nest	inside	cm	60.0	70	21.794	35	75	3
Depth of	cm	30.4	30	8.264	20	40	3	
Nest	inside	cm	18.3	15	10.405	10	30	5
Twigs Bent	<1cm	n	7.7	7	5.056	2	16	10
	1-2 cm	n	4.3	3	2.915	2	11	9
	2-3 cm	n	1.6	1	0.894	1	3	5
Twigs Broken	<1cm	n	3.7	4	2.250	1	7	13
	1-2 cm	n	3.8	4	1.815	1	7	12
	2-3 cm	n	1.7	2	0.751	1	3	11
Twigs	< 1 cm	n	8.7	5	7.851	1	28	15
Detached	1-2 cm	n	1.0	1	0	1	1	5

Table 12: Measurements of nests in detail. For depiction of parameters, see Figure 7. Nests column indicates number of nests for which parameters were investigated.

Distance to stem: The rim of the nest closest to the trunk was on average about a metre away. At the level of the nest, the stem had a diameter of about 25 cm. *Supporting branches:* On average 3 side branches were used per nest. Two of them supported the nest from below, while the other one provided nest substance from above. The average vertical distance along the stem between the supporting side branches and the main branches from the side was 127 cm. *Dimensions:* On average, nests had a horizontal diameter of about 90 cm from rim to rim and an inner

diameter of 60 cm. The vertical thickness varied between 20 and 40 cm; rarely, a cup-shaped depression of 10 to 30 cm in depth was visible. *Twigs*: In addition to branches projecting from the stem, all nests included bent and broken twigs ranging from less than 1 cm to 3 cm in diameter at the proximal end. Up to 21 bent twigs, and up to 14 broken twigs were incorporated into a nest. The larger the diameter of the twigs, the fewer were included. A typical nest had 7 bent and 4 broken twigs of less than 1 cm median diameter, 3 bent and 4 broken twigs of 1 - 2 cm diameter, and 1 bent and 2 broken twigs of 2 - 3 cm diameter. All nests also contained loose twigs for lining. Three-quarters of these twigs had a diameter of less than 1 cm, and the rest were 1 - 2 cm. Not a single detached twig had a thickness of more than 2 cm. The number of detached twigs varied from 1 - 28 per nest.

3.2. Behavioural Correlates

23.05.1991

09:05 - Luna, a juvenile female, starts building a day nest, when Bhagmati, a late juvenile female, approaches the uncompleted rim. With open-mouth play face, she invites play from Mara. Tussling starts - but Mara seems not to be in the right mood. She gives up her first construction and starts her second nest about 1m away - as if she wants to make clear that she wishes to be left alone. **09:07** - Bhagmati improves the captured nest, while Luna finishes hers. Once finished, Luna seems to have changed her mind. She now approaches Bhagmati with open-mouth play face. She playfully grooms her, tussles, grooms again. Both are now in the nest that was started by Luna and finished by Bhagmati. I can hear them laughing. **09:09** - Lea, a female infant jumps between them, and Ufo, an infant male, immediately follows. The nest looks fragile and so both juvenile females cooperatively improve it. **09:10** - They chase each other, chase

Ufo, trying to get the twig he holds in his mouth, and chase Lea. They dash through the entire crown, also use the adjacent ones, then come back to the nest. The one who enters the nest first seems to be the winner, then a brief tussling, and all participants are off again. **09:15** - The nest is short about to fall to pieces, so they improve it again. **09:21** - *dito*. Bhagmati breaks a huge twig to cushion the nest's depression. By now the nest has got so large that it nearly touches Lunas' second nest. This nest in the meantime has been properly improved by Geraldine, Lea's mother. She almost has redone what Luna abandoned, and, in spite of the heavily undulating movements of the players nearby, she seems to get some rest. **09:50** - By the time Lolo, another infant female, joins in the play party, the nest is vacant. Bhagmati now uses the solid construction to give herself some rest, before she is joined by Lolo. **10:06** - While Luna, Lea and Ufo continue chasing through trees, Gina, Lolos' mother, improves within seconds what's left of the abandoned play nest and lies down. All leave at **10:30**.

25.05.1991

06:00 - E 2000m N. We are sitting with more than 10 individuals at an Irvingia feeding site. Irvingia, a mango-like fruit, is today's breakfast. Max is the bravest of the Eyengo males. For several days in the row, he has sat less than 10 m from us, seeming to shield the rest of the group from our potential threat. Also he is busy in getting Vanessa's attention. She is at maximal swelling and wherever she goes, many males follow. Max and Renki are the most successful males in mating her, but the conflict between them escalates from day to day. **06:09** - Chasing between Max and Renki breaks out again. Both bristle their hair and noisily drag branches, ending with high pitched screams. They are "playing chicken", trying to intimidate the other one by running directly towards him. Max seems to be more effective in threatening Renki - and remains calm himself when Renki directs towards him. **06:11** - Renki has had enough. He quickly climbs a tree and in a fork about 8m up, he builds a rudimentary nest within seconds. Max leaves his branch right under the tree, and for the next 14 minutes he remains within 10 m of the stem, regularly throwing threatening glances at Renki. Renki, motionless for about 4 minutes, improves his nest at **06:15** and lies down. He successfully escapes Max's persecution. **06:25** - Max walks toward Vanessa; Renki remains in his nest. **06:33** - Renki climbs to the ground and vanishes in the direction opposite to where Max left 8 min earlier.

Different examples, different situations, different individuals: Nests have an enormous array of variability - not only structural, as seen in the earlier part of this chapter, but also in terms of the related investment and behaviour. The following sections deal with different aspects: Distinctions between day and night nests are made on the level of behaviour and context; solitary or social activities are analysed for day nests only. Individuality then gives way to an attempt to give a generalised picture of sex- and age-related features.

3.2.1. Time of construction

Figure 22 shows the temporal distribution of the onset of construction for 584 nests. The earliest time of nest building was 05:38 hr, the latest time was 18:01 hr. Although nests were built at most times of day, 2 distinct peaks of nest building activity emerged. The first corresponded to an extended period of rest in mid-morning. The second peak late in the afternoon coincided with occupation of the night sleeping site. Day nest construction started earliest at 05:38 hr and latest at 16:23 hr ($n = 307$). Night nest construction started earliest at 16:00 hr and latest at 18:01 hr ($n = 200$). The end of night nest construction usually coincided with sunset. It was dark by 18:00 hr with periodical changes of up to ± 15 minutes over the year.

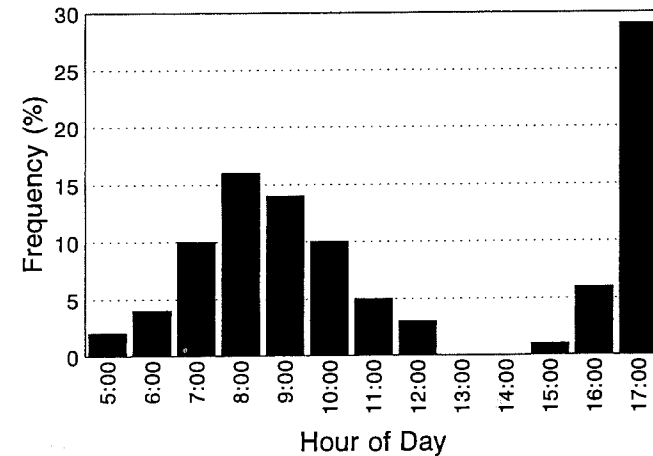


Figure 22: Hour of day of construction of nests ($n = 584$). Each time point on horizontal axes represents start of hour recorded. e.g. 05:00 hr = 05:00 - 05:59 hr, 06:00 hr = 06:00 - 06:59 hr, etc.

3.2.2. Duration of construction and time of utilisation

Duration of nest construction varied from a few seconds to 8 minutes. Bonobos needed about 2 minutes on average ($M = 1$, mean = 2.03 min, $SD = 2.069$, $n = 439$). Figure 23 shows that nests built for the night took significantly more time than those for the day (Mann-Whitney U-test: $z = -15.4074$, $p < 0.0001$). On average bonobos needed 4.3 min to build a night sleeping platform ($M = 4$, range 1 - 8, $n = 239$) whereas it took them less than a minute to build a day bed ($M = 0$, range 0 - 4, $n = 145$; here, zero means 1-59 sec). *Duration of use* of day nests averaged 35.4 min ($M = 27$, range 0 - 156 min, $n = 190$), while the estimated time spent in night nests was 10 to 12 hours.

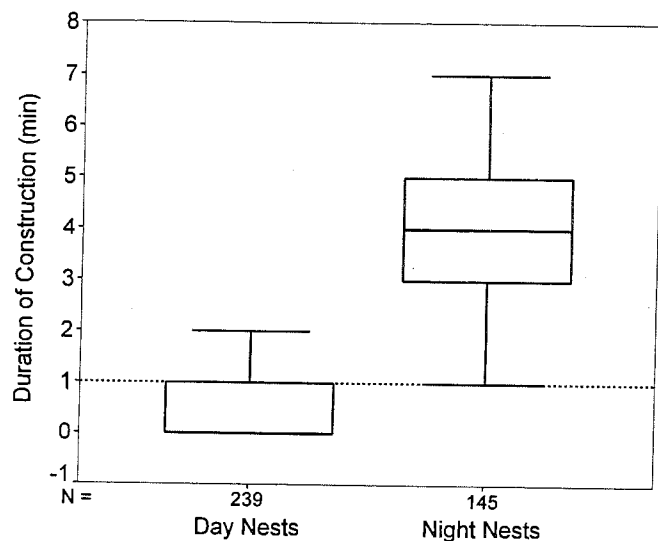


Figure 23: Duration of construction for day nests ($n = 239$) and night nests ($n = 145$). Horizontal bar in boxes indicates median, length of box corresponds to interquartile range, limited by 75th percentile above and 25th percentile below. Bars outside boxes indicate range for observed values (excluding outliers). Dotted line shows overall median duration of nest construction ($n = 384$).

3.2.3. Sex differences

To investigate the possibility of sex differences in the choice of nesting trees and in nest building, only nests of mature individuals were used. Unless specified otherwise, data on sex differences refer to 324 nests measured in detail, 228 nests built for the night, and 96 nests built during day. Behavioural data refer to 507 nests, 200 built for the night, and 307 nests built during the day.

3.2.3.1. Night nests

Of the 228 night nests, 140 were built by females and 88 by males. Considering the *tree species* used for nesting, both females and males chose the same species of trees with minor but significant differences ($\text{Chi}^2 = 21.157$, $\text{df} = 12$, $p < 0.05$). Figure 24 shows sex differences in the choice of tree species for the top 10 species. The only striking difference was in use of *Garcinia punctata* (GP), a medium sized tree of 20 - 35 m. The stem grows straight and main branches from the side grow right-angled to the stem. Branches and twigs are densely covered with medium sized, leathery leaves. It is easy to get enough material from adjacent twigs to make a comfortable cushion, and more than one nest may be built on a single side branch. This species is used by males much less often than expected.

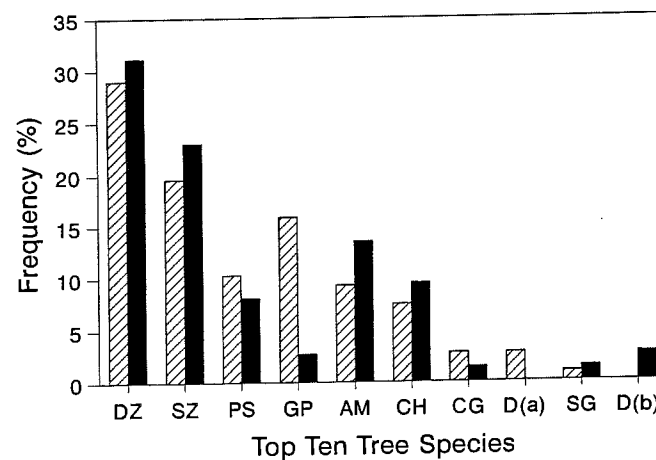


Figure 24: Sex differences in 10 most often used tree species, for females (hatched bars, $n = 140$) and males (black bars, $n = 88$). DZ = *Diogoa zenkeri*, SZ = *Scorodophloeus zenkeri*, PS = *Polyalthia suaveolans*, GP = *Garcinia punctata*, AM = *Anonidium manni*, CH = *Crudia hamsiana*, CG = *Cola griseiflora*, D(a) = *Diospyros* sp. a, SG = *Strombosia grandifolia*, D(b) = *Diospyros* sp. b.

Significant sex differences were also found in the *height* of nests. Females built nests higher ($M = 18$, mean = 18.3 m, $SD = 5.103$, range 8 - 35, $n = 135$) than did males ($M = 14$, mean = 15.2 m, $SD = 4.934$, range 7 - 31, $n = 75$) (t -Test: $t = -4.31$, $df = 157.4$, $p < 0.001$). Nests of males ($n = 87$) and females ($n = 140$) showed the same *type of construction* (cf. Figure 25). They were mostly made from a single tree (about 60%) and less often from 2 or more trees (40%). Among integrated nests, differences emerged focusing on nests, where only tree-tops were integrated. These nests mostly joined 3 smaller trees resulting in a tripod, with the nest located centrally like a spring mattress. Fifteen percent of males' nests were constructed that way while only 6 % in females were so. This differed significantly from the expected value for both males and females ($\chi^2 = 4.075$, $df = 1$, $p < 0.05$). Figure 26 shows the frequency distributions of *duration of construction* for night nests by females and males. Males built nests significantly faster than females did (males: $M = 3.0$, mean = 3.65 min, $SD = 1.289$, $n = 43$, vs. females: $M = 4.0$, mean = 4.51 min, $SD = 1.482$, $n = 69$; Mann-Whitney U-test, $z = -3.0734$, $p = 0.002$). Concerning *duration of use*, night nests were typically used the whole night, so occupation ranged from 10 - 12 hours. Since females started nest construction earlier in the evening (cf. III; 4.3.3.) and males were the first to leave nests in the early morning, females probably used night nests slightly longer than males did. However such analyses will require further data.

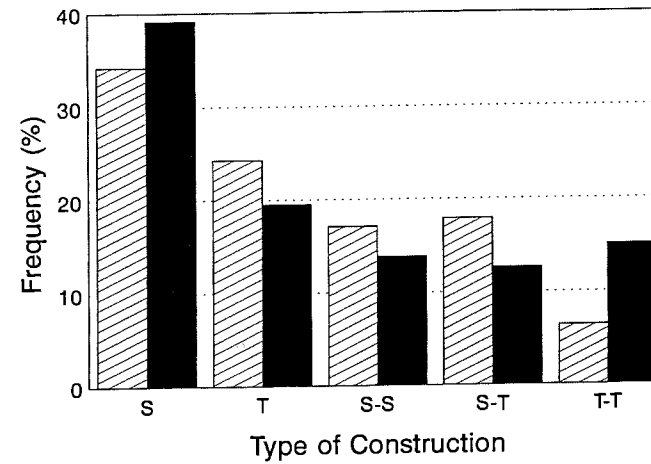


Figure 25: Type of construction of female nests (hatched bars, $n = 140$) and male nests (black bars, $n = 87$). S = side branch, T = tree top, T-T = 2 or more tops combined, S-T = 2 or more side branches or tree tops combined, S-S = 2 or more side branches combined.

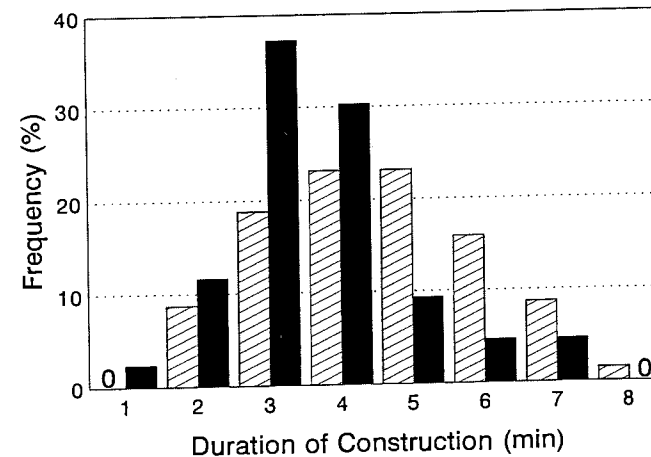


Figure 26: Duration of construction of female nests (hatched bars, $n = 69$) and male nests (black bars, $n = 43$). Each numeral on the horizontal axis represents beginning of each minute used (e.g. 1 min = 1'00" - 1'59", 2 min = 2'00" - 2'59", etc.).

3.2.3.2. Day nests

Every evening, each mature individual built a nest for the night. However, *frequency of construction* of day nests differed between the sexes. Of 192 day nests made by mature individuals, 80% were done by females and 20% by males. Adult plus adolescent females built day nests 4.8 times more often than did males from these age classes (1.86 nests per 10 observation hours by females, compared with 0.39 nests by males). Considering the ratio of males and females in an average day travel party (cf. III; 1.3.), this is more than twice the expected value and the difference is highly significant ($\text{Chi}^2 = 22.8$, $\text{df} = 1$, $p < 0.001$). *Height* of day nests differed for both sexes as well. While females nested at 20.7 m on average ($\text{SD} = 8.747$, $n = 75$), males nested at 14.7 m ($\text{SD} = 5.535$, $n = 15$). This difference of females nesting on average 6 m higher than males was significant (t-test: $t = -3.44$, $\text{df} = 30.06$, $p = 0.002$). The data from males and females for day nests differed also with regard to the *duration of construction*. Females needed 0.61 min on average ($\text{SD} = 0.887$, $n = 129$) whereas males needed only 0.22 min ($\text{SD} = 0.505$, $n = 27$). Although the median for day nest construction was less than a minute for both sexes, the difference was significant (Mann-Whitney U-Test: $z = -2.2269$, $p = 0.026$). For the average *duration of use* of a day nest, there was no difference between the sexes: (males: $M = 27$, mean = 33.3, range 3 - 156 min, $n = 27$; vs. females: $M = 27$, mean = 35.7, range 0 - 120 min, $n = 129$; Mann-Whitney U-test, $z = -0.8115$, $p = 0.42$, n.s.).

3.2.4. Age differences

Since only mature individuals built night nests, one must focus on day nests in order to study aspects of the ontogeny of nest building. Information on the construction or occupation of nests was derived from direct observations of 283 nests built during the day, when the nest builder was identified: 230 were built by females, and 53 by males. Of the females' nests, 67% were made by adults, 17% by adolescents, 14% by juveniles, and 2% by infants. Of the nests built by males, 72% were built by adults, 8% by adolescents, 6% by juveniles, and 14% by infants. Only nests that were visible after the owners left were taken into account. The quality of a day nest was not just a question of age, as it differed across adults from situation to situation. A nest was simple on some occasions, when only a few branches were used to enlarge a feeding site into a platform to increase feeding comfort. It was thick and springy, hard to distinguish from a night nest, on other occasions when it was built for an extensive rest during day. What sometimes seemed to be intentional by adults, appeared only trial-and-error in infants. Infants often bent twigs in front of their body but were unable to hold onto them underneath their feet. Even if they managed that, their nests often unfolded soon after construction, since all the twigs were bent but none was interwoven or broken. Successful nests lasted for a few days. Quality should best be measured by direct inspection (cf. III; 3.1.5.) or indirectly by monitoring the process of decomposition. The latter requires a separate study, of tracking day nests daily, repeating the same travel routes that bonobos used on particular days.

Instead of dealing with quality, the 3 following paragraphs deal with attributes related to the process of nest building and use: Duration of construction and use, number of individuals using a nest at once, and activities performed in the nest.

3.2.4.1. Duration of construction and use

Day nest construction and length of use were analysed according to the age of the nest-builder. While the duration of construction decreased with age, the duration of use increased with age. Figure 27 shows the median *duration of construction* for females and males in each age class. For statistical analyses, classes with a sample size of fewer than 5 subjects were dropped, when sample size in each adjacent class was sufficient (cf. females). Classes were lumped when each of 2 adjacent ones had a sample size of less than 5 (cf. males). For both sexes, the differences across age classes were statistically significant (Kruskal-Wallis Median Test: females (adults, adolescents, juveniles), $\text{Chi}^2 = 22.984$, $\text{df} = 2$, $p < 0.0001$; males (adults, adolescents+juveniles, infants), $\text{Chi}^2 = 21.074$, $\text{df} = 2$, $p < 0.0001$). Also differences between the sexes, i.e. males needing less time than females for day nest construction, were apparent for all ages.



Figure 27: Duration of construction of day nests by females ($n = 186$) and males ($n = 41$) for each age class. Horizontal bar in boxes indicates median, length of box corresponds to interquartile range, limited by 75th percentile above and 25th percentile below. Bars outside boxes indicate range of observed values (excluding outliers). Dotted line shows overall median duration of nest construction.

Figure 28 shows the median *duration of day nest use* by females and males for each of the 4 age classes. For females, the length of use shows a clear increase with age. Younger individuals rested for shorter periods in day nests than did adults. In males, however, adolescents used day nests longer than did adult males. For statistical analyses, age classes with fewer than 5 individuals were lumped. Differences between the age classes were significant for both females and males (Kruskal-Wallis Median-Test: females (adults, adolescents, juveniles), $\text{Chi}^2 = 11.772$, $\text{df} = 2$, $p = 0.003$; males (adults, adolescents + juveniles, infants), $\text{Chi}^2 = 11.008$, $\text{df} = 2$, $p = 0.004$).

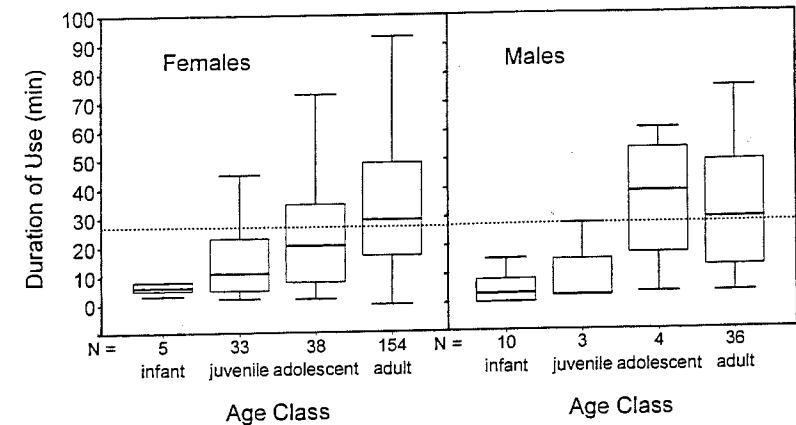


Figure 28: Duration of use of day nests by females ($n = 225$) and males ($n = 53$) for each age class. Horizontal bar in boxes indicates median, length of box corresponds to interquartile range, limited by 75th percentile above and 25th percentile below. Bars outside boxes indicate range of observed values (excluding outliers). Dotted line shows overall median duration of use.

3.2.4.2. Number of individuals

Most day nests (72%) were occupied only by the nest-building individual. In the other nests (28%), others joined the nest owner. On average, 1.34 individuals occupied a day nest ($M = 1$, $SD = 0.625$, range 1 - 4, $n = 279$). When dependent offspring were excluded from the analyses, nests had on average 1.16 occupants ($M = 1$, $SD = 0.491$, range 1 - 4, $n = 279$).

Figure 29 shows the mean number of individuals in nests of males and females for each age class. Of the 153 day nests made and occupied by adult *females*, 33% belonged to females with dependent offspring. Their nests always were occupied at least part of the time by the mother and the infant ($M = 2$, mean = 2.25, $SD = 0.744$, $n = 50$). In addition, 10% of the nests contained at least one more individual. For females without offspring, only 7% of day nests ($n = 103$) contained 2 or more individuals. In 8% of cases, adult females had individuals other than their own offspring in the nest (mean = 1.10, $SD = 0.358$, $n = 153$). The younger the nest building individual, the more the nest was used for social purposes. For adolescent females, 16% of day nests were used socially, whereas it was 26% for juvenile and infant females. On average day nests of adolescents contained 1.21 individuals ($SD = 0.577$, $n = 38$), those from juveniles 1.4 ($SD = 0.83$, $n = 33$), and infants' nests 1.2 ($SD = 0.447$, $n = 5$). The difference in the number of individuals per nest across age classes of females was significant (Kruskal-Wallis 1-Way ANOVA: $\text{Chi}^2 = 10.633$, $df = 3$, $p = 0.014$).

Adult *males* built only 36 day nests. Of these, 8% were used by others in addition to the nest builder ($M = 1$, mean = 1.14, $SD = 0.487$). Except for one nest, built by an infant male and used later by him and another infant male, no adolescent, juvenile or infant male used his nest for social interaction ($n = 17$). Instead, they joined females in their nests.

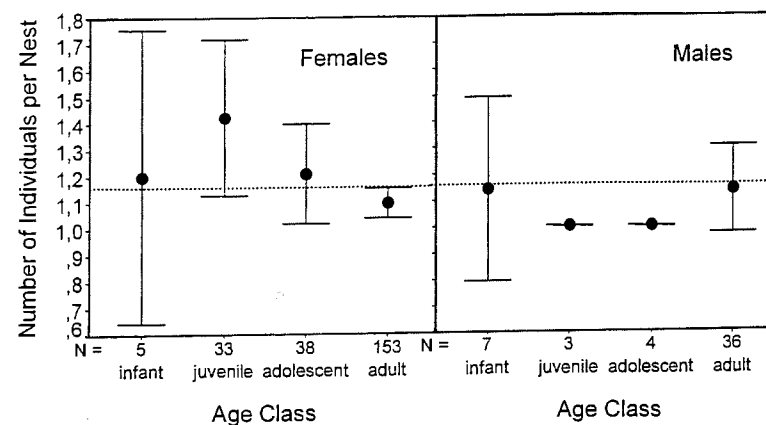


Figure 29: Individuals per nest built by females or males for different age classes. Each point represents mean for all nests of one age class ($N =$ sample size). Bars indicate 95% confidence interval for mean. Dotted line represents overall number of individuals per nest ($n = 279$).

3.2.4.3. Activities

For the 283 day nests, resting seemed to be the main activity during nest use (79.5%), followed by eat (12%), and social interactions like groom (6%) or play (9.5%). In 5% of cases, a nest served as a refuge for the nest-building individual in response to the approach of another. These nests have been termed "taboo-nests", given their apparent function as enclosures for privacy (see FRUTH & HOHMANN 1993). A few nests (3.5%) could not be assigned to categories, either because they were not used ($n = 3$), or because poor visibility did not allow exact determination ($n = 7$). Since various activities could be done in sequence, multiple use of a nest

was possible. These percentages do not include mother-infant pairs occupying the same nest, since for them almost all of the above activities occurred in frequent alternation and for brief periods. Figure 30 shows the relative frequency for 5 kinds of activities by females and males for each age class. Adult males seemed to use their nests in the same ways and with the same frequencies as females, with they tended to groom less and to play more than females. The younger the infant the more important was social play as activity within the nest. Juveniles and infants hardly ever groomed in their nests and except for one male infant, never ate in their nests.

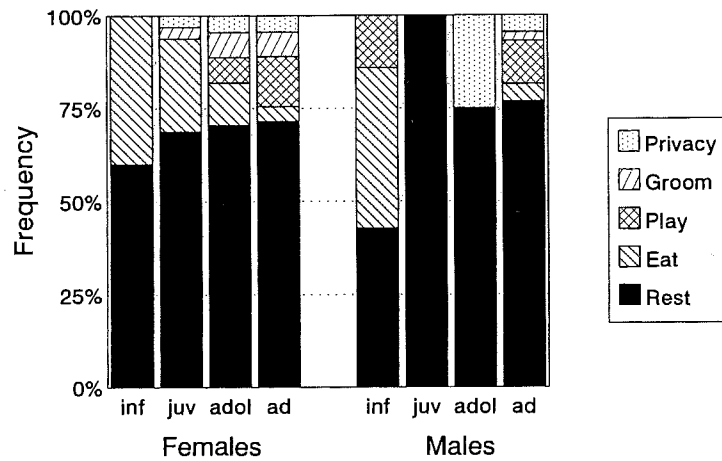


Figure 30: Different types of activities in day nests by age classes of females: infant (n = 5), juvenile (n = 32), adolescent (n = 44), adult (n = 179) and males, infant (n = 7), juvenile (n = 2), adolescent (n = 4), adult (n = 43).

4. NEST GROUPS

04.05.1993

17:00 - We are following a party of about 10 individuals, when high frequency hoots and typical nest building squeaks make it clear that this will be tonight's nest site. 17:04 - The first branches are broken. The noisy concert of cracking lasts about 5 minutes. Sudden silence, then high hoots, and newcomers arrive at the site. Max seems to be displeased by the arrival of Volker, the late adolescent son of Kamba, who seeks a tree close to his mother. Kamba has already started her nest, when Max jumps through the crown of her tree to chase away Volker. His message is clear: Volker, stay tonight wherever you want, but not close to your mother. Although still carrying young Mongo, Kamba is in oestrus ... and Max, by bonobo standards, tries to consort with her. Kamba, almost falling from a branch due to the heavy movements of Max, leaves her initial construction to watch the situation. This time she shows no sign of supporting her elder son, but at 17:18, starts a new nest, and a minute later Max starts his close beside hers. The newcomers again start several vocalisations and disperse among the resident party. Amy, a young adolescent female, not seen before for the whole day, comes from the opposite direction and builds her nest about 10 m from tree, where Max and Kamba built theirs. For the first time, I watch her making an integrated night nest. Viola, mother of young Vasco, remains on the periphery, where she builds a rather low, integrated nest. She plays but a minor role in the highly social nucleus of the community. Volker is out of sight. I cannot find his position from where I am. At any case, he is far from Max and his mother - and as so often probably remains on the periphery of the group. 17:37 - Silence falls on the site. Just another 15 min of twilight before we must take out our torches to find the way back to our "nest". The night is a dry one and the moon is shining, and the next morning, at 05.05.1993 - 05:20, we are back at the site. 05:28 - The first party of the 16 individuals who nested here leave their nests. 06:19 - The last ones do so. The parties remain in acoustical contact before their routes for the day finally separate them.

The previous chapters dealt with physical and behavioural properties of single nests. However, most nests were not built independently of each other, but rather in close proximity and more or less simultaneously by several individuals. Focusing on night nests only, almost all nests were part of a group of 2 or more (99.6%, $n = 2804$). The remaining 0.4% ($n = 10$) of nests were built solitarily. Unless specified otherwise, this chapter will deal only with groups and will consider both the distribution of nest sites within the home range and the physical and behavioural properties of the various nests within these clusters, as a function of sociality. We found 484 nest groups. Out of these, 84% were night nest groups, and 16% were day nest groups. Since analyses of single nests revealed significant differences between day and night nests (see III; 3.1.), the following sections treat night nest groups only.

4.1. Distribution and Size

In 25 months, 408 night nest groups were found (this number includes 13.5% recorded during my absence from June to August 1995). Most nest groups (87%) were seen either during or after construction, in the late evening or in the early morning. The rest (13%) was found by taking bearings of the direction of calling bonobos, approaching them later, e.g. if we were already with one group which was in acoustical contact with a distant one. From the 408 nest groups, 88.5% were made by members of the Eyengo community, and 11.5% by members of neighbouring communities. Figure 31 shows the distribution of night nest groups. On 67 days of observation, more than one group was found. The maximum number of nest groups encountered for one night was 5. Distances between nest groups built on the same night were measured. On average, nest groups of the Eyengo community were 945 m apart ($SD = 669$,

range = 60 - 2459, $n = 60$), while nest groups between the Eyengos and a neighbouring community were 2192 m apart ($SD = 415$, range = 1427 - 2653, $n = 9$). The intra-community nest group distances were significantly smaller than the inter-community nest group distances (Mann-Whitney U-test: $z = -4.1336$, $p < 0.0001$). The following data refer only to nest groups built by members of the Eyengo community. For identification of nest groups see methods II. C; 4.).

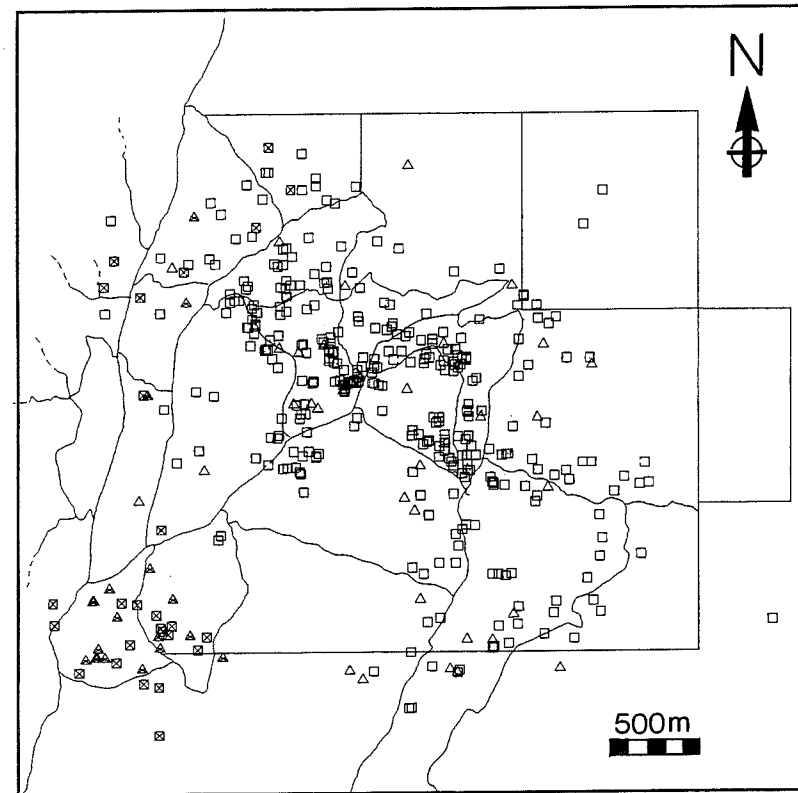


Figure 31: Distribution of nest groups found acoustically (= Δ) or visually (= \square) at Lomako (1990 - 1994). Black lines indicate trail system. Groups marked with x are groups from neighbouring communities, unmarked groups are from members of Eyengo community.

4.1.1. Distribution within the home range

Figure 32 shows the distribution within the home range of the 361 nest groups made by members of the Eyengo community. Nest groups were not distributed homogeneously but were restricted to primary forest. For a conservative estimate of the pattern of distribution, the calculation was restricted to the proportion of primary forest available within the home range. The observed distribution was compared with the expected, Poisson distribution. Nest groups were not distributed randomly but were clumped (Kolmogoroff-Smirnow Test; $z = 3.1792$, $p < 0.0001$, $n = 22$). Re-use of nest sites resulted in accumulations. This occurred in those parts of the forest where several feeding trees fruiting independently from each within a years' cycle are part of the patch. These places often were accessible by several ungulate paths joining from different directions and turned out to be important intersections in the bonobos' spatial infrastructure.

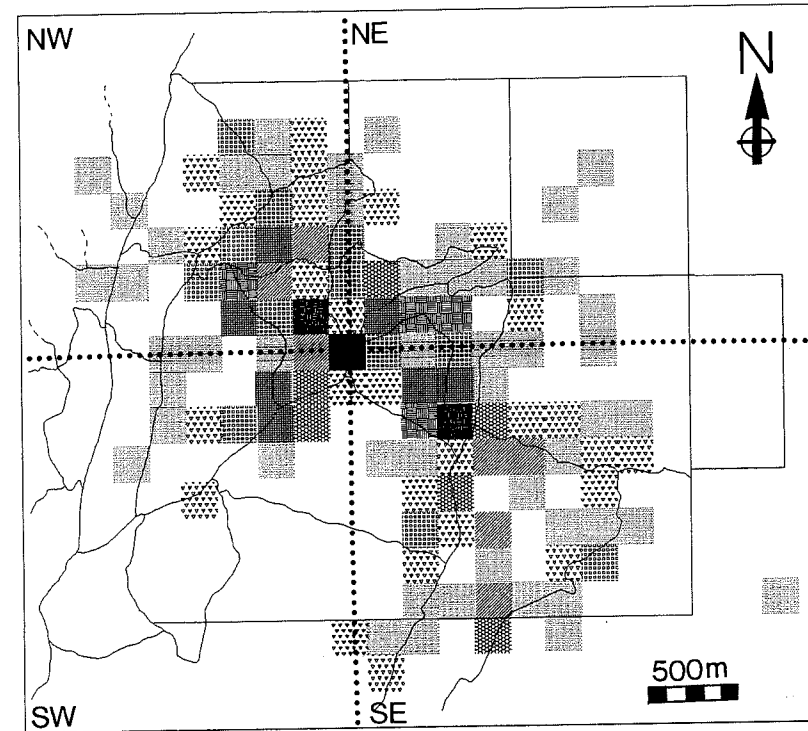
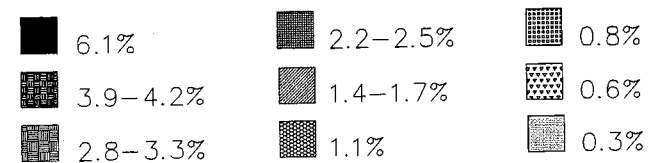


Figure 32: Distribution and relative frequency of nest groups made by Eyengo community ($n = 361$). Each square represents 200m x 200m quadrat within study site, it's pattern represents relative frequency of nest groups built in that quadrat. Black lines indicate trails. Dotted lines show limits of each quarter of home range (cf. chapter 4.1.2.1.). NW = north-west, NE = north-east, SW = south-west, SE = south-east.



4.1.2. Group size

Nests of 309 groups were marked and counted the next morning. Figure 33 shows a frequency histogram for the number of nests per group. The average number of nests per group was 8.8 ($M = 7.5$, $SD = 5.546$, range = 2 - 25).

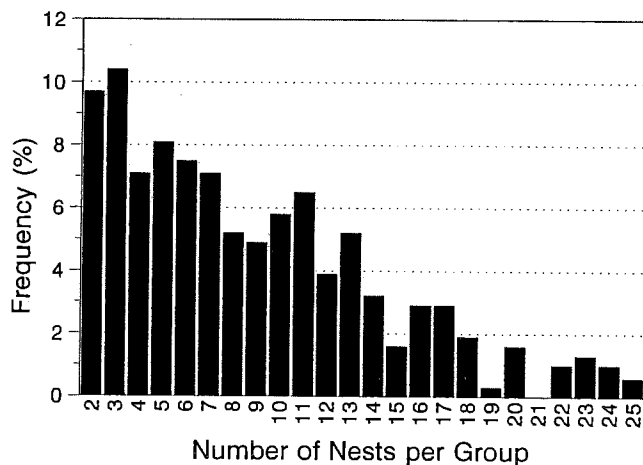


Figure 33: Relative number of nest groups ($n = 309$) for each group size.

4.1.2.1. Group size as a function of the position within the home range

Size of nest groups in the Eyengo community was reckoned to be a function of proximity to neighbouring communities. It was hypothesised that the further away from the centre of their home range, and so the closer to the boundary of the neighbouring community, the more individuals of the Eyengo community nested together. The hypothesis came from 2 major

observations: First, bonobos started regularly to utter long distance calls in the late afternoon, and did so with increasing frequency until their nest group was finished. This behaviour was thought to serve for: a) fusion of parties of the same community, and b) spacing of parties of different communities (HOHMANN & FRUTH 1994). Second, if an inter-community encounter happened (own observations, $n = 2$), it was predominantly a heavy vocal exchange, accompanied by males flitting over the ground like cannon balls. It never resulted in physical injuries, but there seemed to be a winner - the larger party, which was more impressive in their hoot-display. As a consequence, since more individuals make more powerful vocalisations, travel tours to the boundary to the neighbouring group should be used to reconfirm clearly their constitution to the neighbouring group.

Nest groups were on average 766 m from the centre of their home range ($SD = 462$, $n = 329$, range = 20 - 2661). Groups of 3 or fewer individuals never were found further than 1200 m from the centre. Groups of 4 - 18 nests showed large variation in their position relative to the centre; these showed the longest distances. In contrast to prediction, the largest groups of more than 20 individuals, nested within less than 250 m distance from the centre. When the distance was tested for all groups, no relation between group size and distance emerged. Since I regularly observed members from other communities only in the north-western and south-western part of the Eyengos' home range, it was useful to separate their range into 4 quarters, 2 of them in the direction of the confirmed presence of neighbours. Figure 34 shows the results for the 4 quarters of the home range. In contrast to prediction, none of these regressions was statistically significant (linear regression: NW, $r = 0.36$, $F_{1,14} = 2.1486$, $p = 0.1648$, $R^2 = 0.13$, n.s.; NE, $r = 0.39$, $F_{1,9} = 1.5936$, $p = 0.2385$, $R^2 = 0.15$, n.s.; SW, $r = 0.19$, $F_{1,7} = 0.2578$, $p = 0.6272$, $R^2 = 0.04$, n.s.; SE, $r = 0.01$, $F_{1,16} = 0.0030$, $p = 0.9571$, $R^2 = 0.00$, n.s.).

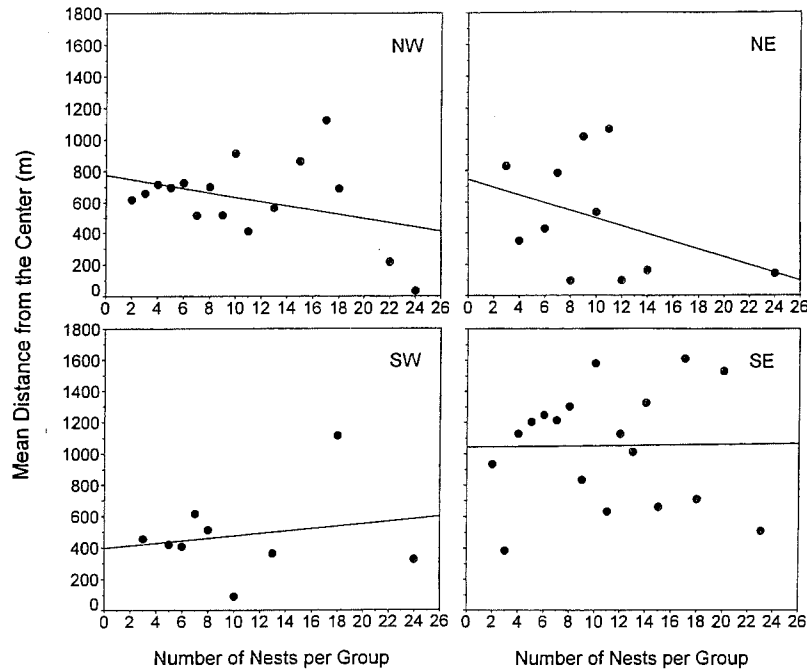


Figure 34: Distance of nest groups from centre of home range. Each point represents mean of distances for groups of one size in each quarter of home range. Sectors: NW = north-west, NE = north-east, SW = south-west, SE = south-east.

4.1.2.2. Group size over seasons

Nest group size differed significantly from month to month (Kruskal-Wallis Median-Test: $\chi^2 = 48.521$, $df = 21$, $p = 0.0006$). Months were analysed separately in respect to seasonality. The 224 groups built in the rainy season had a mean size of 8.5 nests per group ($M = 7$, $SD = 5.5$, range = 2 - 25), and the 83 groups built in the dry season had a mean size of 9.5 nests per group ($M = 8$, $SD = 5.6$, range = 2 - 24), but this difference was not statistically significant (Mann-Whitney U-test, $z = -1.6092$, $p = 0.108$, n.s.).

4.1.2.3. Group size by day and night

Nest group size at night was considered to be the most reliable count of the party size of weaned individuals. To test if night nest groups were the result of fusion or fission of day travel parties or if the 2 were the same, the size of parties at night ($n = 318$) was compared to the size of travel parties by day (c.f. III; 1.2.; $n = 485$). Here, the 10 occasions when individuals were seen to nest alone were included in the analyses. Nest groups at night were significantly larger than parties during the day (Mann Whitney U-test, $z = -7.0877$, $p < 0.0001$). On average, night parties had 9 weaned individuals, while day parties only had 6. Figure 35 shows the mean party sizes by day and at night for 22 months of observation. During all months, bonobos at Lomako consistently congregated to nest together overnight.

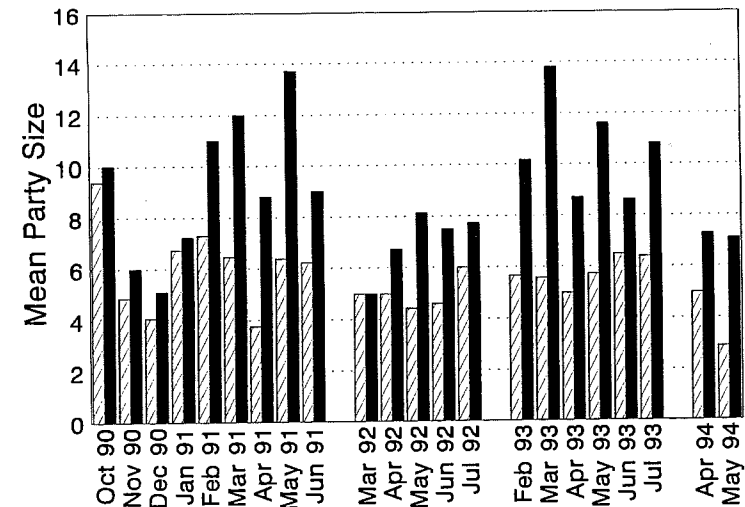


Figure 35: Party size by day (hatched bars; $n = 485$) and at night (black bars; $n = 318$) for each month of observation.

4.1.2.4. Intensity of group fusion

For 20 months of observation, the mean size of day travel parties was positively correlated with the mean size of night nest groups (Spearman rank correlation: $r = 0.48$, $p = 0.033$, $n = 20$). The larger the parties were by day, the larger they were at night. However, the difference between day and night was variable and differed from month to month. Figure 36 shows the difference between the monthly means of day and night party sizes. The overall mean difference was 3.43 (SD = 1.805, $n = 20$). In 9 of 20 months, party sizes at night were smaller, in 11 of 20 they were larger, than the overall mean. There was no month when parties split up at night.

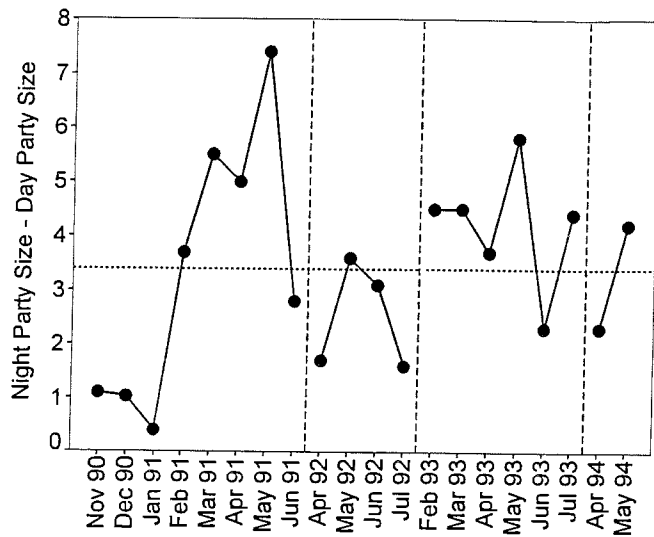


Figure 36: Difference between mean day party sizes and mean night party sizes for each month of observation. Months with fewer than five parties were excluded. Horizontal dotted line indicates overall difference in party size from day to night. Vertical dotted lines indicate gaps in observation between different years of study.

4.2. Physical Correlates

Detailed measurements on relations among nests were taken from 123 night nest groups. From these data, diameter of nest groups, differences in height, between-nest distances and nearest neighbours were calculated. The measurements were set in relation to the number of nests per group.

4.2.1. Horizontal dispersion

The maximal distance between the 2 most peripheral nests of a group was measured for all 123 groups. It ranged from 2 m in the smallest group containing 2 nests to 276 m in a group of 12 nests. Figure 37 shows the diameter of nest groups as a function of group size. The diameter of nest groups increased with group size (linear regression; $r = 0.54$, $F_{1,135} = 56.242$, $p < 0.0001$, $n = 123$; $R^2 = 0.29$). The increase however was far from being directly proportional.

4.2.2. Vertical Dispersion

Differences in height within a nest group varied from 0 - 30 m. Figure 38 gives the vertical diameter of nest groups as a function of group size. The larger the group, the larger the vertical diameter (linear regression; $r = 0.39$, $F_{1,135} = 25.551$, $p < 0.0001$; $R^2 = 0.15$). This correlation is weak, since differences between groups of the same size often resembled differences between groups of different size.

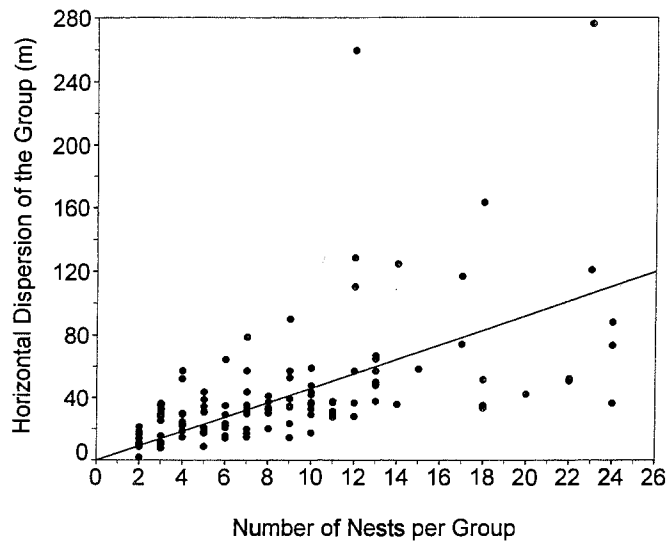


Figure 37 : Horizontal dispersion of nest groups ($n = 123$) as function of group size (Linear regression: $r = 0.54$, $F_{1,135} = 56.242$, $p < 0.0001$, $R^2 = 0.29$).

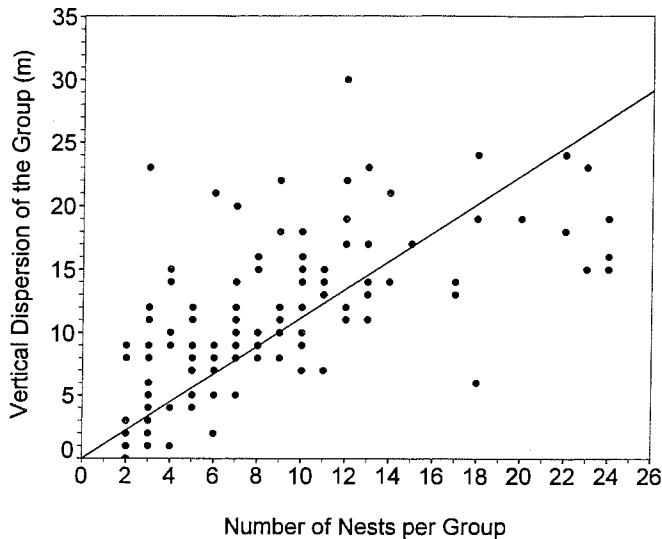


Figure 38 : Vertical dispersion of nest groups ($n = 123$) as function of group size. (Linear regression: $r = 0.39$, $F_{1,135} = 25.551$, $p < 0.0001$, $R^2 = 0.15$)

4.2.3. Distance between nests

For all 123 nest groups, all direct distances from nest to nest were measured. They ranged from 2 nests built side-by-side (0 m) to 276 m for the 2 most distant ones ($M = 23.74$, mean = 18.12, $SD = 22.16$, $n = 5823$). Considering only vertical differences in height, nest positions differed between 0 and 30 m with a mean difference of 4.87 m ($M = 4.0$, $SD = 4.041$, $n = 5823$).

4.2.3.1. Mean inter-nest distances and group size

It was expected that the distance between 2 nests in a group reflects a preferred and constant individual distance and thus determines the mean value of all inter-nest distances of a group. As a constant, it should be independent of the number of nests per group. The mean values of inter-nest distances for each group were plotted against group size. There was no effect of group size on mean inter-nest distance when each data-point represented one group (linear regression; $r = 0.253$, $F_{1,121} = 8.284$, $p = 0.0047$; $R^2 = 0.06$). However, when all inter-nest distances were averaged for each class of group size, the mean inter-nest distances show a near-significant trend to increase with group size (Figure 39: linear regression: $r = 0.42$, $F_{1,18} = 3.9647$, $p = 0.0619$, $R^2 = 0.18$, n.s.). The increase in inter-nest distances resulted from the tendency of bonobos to form 2 or more clusters of nests within a single group. Examination of the cumulative frequency dispersion of nests within a group revealed leaps in distances indicating these clusters. The subgroups were separated by larger distances than the nests within the sub group. Therefore the mean inter-nest distances were increased artificially, although most of the nests were close to each other. As a consequence nearest neighbour distances

(cf. III; 4.2.4.) were thought better to represent the constancy of inter-individual distances.

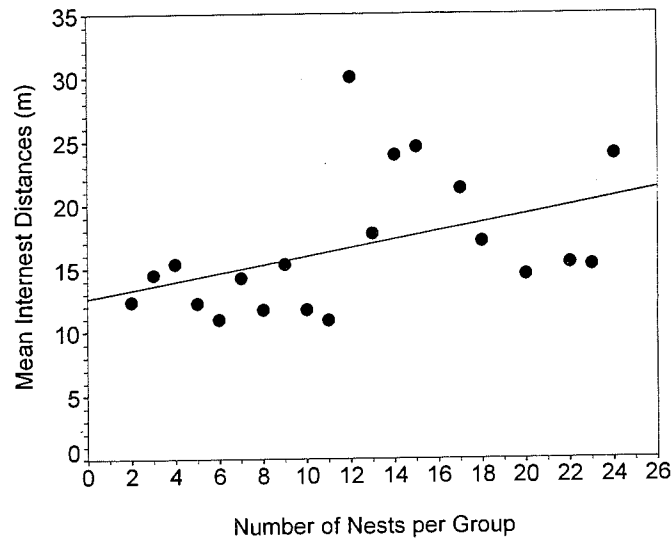


Figure 39: Inter-nest distance as function of group size. Each point represents mean of all mean inter-nest distances of all groups of one size ($n = 123$ groups). (Linear regression: $r = 0.42$, $F_{1,18} = 3.9647$, $p = 0.0619$, $R^2 = 0.18$, n.s.).

4.2.3.2. Mean inter-nest distances and tree density

It was hypothesised that inter-nest distances reflect tree density at a nest site: The lower the tree density of a given area, the larger the mean inter-nest distances should be. For the sites of 36 nest groups the density of all potential nest trees was calculated. It ranged from 500 trees per ha to 1300 trees per ha. This density had no effect on inter-nest distances (linear regression; $r = 0.017$, $F_{1,33} = 0.0095$, $p = 0.92$; $R^2 = 0.00$). However, when the density of only the 5 favourite species of nest trees was considered, the influence of tree density became evident. Figure 40 shows the resulting

scatterplot. Mean inter-nest distances decreased with increasing density of the suitable nesting trees (linear regression; $r = 0.48$, $F_{1,16} = 4.6784$, $p = 0.046$; $R^2 = 0.23$).

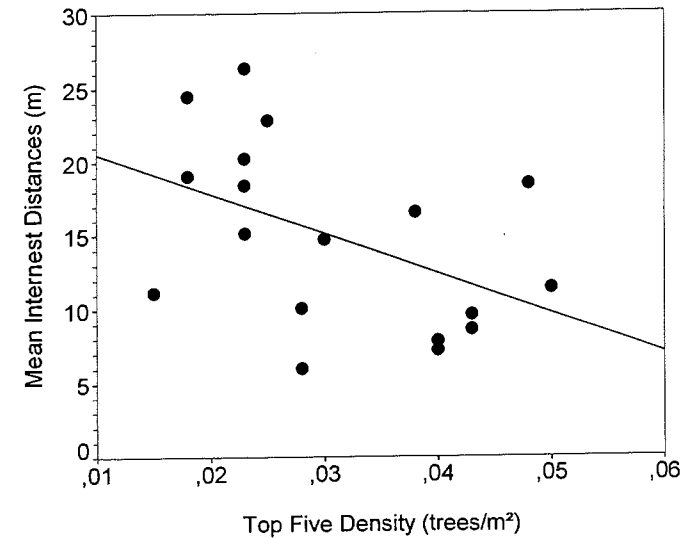


Figure 40: Inter-nest distances and density of five most often used tree species at nest site (Linear regression; $r = 0.48$, $F_{1,16} = 4.6784$, $p = 0.0460$; $R^2 = 0.23$)

4.2.4. Nearest neighbour distances

For the distance between a nest and its nearest neighbour, the range was 0.5 - 45.0 m. The median was 5.6 m (mean 7.62 m, $SD = 5.856$, $n = 1043$). The nearest neighbour distance was greater in smaller groups than it was in larger groups. Figure 41 shows the median nearest neighbour distances for each nest group size. Median nearest neighbour distances varied principally around the overall median. Groups below 5 nests and

groups with 15 nests, however, showed a deviation to larger nearest neighbour distances.

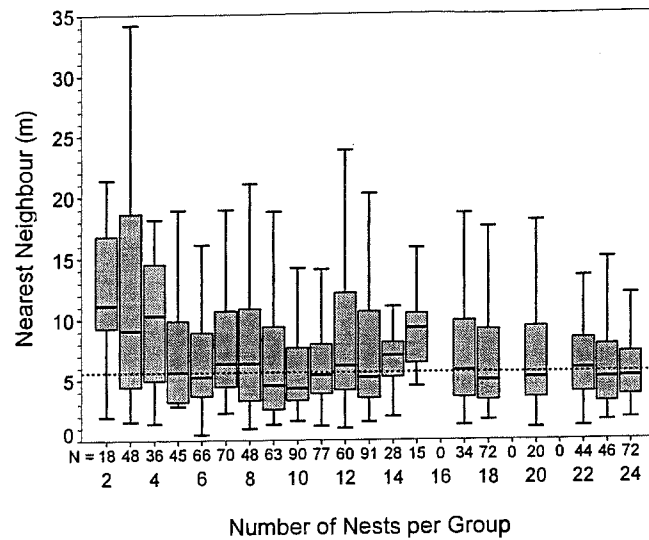


Figure 41: Nearest neighbour distances and nest group sizes. Horizontal bar in boxes indicates median with 75th percentile above and 25th percentile below. Bars outside boxes indicate range of observed values (excluding outliers). N refers to sample size for nearest neighbour distance upon which median is based. Dotted line shows overall median nearest neighbour distance ($n = 1034$).

The average nearest neighbour distances for each group were plotted against group size (test of 2nd order, see chapter II. D.). Figure 42 shows that the larger the group, the closer in space were its individuals (linear regression; $r = -0.63$, $F_{1,18} = 18.127$, $p < 0.0001$, $R^2 = 0.13$). To randomise and confirm this result all nearest neighbour distances were averaged for each group size and plotted against group size again (test of 3rd order). The plot showed a clear negative relation between nearest

neighbour distances and group size (linear regression; $r = -0.63$, $F_{1,18} = 11.949$, $p = 0.003$, $R^2 = 0.40$).

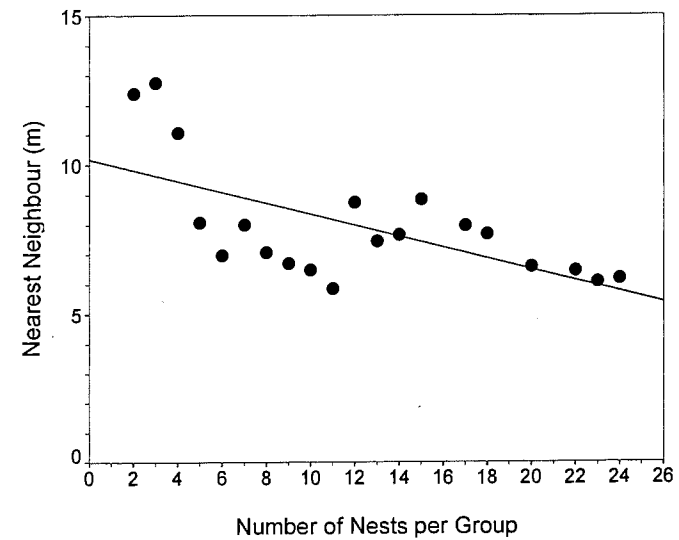


Figure 42: Nearest neighbour distance and group size. Each point is average of mean nearest neighbour distances of all groups of one size. (Linear regression: $r = -0.63$, $F_{1,18} = 11.949$, $p = 0.0028$, $R^2 = 0.40$).

4.3. BEHAVIOURAL CORRELATES

4.3.1. Time of construction

Of the 95 night nest groups, the start of the construction was seen. The earliest time was in the late afternoon at 16:06 hr and the latest was at 17:58 hr. Most nest building (81%) started between 17:00 hr and 17:50 hr. Nest construction was finished by 16:14 hr - 18:06 hr ($M = 17:44$; $n = 78$).

As Figure 43 shows, there were 2 distinct peaks for the onset of night nest groups, dependent on the weather. When it rained at midday or afternoon, bonobos started night nest construction earlier. When it was dry, they started later (M (rain) = 16:06 vs. M (dry) = 16:18, Mann-Whitney U-Test, $z = -1.9489$, $p = 0.05$).

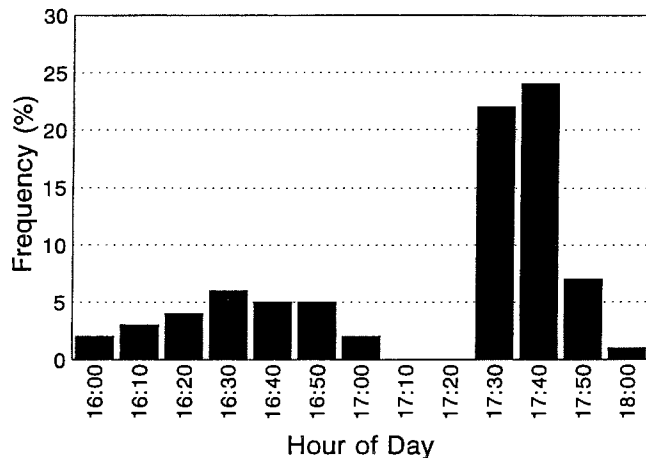


Figure 43: Onset of 95 night nest-building groups. Each point is start interval of 10 minutes (16:00 hr = 16:00 - 16:09 hr, 16:10 hr = 16:10 - 16:19 hr, etc.)

4.3.2. Duration of construction

The time elapsed from when the first nest of the group was started until the last nest was finished varied from 4 - 90 minutes. Bonobos needed 20.4 minutes on average to complete a night nest group. The larger the nest group the longer the combined time of construction, but such variation was not directly proportional, since much construction was done simultaneously. Nest groups on rainy days were built less simultaneously than groups on dry days. On rainy days the average duration for a nest built

within the period of group construction was 3.62 min ($M = 3.14$, $SD = 2.622$, $n = 13$). For dry days it was 2.37 min ($M = 1.69$, $SD = 1.715$, $n = 57$). This apparent difference was not statistically significant (Mann-Whitney U-Test, $z = -1.4048$, $p = 0.16$, n.s.)

4.3.3. Initiator of nest construction

Of the 95 night nest groups (cf. III., 4.3.1.), the initiator was seen in 32 cases. Considering both adult and adolescents, males were the initiators in 9% of these cases, females in 91%. According to the socioeconomic sex ratio of the community (cf. III., 1.1.), females were expected to start nest construction 2 times more often than males did, but actually they started 10 times more often than males. The sex difference is even more striking in adults. Here males started in 6% of all cases, females in 84% ($n = 29$), so females initiated night nest construction 13 times more often than did males. The result differed significantly from the expected value of adult females starting twice as often as males ($\chi^2 = 9.184$, $df = 1$, $p < 0.005$).

4.3.4. Nearest neighbour and sex of the nest owner

Of 123 entirely measured nest groups, 248 nest owners could be identified. In 146 cases the nearest neighbour of these individuals was also known. The nearest neighbour was on average 9.8 m away ($M = 6.8$, $SD = 7.748$). Distances were examined according to sex and age. Adolescents nested closer to adults than adults did to adults. Adult females ($n = 41$) nested with 8.8 m much closer to each other than did adult males ($n = 10$) at 15.6 m. If males were nearest to females ($n = 57$), their distance apart averaged 10.6 m, which was intermediate to the unisex-distances. These sex differences became even more apparent when adolescents and

adults were pooled. Figure 44 shows the median nearest neighbour distances for the different combinations of sex. Females nested on average 7.9 m from other females (F-F; $M = 5.6$, $SD = 7.271$, $n = 65$), and 10.6 m from males (F-M; $M = 9.7$, $SD = 7.356$, $n = 70$). Males kept much larger distances from each other. They nested 16.0 m away from one another (M-M; $M = 18.0$, $SD = 9.504$, $n = 11$). All these differences were statistically significant (Kruskal-Wallis 1-Way ANOVA; $\chi^2 = 13.633$, $df = 2$, $p = 0.001$).

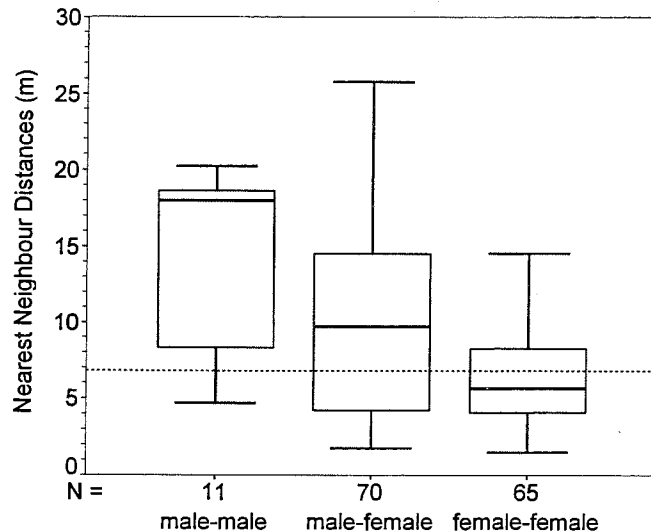


Figure 44: Nearest neighbour distances by sex. Horizontal bar in boxes indicate median with 75th percentile above and 25th percentile below. Bars outside boxes indicate range of observed values (excluding outliers). N refers to sample size of nearest neighbour distances upon which median is based. Dotted line indicates overall median nearest neighbour distance ($n = 1034$).

IV. DISCUSSION

1. THE EYENGO COMMUNITY

The Eyengo community consisted of 34 members, all of whom were identified. Sex ratio in infants was biased to males, but it was biased to females in adults. There was a striking gap in the number of individuals in the age-classes of juvenile and adolescent. During day, members of the Eyengo community never have been seen all together but instead only in parties, that changed regularly in number and composition. The average party consisted of about 6 weaned individuals. Party size fluctuated not only from month-to-month but also during the day. Most parties were made up of both sexes, but nearly a third of all parties contained one sex only. The socioeconomic sex ratio did not change with party size. When individuals travelled alone, however, more often they were males than females. The typical daily range of these parties was about 3 km. They foraged, travelled, and slept within a home range of 15 km², comprising about 2/3 primary forest and 1/3 swamp.

1.1. Demography

The only demographic data available for comparison with this study of *bonobos* at Lomako are from *Wamba*, where five communities were known. *Wamba's* community sizes ranged from 55 - 150 individuals, and were much larger than Lomako's (KANO 1992). *Wamba's* best studied community (E-group) totalled 63 members in 1979, 15 adult and 5 adolescent males, 16 adult and 8 adolescent females, the rest were juveniles (3 males, 4 females), and infants (6 males, 5 females, 1 unknown

sex) (KANO 1982a). No comprehensive data were available for *Lomako* from previous research by the LFPC-Project. For the Eyengo community, only 10 females and 7 males, and for the Bakumba community, 12 females and 5 males were identified (WHITE 1992a). It was not specified whether or not these individuals were adults only. In both cases, the identified individuals were said to represent just a fraction of the entire communities. The size for both, the Bakumba and Eyengo communities was *estimated* to comprise about 50 individuals each (BADRIAN & BADRIAN 1984). *Therefore, the data presented here provide the first complete demographic picture of an unprovisioned bonobo community.* Such differences in community size as these between the two bonobo study sites, Lomako and Wamba (separated by about 300 km) is not unique to bonobos. Community size in *chimpanzees* varies too. The smallest community described so far is that of *Bossou, Guinea*, comprising of 18 - 22 individuals between 1969 and 1986 (SUGIYAMA 1989). The largest was reported from *Mahale, Tanzania*, comprising of up to 100 individuals (NISHIDA *et al.* 1990).

Socionomic sex ratio (SSR) in *chimpanzees* parallels mostly what is presented for bonobos here. At *Bossou* the SSR in 1994 was 0.67 (MATSUZAWA *in press.*), at *Mahale* it was 0.69 for M-community in 1988 (NISHIDA *et al.* 1990), and at *Gombe, Tanzania*, it was 0.62 for the Kasakela community in 1983 (GOODALL 1986). At each site, the sex ratio was biased to females in adults, even though the sex ratio at birth and natural infant mortality are said to be similar for both sexes (GOODALL 1986). There are many variables which may influence adult sex ratio (for a summary see DUNBAR 1988), but here I focus on only a few for matching to chimpanzees. Chimpanzee males are known to engage in fatal inter-community interactions (GOODALL *et al.* 1979; MANSON & WRANGHAM 1991). In addition, cases were reported when chimpanzee males played the more active part, fighting against ground predators like leopards (BOESCH 1991). Both activities may increase mortality in adult males.

In addition, infanticide in chimpanzees occurs between and within communities, and these provide another source of sex-biased mortality. At *Mahale*, only male infants were killed, according to the most recent update; these numbered 8 infants in 10 years of continuous research. (NISHIDA & KAWANAKA 1985, NISHIDA 1994). Even though on the first glance it may be puzzling to see "within-group-cannibalism", the authors suggested that the females' pattern of ranging were crucial. All infants killed were those of female immigrants, who ranged in the periphery of their new home range. But why were only males killed? One explanation is that, in order to avoid increasing competition over mates, males try to keep the numbers of male competitors low. Possibly they even want to increase the relative number of females by eliminating male infants and thus promoting the females' renewed receptivity. But several points contradict these assumptions: First, it is hard to imagine that adult males in the midst of their reproductive period could plan about 15 years ahead to reduce later, potential competition, or to create more potential mating partners, by which time their reproductive period will be over anyway. For this to occur, the killers would have to be young adults of about 15-20 years of age, but this was true for only 1 of 4 infanticidal episodes (NISHIDA & KAWANAKA 1985). Second, sex-biased infanticide is reported for *Mahale* but not for other study sites. At *Gombe*, for example, infants of both sexes (3 females, 3 males, 1 of unknown sex) were killed from community members, including females (GOODALL 1977). What seems to be easier to interpret is infanticide committed to strangers trying to immigrate into a community. Attacks by males on strange females and juveniles were reported from *Mahale* and from *Gombe* (NISHIDA & HIRAIWA-HASEGAWA 1985, GOODALL 1977). Again, however, infants of both sexes were killed. Thus, closer scrutiny of intra-community cannibalism leads too far away to be an explanation for the bias toward females in adults in chimpanzee communities.

In *bonobos*, not a single case of infanticide has been so far reported. Whether or not this is related to female dominance, or to sexual tolerance

which, in contrast to chimpanzees, permits males to mate even during the inter-birth intervals, or whether bonobos in general show more tolerant inter-individual relationships, remains to be seen. Bonobos *do* have in inter-community encounters and in the cases seen in this study, the males played the physically active part (cf. p. 108). Serious injuries were not seen to occur during these events. Although limb deficiencies were partly due to injuries from snares, these occurred much more often in males than in females. This may indicate that competition in bonobo society is not always peaceful. Bonobo males were seen to compete with each other over females. They also probably faced greater risks from predators, snakes, humans, etc. during their lone travels. These weak indices, however, help little in trying to explain the higher proportion of females compared to males. The first argument to question the above mentioned reasons for female demographic predominance comes from female migration. Lone female travellers, just like lone males, without the protection given by a group should face increased predator pressure including that from humans. During the period of study, 3 individuals were seen with a fresh snare wire around the hand: 2 adolescent females, and 1 late adolescent male. Again, both sexes seem to be affected similarly. The strongest argument against the above mentioned assumptions to explain the female preponderance, however, is the socioeconomic sex ratio at *Wamba* which was balanced for all age classes (SSR = 0.55) and which at first glance seems lower than for *Lomako*. Questions remain, as to what may cause the female predominance (SSR = 0.67) and the gap in the class of juveniles and adolescents at *Lomako*.

Another factor may explain both effects: When observations began, Volker, a young adolescent male, was pressured by all other community members, except his mother Kamba. He rarely got access to a feeding tree, was quickly displaced if entered one, and was often harassed by Max, a dominant male. If he was not content to eat only fallen leftovers from underneath the tree, he was obliged to be a thief at the periphery of feeding

trees. Only when he travelled alone with his mother, did he get access to food without being obliged to compete. A similar situation developed when Ufo, the infant son of Senufo, became weaned in 1993. At that time we estimated his age at about 5 to 6 years. In that year he suddenly fell from his "kid the king status" to that of an "underdog". He regularly was displaced from food resources. Since his mother was no longer willing to carry him, he had to travel long distances on his own, was not allowed to have nipple contact, and had to build his own night nests. Although sometimes his mother showed pity and relaxed the unwritten rules, Ufo became rather unsociable, showed no further interest in play, and finally disappeared at the end of 1994, when his mother had a new-born baby. Although these observations are not backed up by a large sample size, they indicate the following: An infant of either sex, up to its fifth or sixth year, is allowed to do and to get everything. Access to food is free and contact to all other community members is affiliative. From the moment the infant is weaned, it becomes an underdog in the society and in addition to all of the other struggles that come with the necessity of making its own living, it has to face inter-individual competition. Support provided by the mother depends on her status. The higher this is, the more her infant will be protected, but infantile frustration during weaning is extreme. It is tempting to see here a harsh process almost overcome in human society, which is: - "What doesn't kill you, makes you stronger". Female juveniles have to make their own living as well, but they show the ability to form coalitions with adult females, and this may buffer them (e.g.) by giving them access to feeding trees. Because of their coalitions, adult males dare not to displace females. When food is abundant, this disparity between the sexes may not appear, but when food is short, first of all juvenile males and then possibly juvenile females will suffer higher selection pressure through competition and so will be the first ones to die. At *Wamba* feeding patches are reported to be larger (WHITE 1992a). Many cultivated fields occur there and also communities were provisioned "sufficiently" (KANO 1982a), so the problem

of food shortage may never have arisen and every generation was able to survive. If this was true, Lomako's bonobos, given the lack of individuals of 6 - 10 years of age during the present study, may have suffered an extreme shortage of food sometime during 1985 - 1989.

1.2. Party Size

Comparing data on bonobo party size presented here to that from published results from previous studies at Lomako revealed similar findings, when the habituated Bakumba community was considered. In 1984-1985, the average party size for all observed party compositions, for Bakumba (= Hedons), and Eyengo (= Rangers), and the splinter group (= Blobs), was 5.4 ($n = 164$) with most parties between 4 and 6 individuals (WHITE 1988). When communities were analysed separately, however, party size differed significantly between the Eyengo community and the others. At that time, the Eyengo community had an average party size of 9.7 ($n = 26$), and over 60% of parties had more than 10 individuals (WHITE 1988, 1992a, WHITE & BURGMAN 1990). WHITE (1992a) hypothesised that sightings of smaller parties would increase with better habituation. In her comparison with Wamba, however, she rejected this hypothesis, arguing that if this were true, at Wamba parties should be even smaller since they were better habituated. I do not see any contradiction. Observations on the Eyengo community presented here show clearly that habituation has had an important effect. Not only that the Eyengo community is now observable in small parties, and females and males can be followed solitarily, but the *overall* party size for that community size presented here has dropped to 5.8.

Differences in party size are better related to differences in community size: The mean party size of 5.8 at Lomako represents about 1/5 of the community. Communities at *Wamba* were much larger, but the

average party size of 16.9 paralleled about the same proportion of this large community. Nevertheless, the data from *Wamba* contrast significantly with the findings from Lomako. Party size at *Wamba* was 16.9 on average ($n = 147$) and sometimes a single party comprised up to 70 individuals (KURODA 1979). Since KURODA reported that he "failed in provisionization", this inflating factor has to be excluded as a possible influence. KANO (1982a, 1992) reported an average size of mixed parties at the artificial feeding site of 18.9 individuals ($n = 172$), independent from the community they belonged to. In his case 96% of all parties observed were mixed parties, containing females, males, and dependant offspring. In view of such large party sizes, however, it would be surprising to find a party consisting of only one sex. For *Yalosidi*, KANO (1983) reported an average party size of 8.5 individuals with a proportion of 70% mixed parties.

KANO (1982a) hypothesised that under the assumption that the degree of individual gregariousness is constant, relative party size should reflect relative community size. To test party sizes in relation to corresponding community sizes, BOESCH (*in press*) proposed to calculate the relative mean party size (mean party size divided by the community size). Following that, the party size for the Eyengo community at Lomako would fit into the range of bonobo communities at *Wamba*.

Originally, in contrast to bonobos, party sizes in *chimpanzees* were reported to be larger (for a review see NISHIDA & HIRAIWA-HASEGAWA 1987). The original premise was that bonobos have less feeding competition due to their species-specific tolerance and therefore generally have larger parties (CHAPMAN *et al.* 1994). A detailed review of average party sizes of bonobos and chimpanzees revealed, however, that both species of *Pan* show extreme flexibility and variance within species that may parallel those between species (CHAPMAN *et al.* 1994).

For *bonobos* at *Lomako*, fluctuation in party size was observed in the late 1970s, and was related to the production cycles of particular food

plants rather than to seasonality *per se* (BADRIAN & BADRIAN 1984, BADRIAN & MALENKY 1984). Recently, however, MALENKY (1990, cited in CHAPMAN *et al.* 1994) suggested that fruit production is uniform throughout the year and therefore party sizes could remain large. In agreement with the earlier observations, the data presented here suggest rhythmical changes. The reason why the seasonality correlation presented here did not reach statistical significance, however, may be that fruiting cycles did not necessarily correlate with the monthly periods used here, but instead followed a different rhythm independent of the rough wet-dry pattern. Fruit production may occur throughout the year, but it may be the quality of particular fruit-items which changes over the year and determines party size fluctuation. Even at *Wamba*, where party size was reported to remain constant and large for up to 3 weeks, seasonal fluctuation was reported for party sizes in relation to the abundance and distribution of food (KURODA 1979). The need for a more detailed study on feeding ecology, monitoring the phenology of food-plants (fruit trees, leaf production, herbaceous vegetation), and the corresponding fluctuation in number and composition of parties, is apparent and may resolve the contradictory observations within and between study sites reported so far.

Despite frequent changes in party membership during the day and from day-to-day, no pattern in the variation of party sizes during the day was observed in the years 1984-85 at Lomako (WHITE 1988, *in press*). Even in 1986-1987, when the bonobos at Lomako must have been better habituated than before, the mean duration of observation was still only 168 min, and observation was mostly restricted to times when the subjects were in trees (DORAN 1993). This may explain why the clear pattern of parties being larger in the morning, fissioning during day and joining again at night, as shown in the present study, was not seen at that time.

1.3. Party Composition

From early studies on *bonobos* at *Lomako* in 1980-82, parties were found to be composed of "fairly equal numbers of males and females". The tendency for larger groups to contain more females was interpreted as a consequence of high female-female affinity (BADRIAN & BADRIAN 1984, p.333). In 1984-85, WHITE (1988) found party composition to be shifted to females in the best habituated Bakumba community, and in the splinter group (Blobs), but not in the Eyengo community. In contrast to the study conducted by BADRIAN and BADRIAN (1984), WHITE (1988) reported that larger parties contained proportionally more males. Discussing this difference, she opined that it could be due to historical shifts in party composition or be a consequence of increased tolerance during habituation. She also addressed the problem of inaccurate counts due to incorrect identification. Since "males are often hard to recognise as individuals", the same males may have been counted several times (WHITE 1988, p.191). This contrasted with the present study: Males were the first known individuals, being easier to identify (*cf.* p. 37). Thus, differing degrees of habituation may be the crucial point to explain the difference in these early observations.

At *Wamba*, most parties (96%) were mixed (KANO 1982a), with an average socionomic sex ratio of 0.47. There they were said to show a high degree of uniformity independent of the number of individuals. The socionomic sex ratio of parties came close to that of the community (SSR = 0.55; *cf.* p. 61), as it did in the data presented here. This mixed type of parties dominates bonobo society, and combines searching for food sources, caring for dependent offspring, and multiple possibilities for sex and reproduction (KANO 1982a).

This contrasts with what is seen in *chimpanzees*. Despite the fact that the overall socionomic sex ratio in communities resembles that of

bonobos, breakdown into parties changes the picture. When the provisioned chimpanzee communities at *Gombe* and at *Mahale, Tanzania*, are considered, they formed unisexual parties as often as they did bisexual ones (HALPERLIN 1979, NISHIDA 1979). In the unprovisioned chimpanzees of *Taï forest, Côte d'Ivoire*, uni-sexual groups accounted still for more than a third (38% vs. 24% here) of all parties, and 52% of all parties were mixed (BOESCH *in press.*). The separation of functions, e.g. nursing, feeding, reproduction, and territorial defence, is much more evident in chimpanzees. Bisexual parties mostly involve a male consorting a female in oestrus. Unisexual parties are of males, patrolling boundaries, collectively gathered for territorial defence. Males usually cover a much larger range than females with their dependent offspring (WRANGHAM 1979).

1.4. Travel Patterns

Except for one all-day follow when *bonobos* travelled 1200 m (DORAN 1993), no data were available for nest-to-nest follows from previous studies at *Lomako*. DORAN (1993) reported that the average travel distance on the ground was 359 m for each sighting. Since the mean length of a sighting was 168 min, the bonobos would travel 1540 m on an average 12-hour day, if travelling were constant (which it is not). KANO (1992) reported that bonobos at *Wamba* travelled 400 m - 6000 m ($M = 2000$ m) per day. These distances were about 1000 m below the distances reported here. At *Wamba* either larger food patches with a different distribution or the artificial feeding site and mobile provisioning may account for parties not being obliged to forage extensively. No all-day follows on focal individuals are available, so nothing is known on sex differences in daily ranging. However, a sex difference likely exists, since analyses of single individual "parties" revealed a higher proportion of males travelling

solitarily. Sex differences may be less pronounced in bonobos than in chimpanzees (see below), since parties are most often mixed, containing individuals of both sexes and all age classes.

Chimpanzees travelled larger distances. The day-range for *Gombe, Tanzania* reported for the years 1972-73 by WRANGHAM (1975) varied from 0.2 km - 10.7 km. He found that variation depended on season, sex and community of the subjects. When the sexes were treated separately, males had larger day-ranges than females. As an average day-range, WRANGHAM indicated 4 km for males and 3 km for females. GOODALL (1986), summing up 30 years of research at *Gombe*, reported for males an average day travel of 4.9 km, and for females 3.0 km. At *Mahale, Tanzania*, the median day-range was 4.1 km for males, 2.8 km for females (NISHIDA 1979).

1.5. Home Range

The home range presented here gives the first figure for bonobos ever calculated from the travel patterns of one community. Since observations over 3 years omitted the months of September to January, the results probably indicate the lower limit of the actual range. Previous studies at *Lomako* gave estimates of about 22 km². At *Wamba* home ranges were estimated from quadrates of 1 km² entered by specific parties. The most conservative estimates ranged from 14 km² for the K-community, over 20 km² for the best known E-community, to 29 km² for the B-community. These areas however were said to be only parts of the nomadic ranges and therefore the estimates had to be extrapolated. Accordingly, it was supposed that the range of the K-community was 50 - 60 km², that of E-community about 40-50 km², and that for B-community was about 50 km² (KANO 1982a). However, if daily travel distances are so short (2 km), and if size and distribution of food patches

allows large parties to forage optimally, it remains an open question as to why home ranges should be so large. For *chimpanzees* home range sizes differ with habitat. In rain forest habitats they ranged from 21 km² at *Mahale, Tanzania*, (M-community; NISHIDA *et al.* 1990) to over 27 km² at *Tai, Côte d'Ivoire*, (BOESCH & BOESCH 1989). Only ranges in drier habitats were much larger (*Mt. Assirik, Senegal*: 228 km²; TUTIN *et al.* 1983).

When only forest habitats were compared, calculation of the number of individuals per km² revealed a lower rate for bonobos than for chimpanzees. *Lomako* has 2.3 bonobos per km² home range, while *Wamba* for E-group had only 1.4, based on the estimated range. For *chimpanzees*, there were 4.6 individuals per km² at *Mahale* and 2.9 at *Tai*. However territoriality is reported to be higher in chimpanzees than in bonobos (for a review see, NISHIDA & HIRAIWA-HASEGAWA 1987) and therefore, lower density in *bonobo* ranges may be compensated by larger range overlap. KANO (1992) reported that more than 60% of the home range of *Wamba's* E-group overlapped with that of other groups.

Data on habitat availability and use have been investigated at both *bonobo* study sites, *Lomako* (WHITE 1992b) and *Wamba* (KANO & MULAVWA 1984). WHITE (1992b) calculated the proportion of the different types of habitat for a 7.5 km² focal animal range (whatever that may be) at *Lomako*. In contrast to the results presented here, WHITE'S proportion is higher for primary and slope (*Gilbertiodendron drewerei*) forest (85% vs. 64%) and lower for swamp (13% vs. 32%). The difference from the present study in the percentages may be due to different methods, since WHITE (1992b) did not calculate the proportions for the entire community and did not observe study subjects in the swamp forest. At *Wamba*, the proportion of swamp was closer to that reported in this study (22% vs. 32%), the proportion of secondary forest was much higher (20% vs. 5%), that of primary forest much lower than at *Lomako* (44% vs. 65%). In addition 14%

of *Wamba's* surface was cultivated (KANO & MULAVWA 1984). The differences between *Lomako* and *Wamba* seem to be crucial and may be major reasons for social and behavioural differences observed.

2. NEST TREES

In this study, analyses of nest trees were based on 5 attributes: height, stem diameter, height of tree tops, species, and leaf size. I have shown that bonobos were highly selective in their choice of trees on all these criteria.

2.1. & 2.2. Height and Stem Diameter

Bonobos at *Lomako* favoured trees of 15 - 25 m height, and chose stem diameters above 15 cm. Nests combining more than one tree sometimes involved trees with very small diameters which alone could not support a nest. Consequently, the validity of the attribute stem diameter seems to be limited. Stem diameter of trees is positively correlated with height. Therefore height of trees remains the crucial indicator for evaluations of potential nesting sites.

2.3. Height of Crown

Since height of tree crowns was also positively correlated with height, height was still considered to be more important as a criterion for tree choice. It is possible, that in respect to the avoidance of ground predators selection of nests sites may not only represent a choice based on the

absolute height of a tree, but more specifically on the position of the **lowest branch**. Leopards are predators that are known to prey on chimpanzees (BOESCH & BOESCH 1989, BOESCH 1991), and that have been seen to prey in trees (GANDINI & BALDWIN 1978). The height of the lowest branch that a leopard might be able to leap on, may be crucial in that respect. At *Lomako*, the lowest branch was on average about 10 m above the ground. Sometimes, trees were entered from neighbouring trees, but this is an unlikely path for a leopard, since crossing gaps implies locomotor techniques, such as leap-and-cling, which cats can not do. *Bonobos* swung or stretched to grasp a branch to cross over the gap or used their 4 limbs to disperse their weight over several branches. Unfortunately, the bonobos' choice for the height of the lowest branch was not compared with the branches' availability in the forest. Since both, however, height and lowest branch were positively correlated and selection of trees favoured higher trees, it is possible that the lower limit of nests was determined by an optimum height of the lowest branch. In contrast, selection for nest sites overhung by higher vegetation could possibly explain the upper limit of nest trees (cf. p. 135).

WROGEMANN (1992) investigated selectivity of the lowest branch by *chimpanzees* at *Lopé, Gabon*, and reported that a higher proportion of trees used for nest construction had lower lowest branches, and that fewer trees had higher ones. The lowest branches at *Lopé* ranged from 3 - 6 m and thus were much lower than those found at *Lomako*. However, the height of trees in general was lower too, and therefore the apparent choice presented in study may simply reflect availability in a given habitat structure.

2.4. Species

Investigations on the selectivity of tree species showed that *bonobos* at *Lomako* chose for night nests 26 species that were only a small proportion of the available spectrum. Day nests were not included in the analyses of tree selection presented here, since bonobos built them unselectively in almost every feeding tree. Day nests would have increased the number of species used significantly. KANO (1983) reported 103 different species that were used for nests at *Yalosidi*. However, "a fair number of these were presumed to be day nests" (p.19). Thus, it is unclear to what extent day nests influence this picture, but over 80% of the nests mentioned by KANO (1983) came from only 19 species. That gives a similar number to that shown in the present study. At *Wamba* KANO (1992) recorded 108 species for night nests only, and of those the 10 most often used tree species accounted for 72% of all trees. Even though *Wamba* is only about at 300 km distance from *Lomako*, only 2 species of tree were identical among the top 10 species: *Anonidium mannii* and *Scorodophloeus zenkeri*. SABATER PI & VEA (1990) reported nest frequencies for 13 used tree species they found during their transect survey. Of these, 5 species were also used at *Lomako* for night nests, but with different frequencies. The species composition suggests that part of the sample is due to day nests constructed within feeding trees. The tree most often used at all other sites (*Yalosidi* (34.5%), *Wamba* (45%), *Ikela* (28%)) is *Leonardoxa romii*, which was never reported as present at *Lomako*. *Scorodophloeus zenkeri* may be the potential ecological equivalent at *Lomako* due to comparable morphological features like small, soft leaves (FRUTH & HOHMANN 1993).

2.5. Leaf Size

At *Lomako*, all size classes of leaves were represented amongst the top 10 species. The most frequently nested-in tree species, *Diogoa zenkeri*, had leaves of the largest size, the second one, *Scorodophloeus zenkeri*, very small-sized, smooth leaves and the third one, *Polyalthia suaveolans*, leaves of intermediate size. The most simple explanation for small leaves may be that they may make nests more comfortable: They likely provide a sort of air cushion, insulating with many air-filled layers, that is warmed up by body temperature on a cold night. Thermoregulation, however, could also account for the choice of large leaves: Their broad surfaces could provide an air-tight shelter which may reflect body warmth. The few occasions when bonobos were observed in the mornings to remove the cover that had protected their body during cold rainy nights, it was of branches bearing large leaves. When building nests in trees with big sized leaves, bonobos sometimes lined the basic platform with twigs bearing smaller leaves. However, among the top 10, the most often selected tree species had very large leaves. Most probably, leaf size is not primarily important for tree choice.

Instead, other criteria than leaf size may influence choice of tree species: e.g. solid side branches, flexible, and densely leafed twigs. Solid side branches allowed construction of nests in close proximity (e.g. more than one nest on the same side branch). Flexible branches or twigs made it possible to bend and interweave them, without detaching them. I tried to construct a nest in a *Garcinia punctata* tree (a species almost exclusively used by bonobo females). I reached an angle of about 90° before part of the branch broke. This may have been exactly what the bonobos sought: A branch that bent rather than broke, and if it broke then only partly so that it never detached completely. In addition, the leaf densities of branches and twigs were responsible for the thickness of the nest bottom and rim. The

denser were the leaves on branches or twigs, the easier it was to get a thick mattress within arm's reach of the nest site. It seems likely that many other criteria that have not been considered during this study also exist, but it can be concluded that bonobos are highly selective in their choice of trees for nesting. In trying to rank the criteria investigated in this study according to their importance, I would say height first, quality (= species) second and lowest branch third.

Chimpanzees are also selective in their choice of tree species for nesting, and WROGEMANN (1992) provided data on the availability and choice of trees used for nest construction at *Lopé, Gabon*. The proportion of species selected from the available number was much higher than in bonobos. Chimpanzees at *Lopé* used 56 species of 86 available and thus seemed to be less selective. Since WROGEMANN'S study used nests discovered independent of direct observation, it seems likely that day nests were included and this may have increased the number of species used and thus diluted any existing selectivity. However, if it is true that *Lopé* chimpanzees use a broader spectrum of the available species, then it would be interesting to know whether this is related to their being sympatric with gorillas. Possibly, where chimpanzees have to share their habitat with gorillas, they are obliged to be less selective because of inter-specific competition over nest trees. Since more than half of gorilla nests are built on the ground or at much lower heights than are chimpanzee nests, competition may seem improbable, but there could be a secondary effect due to limited nesting sites around shared food resources. In bonobos and chimpanzees, nest sites are re-used regularly and such accumulations show that preferences exist (for more detailed discussion of this subject, see IV; 4.1.). Possibly, choice of the optimal nest *site* (e.g. proximity to feeding trees or to important junctions in the path system) leads to a compromise in the choice of the optimal tree *species*.

3. NESTS

3.1. Physical Correlates

In this chapter I showed the basic physical features of day and night nests. These differed significantly from each other. Day nests were higher than night nests and usually involved only a single tree. Most night nests were in the middle layer of the canopy, and the middle part of the crown. More than half of all night nests had no vegetation overhead, but the proportion of such open nests increased during the rainy season. Investigations of architectural details revealed that nests were built on up to 3 supporting branches, included many bent and broken twigs, and always had some detached twigs as a lining.

3.1.1. Type of construction

One of the main differences between Lomako and other bonobo study sites is the mode of construction: integrated vs. non integrated nests. At *Yalosidi*, only 15% of all nests were integrated (KANO 1983). Of nests made up of only one tree, most (63%) were built on a side branch or in a fork of a tree, while only 20% were built at or near the top. It is possible that this difference between Lomako and *Yalosidi* is due to the fact that no distinction was made between day and night nests. At *Lilungu*, only 4.5% of the 419 nests were integrated (SABATER PI & VEA 1990). Here, however, nest data were taken along transects for population density estimates. Nests were not only reported independently of their time of construction (day vs. night), but also independently of age. From this and other studies (e.g. GOODALL 1968) it is known that nests consisting of parts from several

trees often disintegrate soon after the nest is abandoned, and so decompose faster than non-integrated nests. For studies of the type of construction, this disintegration may give misleading results, since the integrated trees of former nests may have snapped back into their original position, leaving a partial nest in a single tree. Thus, the higher proportion of integrated nests found in Lomako compared to *Yalosidi* and *Lilungu* may be related to the different sampling techniques. Only at *Wamba*, where KANO (1992) distinguished between day and night nests, was the result similar to that reported for Lomako: Night nests were integrated in 45% of the cases ($n = 1693$), 37% were located on side branches, and 19% in the top of a tree. Day nests ($n = 451$) were integrated in only 10% of the cases, with most at side branches (76%) and least at the top (14%).

For *chimpanzees*, little is known about the type of construction. GOODALL (1962) reported integrated nests, but considered them as exceptional. WROGEMANN (1992) found at *Lopé*, that less than 10% of 523 nests incorporated more than one tree, although she only took completely fresh nests into account. The most integrated trees in one nest she reported was 2. It may be that bonobos integrate their nests more than chimpanzees, because of their different social life. If nest places are a limited resource, than larger groups have only 2 possibilities: Either to spread widely over the forest, with each individual finding its place in a perfectly suitable tree, or to try to "create" additional nest material, in order to be close to another individual. Thus, integrated nests may exemplify a response to the needs of sociality and may be a striking example of the capability of apes to alter the environment to fit their needs.

3.1.2. Height

Comparison of data from potential and used nest trees suggests that bonobos make their nests at a preferred height. Factors responsible for this selectivity might be preference for optimum climate (temperature, humidity, protection of wind), material (soft twigs and leaflets) or safety (ground predator, prevention of fall). Climate was reported to influence nest construction in gorillas, with more nests built at protected sites and more vegetation used for better insulation during the rainy season (GROVES & SABATER PI 1985). TUTIN *et al.* (1995) described a case of gorillas abandoning their tree nests in a stormy night for safety reasons (not to fall or to be hidden by falling trees). They concluded that wind sometimes is so violent that comfort becomes secondary to safety. While BALDWIN *et al.* (1981), found the nests of chimpanzees to be lower during the rainy season, TUTIN *et al.* (1995) found no difference in the proportion of tree versus ground nests when they compared dry days with wet days. As mentioned earlier, the making of nests high above the ground is widely thought to be an adaptation to terrestrial predators (BALDWIN *et al.* 1981) including humans (KANO 1992). BOESCH (1991) reported 9 documented cases when *chimpanzees* were attacked by leopards. It is not known whether other attacks occurred at night when the chimpanzees were resting in their nests, but nests in *Tai* forest are the highest compared to other study sites of chimpanzees in *Côte d'Ivoire* (FRUTH 1990). Although attacks by predators on *bonobos* have not been seen at Lomako, it seems likely that predator pressure sets the lower limit on nest sites. Nevertheless, it is hard to see how predator pressure could affect the variation in height existing within study sites (e.g. differences between day and night nests at Lomako).

So far, no study has evaluated height-dependent differences in the availability of potential nest material. Analyses of the structure and productivity of different forest layers in the primary rain forest habitat of *Makoku, Gabon*, show that the middle layer (10-30 m high) contains the majority of flexible branches and twigs with a high proportion of leaves (HLADIK 1978). Extrapolating from that, the bonobos' choice to make nests in that layer may reflect selection for optimal nest material. Day nests may be considerably higher than night nests, because nests are usually constructed after heavy rain in the early morning. At that time bonobos preferred the uncovered part of the upper canopy to bask in the sun. Also, day nests were often built in feeding trees, which are usually the larger trees of the forest. Nests and nesting trees were higher in Lomako than in *Yalosidi, Lake Tumba, and Ikela*. Unlike the disparities in the type of construction (see above), the comparatively high location of nests as well as the absence of ground nests at Lomako are unlikely to result from methodological disparities. Although these study populations are no further apart than 300 - 400 km, cultural differences seem to emerge in bonobo life: Prey-type and food sharing differ between Wamba (flying squirrels - no sharing; IHOBE 1992) and Lomako (duiker - sharing; HOHMANN & FRUTH 1993); play differs between Ikela (capture of monkeys as toys; SABATER PI *et al.* 1993) and Lomako or Wamba (no such observations). Further investigation is needed before we will know, if the differences in nest construction are due to ecological constraints or to other, social factors. Since bonobos lack food processing tools, which in chimpanzees made it possible to make detailed studies on cross-cultural differences (McGrew 1992), nests could clarify whether or not bonobos, even with their much smaller distribution, follow a similar pattern of inter-populational differences.

3.1.3. Position within the crown

The preferred position within the crown may be determined by the availability of suitable nest material or by microclimate. That most bonobos' nests are in the middle part of a crown reflects what was said earlier about the different types of construction. Side branches were used for most nests: lower side branches are thicker and thus less flexible than higher ones. Less light penetrates and thus leaves occur at lower density. The higher the side branches are within a crown, the more flexible and rich in leaflets they are, but also less sturdy. Therefore, the optimal location for nests is probably in the middle crown. In contrast to the top position, the middle position also allows the construction of more than one nest, which may also be responsible for the higher proportion of nests found there. No other study on bonobos has considered the position of nests. WROGEMANN's (1992) study at *Lopé, Gabon*, however, permits a comparison with *chimpanzees*. They used also the middle third of a crown more often than the lower or the upper third. Data from a drier, open habitat at *Mt. Assirik, Senegal*, showed that nests are more often in the upper third (BALDWIN *et al.* 1981). GOODALL (1968) reported that nests at *Gombe* are located in the bottom of a crown. Until more data are available, it is hard to draw any conclusions about the factors influencing choice of nest position.

3.1.4. Cover

Another aspect considered in the current study was whether or not nests were overhung by vegetation from above. The ratio of covered versus uncovered nests was constant, regardless of the season. *Bonobos*, probably did not care whether or not a heavy cloud-burst may hit them directly or with some delay. Upper vegetation may lessen the impact of a

cloud-burst, however water then drips for hours afterwards. The tendency of more nests being open on rainy days may indicate that bonobos prefer to spend minutes under a waterfall rather than hours under a dripping shower. No comparable data were available from other studies of bonobos. In studies of *chimpanzees*, the shift from closed nests in the dry season to open nests in the rainy season was pronounced (BALDWIN *et al.* 1981, WROGEMANN 1992). However, in all other habitats where data on nest cover has been investigated (*Mt. Assirik, Senegal; Okorobiko, Equatorial Guinea; Lopé, Gabon*) the proportion of uncovered nests was always less than that reported here. This may reflect Central Zaïre's having some of the highest rainfall in Africa.

3.1.5. Architectural details

The data shown here for *bonobos* give details on only a very small proportion of nests: those that were accessible to me and thus were rather solid, supporting about twice of a bonobo females' weight. Therefore, these data probably show the upper limits of supporting branches and thicknesses, but they provide the first detailed picture of the components of a bonobo's nest. MACKINNON (1974) who studied Sumatran and Bornean *orang utans*, cut down 7 nests for close examination. He distinguished branches according to their function as "rimming", "hanging", "pillaring" or "loose", but, strikingly he reported no broken branches but only *bent* ones. On the other hand, SCHALLER (1961) examined in detail 13 nests of orang utans in *Sarawak, Malaysia* and found that a nest was usually supported by an average of 4.7 *broken* branches (range 3 - 9). His subjects also used twigs for lining. The mean number of these detached twigs was 10 per nest (range 0 - 34). Nothing was said about the dimensions of these branches, but the data suggest, that orang utans use slightly more branches to built a

platform, which is not surprising, given their greater weight than both species of *Pan*.

3.2. Behavioural Correlates

When behavioural features were analysed, more differences between day and night nests emerged. Day nests needed less time for construction, and were used for shorter periods than were night nests. Females built higher, needed longer to make their nests, built day nests more often and used them for slightly longer. When age classes were compared, it became evident that younger individuals of both sexes needed more time for construction and used the nests they made for much shorter periods than did adults. Most nests were used for rest, followed by eat, groom, play and privacy. The younger the nest-building individual was, the more often nests were used for social purposes. Females' nests were used for social purposes more than males'.

3.2.2. Duration of construction and time of use

Less time spent in the construction of day nests may be partly explained by the less sophisticated mode of construction: fewer trees involved, less branches broken, less single twigs for lining, and by the briefer period of use. Day nests being less sophisticated in structure than night nests is a constant pattern across the great apes (orang utans: MACKINNON 1974; gorillas: SCHALLER 1963; chimpanzees: GOODALL 1992, bonobos: KANO 1992).

3.2.3. Sex differences

In addition to the general preferences shown by *bonobos*, the data indicate sex differences in the height of nests. Females chose not only to build their nests higher, but also earlier than males (cf. III; 4.3.3.). If females build nests in the upper part of nesting trees where soft branches provide optimum comfort (cf. p.143), then a male who wants to stay close to a female may have no better option than to build his nest below hers. In both species of *Pan*, males compete consistently for access to females (GOODALL 1986; DE WAAL 1989; WHITE & BURGMAN 1990). Although most mating occurs during the day, it also happens at night (GOODALL 1968). Thus, males who build their nests beneath those of females may be able to control females and to prevent competing males from approaching females from below. Females may be able to construct day nests more often than males, because they can be more relaxed. Males are probably more often vigilant than females. The larger investment of females in nest construction may also be related to their having dependent offspring. They usually have to build a nest for 2, that not only provides a comfortable mattress but also a safe playground for the infant. If this were the case, then one would expect females without offspring to invest less in nests, but this was not so (*own unpubl. data*). Higher sites may afford thinner branches and twigs and so more material is needed to complete a nest. The difference in duration of construction emerges during ontogeny (infants, juveniles), when one expects infants to copy nest construction from their mothers.

Some sex differences reported here are in accord with observations on *chimpanzees*. MCGREW (1979) was the first to report on sex differences in tool use at *Gombe, Tanzania*. There, females more often engaged in termite fishing and ant dipping, which requires the skilful use of twigs, and invested in longer fishing bouts than males. Insects were a larger proportion of females' than of males' diets. Males, in contrast, were more often involved in hunting and killing of vertebrate prey. MCGREW (1979)

discussed these results in terms of incipient division of labour. *Tai* chimpanzees, *Côte d'Ivoire*, also show remarkable sex differences, with males concentrating less on being less efficient in nut cracking (BOESCH & BOESCH 1984). The authors explained this contrast as males being notably more interested in social events than in nut cracking, while females were the reverse. As to nests, the only data come from *Mahale, Tanzania*, where male chimpanzees built day nests less frequently than females (HIRAIWA-HASEGAWA 1989).

3.2.4. Age Differences

Detailed observations on the ontogeny of nest building are rare. Although the disposition may be innate, infants will watch their mothers as they cling to her body or dangle beside her. Daily exposure to nest construction by their mothers later stimulates them to practice nest building during the day (GOODALL 1962). Gradually increasing skill implicates social and individual learning processes, as observed in captive studies or rehabilitation projects. BERNSTEIN (1962) described captive chimpanzees learning to build nests, and LETHMATE (1977) described nest building attempts by a juvenile orang utan. HARRISSON (1960) gave a detailed ethogram of the ontogeny of captive orang utan orphans and described nest building behaviour of released juvenile orang utans in detail. A comprehensive picture of the learning process, however, is still not available. By cross-sectional study of age classes, I tried to show some stages of nest building skills that emerge during ontogeny. Except for 6 infants born during our study, whose ages are known, age classes were estimated and some classes were made up by only one individual. Until the sample sizes for some age classes increases and the individuals of known age are monitored regularly, the extent to which individuality influences development will remain speculative.

Duration of construction and use

The steady decrease in time used for nest making by both sexes shows that practise improves skills. To watch infants in their first exploratory attempts of nest making was almost like seeing them struggling with the "tree-devil" itself. Stout twigs refused to bend and brittle others snapped immediately back into their faces. That these twig-monstrosities were abandoned immediately before they "exploded" is understandable. The first nests used by a youngster were more like leafy layers than a nest in the proper sense (cf. p. 5). Juveniles built night nests, but took their time constructing day nests. Whether or not they really invested more time to make thicker leaf layers (which would be most useful at night for a better insulation) requires more study. The fact that time-of-use is inversely proportional to the time of investment, suggests that nest construction in infants and juveniles had to do not just with rest but with practise and play. While in infants, the first attempts at nest-making were part of their increasing environmental exploration, juveniles built nests as did adults. As shown in chapter III; 3.2.4.3., infants and juveniles mostly rested or ate while in their nests. However, since nest occupation on average did not exceed 10 minutes, it is more likely that it was nest-making for the sake of the activity than for more comfortable rest or more pleasant food intake. Another reason for the immatures' shorter time of use is that they often built nests near the end of a siesta and thus had to leave them when the adults, who had already had their longer naps, departed. Exceptionally, adolescent males used their day nests for longer than did all other age classes of both sexes. This figure, however, is based on only 4 nests made by one individual (Volker), and thus may not be representative. I can imagine that Volker may have used his day nests longer than other males because they aided his escape from the attention he suffered from the other males (see below). His nests may not have been reported to be responses to pressure, so much as preventive measures. Whether or not that is true awaits additional data.

Number of Individuals

The large difference in sample sizes of non-adult females and males for *day nests* makes it hard to give a conclusive interpretation on the age and sex differences emerging in *bonobo* sociality. Also, male adolescents are represented by only one individual, while there are 3 female adolescents. Nevertheless, the fact that females more often use their nests socially fits into the picture shown on other fronts, in which bonobo females repeatedly seem to be more sociable than males (see III; 3.2.4.3. and III; 4.3.4.). However, males are not unsocial: They often join females in their nests. The higher number of individuals per nest of juvenile and adolescent females therefore may be due to males and other females who join them. Males invest less time in day and night nests and build day nests less often. Possibly a juvenile female's nest is simply more suitable (more broken branches, more twigs for lining, better interwoven) to support more than one individual.

In addition to the sharing of day nests, I saw about 10 cases of *shared night nests*. With one exception in which Ufo, a juvenile male, only started rudimentary nest construction before he joined a juvenile female in her generously shaped nest, all other individuals first built their own night nests, then joined later neighbours. Juvenile males were observed to emerge from their mother's night nest on the next morning. Once, just after a juvenile male had completed his nest, he joined his mother although she was already sharing her nest with her new offspring. Adolescent females have thrice been seen to emerge from an adult male's nest. Once, she had joined him shortly before for an early morning copulation. By including night nests in the analysis, males in nests might be joined as often as females in nests, since younger females make a habit of visiting a male's nest for dawn matings.

Nest-sharing also occurs at *Wamba*, where it is called "co-bedding" (KURODA 1980). During 210 hr of direct observation, KURODA (1980, p.185) saw "not many cases" of nest sharing and described 7 cases in detail, 3 of

which were in night nests. He discussed it together with food-sharing, emphasising the pronounced tolerance of males to females. This contrasts with *Lomako* where females were mostly the tolerant party permitting males to enter their nests. While at *Wamba*, the dominant role is attributed to males no matter whether it is in food sharing or nest sharing, at *Lomako*, it is attributed to females (HOHMANN & FRUTH 1993, *in press*). (Whether or not this is due to gender differences in the subjects of the study or in the research teams remains to be seen.) At *Lomako*, most shared day nests built by adult males involved infants. When adult males built nests during the siesta, they often baby-sat infants, an example of their great tolerance. This behaviour was rarely reported for *chimpanzee* day nests and only exceptionally for their night nests (GOODALL 1975, RISS & GOODALL 1976). It seems to be another example of the high inter-individual tolerance in bonobos.

Activities

As reported above, *bonobos* use nests not just for rest but also for other activities such as eat, groom and play. Nest owners were joined by other individuals and engaged in long and exhaustive play bouts often resulting in damage to and communal reconstruction of nests (cf. p. 88). Of particular interest were those cases when a bonobo built a nest in obvious response to the approach of another individual. A comparable study on captive bonobos confirmed the reluctance of bonobos to displace an individual once ensconced in a nest (ZIETEMANN 1995). In only 4.6% ($n = 907$) of nests were individuals displaced. Where does this reluctance come from?

When approaching their mothers resting in a day nest, youngsters do not immediately enter the nest. Instead, they stop at the fringe and show various gestures of begging and distress, like the "pout face" (DE WAAL 1988), body rock, baby hoot and self embrace. In these situations, the

females often leave the nest before making physical contact with their young. This suggests that the reluctance of females to share day nests with their juvenile offspring may be a key part of the weaning process, in encouraging or forcing the youngster to build its own nest. It remains to be seen whether this behavioural pattern is a species-specific trait limited to bonobos or whether it occurs in the other great apes as well.

Thus, nests may not only facilitate rest but also demarcate "personal space". Other observations at Lomako indicate that this pattern may not only be practised in weaning but also later in life. If potential displacements can be rebuffed by breaking a few branches, nests are not only resting sites but also tools. In order to regulate social conflict, each species evolves particular behavioural mechanisms. Bonobos seem to have developed many such patterns emphasising socio-sexuality, which are not known to occur in other ape species (e.g. genito-genital rubbing; KURODA 1980). While socio-sexual behaviour 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 behavioural element on which the peaceful and cohesive social organisation of bonobos is based. Day nests are also built by the other great apes, and although it has never been reported that they are used as a claim of privacy from conspecifics, some descriptions indicate that they are used to assert occupancy of feeding trees or to hide from observers (for a review, see FRUTH & HOHMANN *in press*). *Orang utans*, for example, stay in feeding trees for days and so monopolise the patch that otherwise would be invaded by competitors. FRUTH and HOHMANN (*in press*) accordingly speculated that nest building may have evolved as a response to inter-specific competition. They hypothesised that only apes who developed nest building during the early Miocene were able to compete successfully with the radiating monkeys, because they were able to occupy and to defend feeding trees. Thus the high rate of day nest construction seen in *bonobos* may be partly related to the functional extension of this behaviour. Day

nests were regularly made in feeding trees, and females twice were seen to start nests when black mangabeys approached and intended to enter the same feeding tree. In both cases the mangabeys moved on. Nests may thus have developed in response to environmental changes with inter-specific significance and later became a conventional sign important for intra-specific communication.

4. NEST GROUPS

This leads to another aspect entirely neglected by other nest studies in great apes: Nest building in bonobos is a social activity, sometimes involving 20 or more individuals. Nest groups analysed here were distributed throughout the primary forest but showed patterns of concentration at certain spots. The average number of nests per group was about 9. It changed from month-to-month and was always larger than the travel groups reported during the day. The degree of fusion at night changed from month-to-month as well. No significant relationship was found between group size and the position of the group within the home range, although the largest groups tended to be close to the centre. Horizontal and vertical dispersion increased with group size, and mean inter-nest distances increased slightly because of subclusters in larger groups. When the nearest neighbour distances were analysed, nests on average were 8 m apart. Inter-nest distance was negatively correlated with group size. Two peaks of construction were seen: One in the afternoon, one in the evening. Onset of construction was earlier at rainy days, and the time from onset to onset between the nests of a group was less simultaneous. In most cases, females started nest construction. They also nested closest to each other, with males nesting less close to females, and males nesting least close to other males of the same night party.

4.1. Distribution and Size

Distribution over the home range

Accumulations of nests at specific sites in the habitat are not unique for bonobos. This behaviour was described for *chimpanzees* in a savanna-woodland habitat (SUZUKI 1969, BALDWIN *et al.* 1982), and in a mosaic of grass-woodland and forest (GOODALL 1962). Chimpanzees were seen to use nest sites concentrated around resources, like large feeding trees or water. It was suggested that seasonal changes influenced the site choice. Early archaeological records with accumulation of tools at specific sites have been interpreted as evidence of hominid home bases used for shelter and food sharing (e.g. ISAAC 1978). SEPT (1992) analysed aggregation patterns of chimpanzee nests at *Ishasha, Zaire* in order to compare prehistorical artifact assemblages with the short lasting debris made by chimpanzees. She hypothesized that spatial concentrations of chimpanzees' nests may accumulate over years through independent episodes of this behaviour, and her results on nest accumulations showed that some sections of the forest were used more often than others. Although her study did not cover all seasons, it was another example of humans not being unique in "spatially focussing their social and economic activities" (MCGREW 1991, 1992). These accumulations are not unique to great apes, for many primate species, whether they are diurnal or nocturnal, have preferences for specific night sleeping sites. Guinea baboons (*Papio papio*), for example, used a single Kapok (*Ceiba pentandra*) tree in 92 of 133 nights (ANDERSON & MCGREW 1984). Night monkeys (*Aotus azarae*) in Bolivia used certain trees at certain places significantly more often than others to sleep during day (GARCIA & BRAZA 1992). The authors suggest that the pattern of distribution and use of specific sleeping sites is related to food availability and structural characteristics of the habitat.

The same reasons may account for the uneven distribution shown for *bonobos* here. Proximity to feeding trees was noted but is not yet analysed. Two occasions may be indicative: One was bonobos for their last food intake about 2 hours before sunset, entering a large, fruit bearing tree. They built their nests about 10-30 m away. The next morning some of the night party may have revisited the tree and eaten some left overs, but most individuals left the site to forage elsewhere. The other regularly occurring situation was when bonobos travelled over large distances in the evening, eating mostly *Haumania* piths. They joined others at a nest site and, the next morning entered a large tree close by. This could have been a tree bearing young, fresh leaves or flowers (*Scorodophloeus zenkeri*) or a tree containing fruit. In both cases, the sites seemed not to be chosen by chance but were known in advance and sought. Old, deformed branches with healed breaks at used nest sites gave proof of much earlier visits of these sites (FRUTH & HOHMANN 1994 b). Re-use may occur more often, when different feeding trees provide food at different times at the same spot, versus when only one tree fruits seasonally. The travel patterns of bonobos appear to be conservative, and much of the time they follow specific trails at specific times. Along these paths they check feeding trees that they may re-visit later. Thus, sites of accumulation may reflect both proximity to regular resources and important junctions of the bonobo path system.

Group size

No data are available on nest group sizes from previous studies of bonobos. For *chimpanzees*, many studies refer to nest group size, but definitions on what is considered to be a nest group vary considerably (ANDERSON *et al.* 1983, TUTIN & FERNANDEZ 1984). Mostly, the age (measured by the state of decomposition) of nests was used as a measure to age a nest group, assuming it to be a cluster of nests built at the same night. However, there is only one sure method to age nests: direct

observation of apes or fresh feces and urine underneath the nests, by marking the nests the next day, after they were built the evening before, to keep track of followed site re-use. WROGEMANN (1992) saw no nest construction but she separated those groups that were completely fresh and did not combine different age classes into one group. Therefore her data are useful for comparison (FRUTH & HOHMANN 1994a), which revealed the most striking difference between the 2 species of *Pan*: While bonobos prefer to join at night to form larger groups, chimpanzees prefer either to nest in the same small groups from the day or even to split up at night.

Location in the home range

The finding that group size was not related to the distance from the centre of the home range may be explained in several ways: First, the criteria I used to define the centre may differ from what bonobos considered to be their centre. Some of their centres may be frequently re-used nest sites at important junctions in their path system. Second, in this analysis I used the total cumulative range over 4 years. Their actual range may differ by season and shift in other directions depending on food availability. Third, borders with neighbouring communities may not be boundaries in the human sense, but instead large zones of overlap in which strangers are tolerated unless important feeding trees occur in the area. The only recorded inter-community encounters occurred, when favoured trees at the periphery were in fruit: *Pancovia laurentii* in January 1991, *ifetete* in June 1992 (own obs.), *Polyalthia suaveolans* in March 1995 (HOHMANN pers. comm.). Therefore, the premise used here to analyse group size in relation to spatial position does not take enough into account the dynamics of bonobo nomadism. A better way to understand neighbour-related ranging would be the simultaneous observation of 2 neighbouring communities. Probably, distance to the centre does not affect the size of a party but more likely the behaviour of a party according to its size. When strangers were

found in a known area regularly used by members of the Eyengo community, they were loud and aggressive when they were a large group, but they were silent, cryptic when they were few. Nevertheless, it is worth noting the tendency for larger groups to aggregate in the centre. This may be explained in relation to travel and fission-fusion, discussed below.

Groups size over seasons, by day and night, with varying intensity

It is evident that there is much fluctuation in association patterns, not only from day-to-night but also from month-to-month. Why do different parties join? Living in groups has been explained in different ways: as an anti-predator strategy (VAN SCHAİK 1983), as an optimal foraging strategy in terms of resource competition and foraging efficiency (WRANGHAM 1977, 1980), and as a strategy to improve opportunities of care-giving (SMUTS 1985; for a summary of these theories see DUNBAR 1988). Primates' gathering to form larger groups at night may be one adaptation against predators, although there is no evidence that bonobos face any nocturnal threats. For great apes potential ground predators like leopards (*Panthera pardus*) and lions (*Panthera leo*) in Africa, and clouded leopards in Asia, however, exist and grouping patterns of bonobos may be an adaptation which finds its roots in the past. The question remains as to what selection pressure could favour bonobos' gathering at night?

The community splits up to forage in different parts of its range. They may spend days outside the core area, but they regularly return to the core area. There may be a certain rhythm to this and large meetings may not be by chance but sought. I suggest that these regular aggregations may facilitate information exchange, as suggested by WARD and ZAHAVI (1973) for birds. Grouping at night may make possible not only the long-term cohesion of a community of rather independent individuals but also the

optimal (but still individually based) use of a range that is not only vast but also is inhabited by many feeding competitors.

Periodical gathering seems to happen at 2 levels: Almost daily when some parties gather at night and every 2 - 3 weeks when almost the entire community comes together. Once, in the beginning, when we had lost the bonobos for days because we did not know the extent of their range and searched in the wrong places, we suddenly heard a party approaching from the north-east, at that time peripheral to the range we were familiar with. This party often vocalised and immediately there were answers from different directions. They joined, continued travelling, crossed the central basin of the home range and formed a large sleeping group in dry primary forest at the other end of their range. In this phenomenon of large-scale fusion, everyone seems to know the aim well beforehand. The five largest such groups had 24 or 25 nests, and the community consisted of 24-26 mature individuals, depending on the year, so on these occasions all community members were probably present.

For *chimpanzees* at Gombe, Tanzania, WRANGHAM (1977) found no evidence that dispersion and recombination of chimpanzee parties helped to increase food-finding efficiency. He focused on food-calls to answer the question of whether or not individuals who discovered a food resource would seek to share. Attracting others to a rich resource at first glance appears to be altruistic. The individual inviting others, however, could benefit from reciprocity (TRIVERS 1971) or within-group kin support (HAMILTON 1964). These explanations were ruled out by CLARK's (1991) study at Kibale, Uganda, showing that food calls were only given by high-ranking males and were independent of food availability. WRANGHAM (1977) concluded that information transfer was not necessary, since each individual is familiar with the range and knows where food is. For *bonobos*, familiarity with the home range is also high, but monitoring a 20 km² range phenologically would be energetically expensive if not impossible for an individual. Fission and fusion may be the only strategy to get regular

access to the best food available and quality of information may outweigh the costs of feeding competition. Also, congregating at times of no feeding competition could bring mating advantages for males and females. Early morning copulations occur regularly at Lomako. Females leave their nests, descend to a male, sit in or beside his nest, and invite him to copulate. The probability of more potential mating partners being present increases with group size. Males seek to maximise copulations as a basic strategy, and females may get easier access to their sexual partners of choice. Moreover, sperm levels regenerate over night, so the first copulation in a day is probably the most potent in terms of probable conception.

To better understand that fission-fusion system, it is necessary not only to follow different parties simultaneously for extended periods, but also to learn whether or not parties that join a larger group change their travel direction to follow the others. It may also be important to know when a resource is known to be consumed also by other species such as monkeys, in terms of the impact of feeding competitors.

4.2. Physical Correlates

4.2.1. - 4.2.2. Horizontal and vertical dispersion

These measures were taken to give a description of the extent to which a *bonobo* nest group is dispersed within the forest. Comparison to other data is not possible since nothing is known on the dimension of nest groups at other bonobo study sites. For *chimpanzees*, GOODALL (1968) reported for Gombe, Tanzania, that mature or adolescent males sometimes nested more than 90 m away from a rather densely packed nest group. The 2 nest groups measured at Tai, Côte d'Ivoire, had 40 m (11 nests) and

64 m (15 nests) horizontal dispersion respectively (cf. II. 4.2.1). At *Equatorial Guinea*, nest sites were measured for *gorillas* by JONES & SABATER PI (1971). These gorilla nest sites ranged from 9 - 31 m across, but this was not the distance between the most peripheral nests but the nest site (terrain) where the nests were located in.

4.2.3. Distance between nests

The values given here are for what was defined as a nest group on p. I. Individuals nesting within a radius of 10 m seemed to belong to the group, but whether or not individuals 100 m away were also members is unclear. Alternation of choruses however, indicated that only individuals further away than 100 m seemed to belong to another group. Only for mountain *gorillas* are mean inter-nest distances available: SCHALLER (1963) reported inter-nest distances ranging from 0 - 39 m, and CASIMIR (1979) reported mean distances from 8 - 10 m. Both investigators considered only ground nests, and thus measured 2, rather than 3, dimensions. This suggests that gorillas on average have tighter spaced nest groups, perhaps because they nest mostly on the ground and have more suitable nest material from terrestrial herbaceous vegetation (THV) available.

Mean inter-nest distances and tree density

Mean inter-nest distances decreased with increasing density of suitable nesting trees. This reflects in part what emerged from the analysis on selectivity of specific tree species. It also suggests that bonobos might even nest closer, if the density of suitable nesting trees allowed it.

4.2.4. Nearest Neighbour Distances

The nearest neighbour distances presented here are the first ones available for wild *bonobos*.

In *chimpanzees*, measurements of nearest neighbour distances were investigated by BALDWIN *et al.* (1981) at Mt. Assirik, Senegal and WROGEMANN (1992) at Lopé, Gabon. WROGEMANN (1992) found a median nearest neighbour distance of 6 m, with extreme values of 0.5 and 45 m. This is strikingly similar to what was found at Lomako. However, WROGEMANN (1992) and all other researchers working on the subject, took the horizontal distances from one nest to the other, assuming that height would not influence these distances significantly. Inter-nest distances at Lomako were compared for both 2 and 3 dimensions. The difference was significant (Wilcoxon Matched-Pairs Signed-Ranks Test; $z = -25.4926$, $p < 0.0001$, $n = 1043$). On average it was only one metre, but the difference became more important the closer 2 nests were on a 2 dimensional level, if the difference in height was great. Therefore, it is likely that chimpanzees on average show less spatial tolerance than do bonobos.

At Mt. Assirik, BALDWIN *et al.* (1981) found that the median distance between neighbouring nests was 4 m. Here, nests were thought to belong to one group when the age was estimated to be the same, and all nests that were further away than 15 m were considered to belong to the next group, even if they were the same age. This probably diminished the result for inter-nest distances within groups, since peripheral nests were excluded by definition. Habitat structure may be another factor that influences inter-nest distances, as shown with tree density above. Therefore, the question of inter-specific differences in the spatial distribution of nests awaits data from both species of *Pan* when they are investigated using the same methods.

Why do individuals move closer to one another with increasing group size? The most striking difference is between the very small groups of up to 4 individuals who nest relatively far from each other and those with more

than 4 individuals. At first glance, this is striking because if grouping at night has evolved as an anti-predator strategy, one would expect less individuals to get even closer. However, it may be more advantageous for a small group to separate, in order to conceal themselves from a potential predator. Although small groups give fewer distance calls at night than do large ones (*unpubl. data*), they do sometimes vocalise. Therefore, avoiding detection may not be their anti-predator strategy. Given the make up of the small groups, there is another explanation: These solitary individuals avoided the socially active ones, who usually formed a larger parties. The solitaires often roamed in a small area of the range rarely used by others. They did not interact frequently with each other but seemed to be content mainly with eating. Moreover, in these small groups 2 adult males often accompanied an adult female with dependent offspring. The males kept larger distances to each other than to the female and may have influenced greatly overall proximities. The differences from one point to the next in Figure 42 will only be ultimately understood, if the composition of individual nest groups is known in detail.

4.3. Behavioural Correlates

4.3.1.- 4.3.2. Time and duration of construction

There is a striking gap between early onset and late onset of nest construction. *Bonobos* built nests earlier when it was a rainy day or a cloudy day. On these occasions, they took their time and built in sequence close to the last feeding tree; One individual typically left the feeding tree, made a nest, lay down, and then minutes passed before another came to join in. When the weather was good, it was usually light until 18:00 hr or

later, and individuals often used the 'extra' time to travel before they actually reached the nest site. Then they would build more simultaneously and faster, in order to finish just before nightfall. The difference shown in this study, with a low and wide spread distribution when nest groups started early and a peaked, narrow distribution short before sunset reflects these different habits. It is likely, that prolongation of rest in nests on cold, rainy evenings or mornings, helps to conserve energy.

Duration of nest construction is similar in all the great apes and different times of onset and construction have been attributed to weather, season and group size. Similar shifts have been reported for *chimpanzees* (GOODALL 1968), *orang utans* (MACKINNON 1974) and *gorillas* (GROVES & SABATER PI 1985).

4.3.3. Initiator of construction

Females initiate nest-making. Comparable data from other studies on bonobos or chimpanzees are not available. SCHALLER (1963) and GROVES and SABATER PI (1985) noted that in *gorillas* the silverback male decided where to stay for the night. Such decision-taking seems to be dominance related, and *bonobo* females' first choosing a nesting site and then males joining in is another example of this society's being female-dominated. But what do females gain by being the ones to start nest construction? As shown in section 3.1.2. of this chapter, higher places may provide better nest material than lower ones, optimal nest trees are not scattered homogeneously, so females starting first obtain the best places. The pattern of distribution described by WRANGHAM (1980) with males seeking proximity to females who distribute themselves according to food resources, could be reflected here on a smaller scale: Females go to the best nest places and males 'map' themselves accordingly. Sex differences in the choice of nest positions and nearest neighbours suggest that males

try to stay close to females and in the process space themselves evenly among the group.

4.3.4. Nearest neighbour and sex of the nest-owner

For nearest neighbour distances between *bonobo* nests in relation to the sex of the nest owner, the results are as expected from the social structure of a bonobo community (cf. II.B.;1.). Females form close coalitions and thus dominate males, while males compete with each other over females. Thus females nesting closest together may reflect their strong, mutual affiliation. The distance between males and females, in contrast, may be influenced by several factors: males' striving to be close to a female leads to close proximity which will be a strain for both, from avoidance of potential conflicts with other males by being too close, and from individual differences on tolerance by the female concerned. The nearest neighbour distances calculated here, probably reflect the upper limit of nearest neighbour distances in bonobos at *Lomako* for the following reason: The largest group for which nearest neighbour distances were analysed according to the sex of the nest owners had 7 nests. Nearest neighbour distances of larger groups, however, were smaller overall. If sex related analyses had been taken into account, these would have been even smaller. The relative proximity with females being closest to females, followed by male to females and male to males, would probably remain the same. Fading light and simultaneous construction makes it impossible for an observer to identify completely all nest owners in nest groups of over 10 individuals. Unless several observers take data at different corners of the same group, complete inter-individual relations rarely will be obtained.

ZIETEMANN (1995) confirmed for *captive bonobos* the relative distances found in this study. She defined 3 classes of proximity: < 2 m, 2 - 5 m and > 5 m, as adapted to the constraints of the enclosure. In her

study, females predominantly built nests within 2 m of females, and males built at the 2 - 5 m distance to females. Males in contrast avoided building near one another. They nested in 74% of cases ($n = 283$) more than 5 m apart, while females did so in only 50% of cases ($n = 450$).

If the data in this study are compared with nearest neighbour associations during the day from previous research at *Lomako* (1983-1985), the results for the 2 best habituated communities is similar to what is reported here. Only for investigations of the formerly least habituated Eyengo community, do differences emerge on the intra-site level: Distances were also largest between males and males, but were followed by females and females. Here males and females were closest (WHITE & BURGMAN 1990). According to WHITE and BURGMAN (1990, p.200) these differences cannot be explained by differences in habituation since "... at Wamba, where the study population is highly habituated, association patterns are most similar to the unhabituated Rangers" (= Eyengo community). Again (see also p. 130) it seems likely that the differing degree of habituation is the major reason for the differences between these data and those obtained previously for *Lomako*. Why at *Wamba* did males mainly associate with females, then females with females, and only thirdly, males with males (KURODA 1979)? KANO (1980) described the same pattern for grooming associations. It may be because of the artificial feeding site at Wamba. Members from different communities often joined there and although the bonobos may have been perfectly habituated to the presence of human observers, social tensions accompanying intergroup encounters was likely present. Males may have guarded females from other-group-members and thus may have raised their status, putting them in a more powerful position than normal.

Association among related females has been discussed as a strategy for cooperative defence of food patches (WRANGHAM 1980, WHITE & WRANGHAM 1988, WHITE & BURGMAN 1990). In bonobos, females "bond" even though they are not closely related. This bonding was discussed in the

context of larger and easier accessible feeding patches including superabundant herbaceous vegetation, THV (WHITE & WRANGHAM 1988, MALENKY & STILES 1991, MALENKY & WRANGHAM 1994). Moreover, rich socio-sexual interaction has been discussed as a means to reduce tension and to increase cooperation and bonding (KANO 1980, KURODA 1984, DE WAAL 1987, 1989; PARISH 1995). Why should nest sites be a resource to compete for? Close proximity among females suggests that nest trees may be considered as resources, for which females possibly compete with males. Spatial differences within a group, females nesting higher than males, support this idea. Other reasons, however, are feasible for females to nest so close: At rainy days when nests were built early, females were seen twice to groom each other in one of 2 adjacent nests. Infants, usually the first ones to leave their mother's nest in the early morning, were seen regularly to start play immediately with the neighbouring infant somewhere within reach of either one or the other nest. Possibly, the solution of tension in competition made it even more possible for females to stay close together in non-competitive interaction.

For the other great apes, only in *gorillas* have detailed studies on inter-nest associations been done. No relation between social relationships and nest associations were found (CASIMIR 1979, WINA 1989). Although CASIMIR'S (1979) study measured distances from nest-to-nest, he did not take into account height differences (for nests or for terrain), nor did he consider personal relationships. YAMAGIWA (1983) found different positioning according to age-sex classes, with silverbacks and females with offspring in the centre, surrounded by females without infants, old infants and juveniles, and blackback males and young females at the periphery.

Many indices of *bonobo* grouping suggest that there are patterns, as seen in details like height, distances, or differences in nearest neighbours, that characterise the make-up of a nest group. We will not be able to specify what it is exactly that determines these patterns, and only by comparison to nest groups of the other great apes, we will be able to

ascertain if the patterns found here are species-specific, rather than a result of environmental determinants or other influencing factors.

ACKNOWLEDGEMENTS

I thank my parents and grandparents for having shared their nest with me for so long. They did not throw me out when my little sister was born, and even nowadays they are never reluctant to share it with me whenever I feel the need for the well known nestwarmth. PROF. GERHARD NEUWEILER is the person who first encouraged my academic career. To him I owe deepest thanks for his administrative, financial, and moral support; the patience and freedom he provided were essential. PROF. IRENÄUS EIBL-EIBESFELDT made it possible for me to continue this study when the DAAD reclaimed the fellowship because of political instability at Zaïre. He gave me office space and basic supplies in his institute, and allowed me to write up my data in one of the most atmospheric places of the world. PROF. DETLEV PLOOG supported the project intellectually and financially, and I like to thank him warmly for his continuous interest and support. PROF. EBERHARDT GWINNER was generous in giving me access to his territory: computers, e-mail, and all these nice people working with creatures making "real" nests. PROF. WOLFGANG WICKLER deserves special thanks for having given the project a future by incorporating it (and us) into his domain. Last, but not least, among the alpha males, I express my deep gratitude to PROF. WILLIAM MCGREW, who came to Erling just in time to enrich me and the thesis with good discussion. His patient reading, re-reading and editing of the thesis helped to make it accessible to non-German speakers.

One person shares the "we" in the descriptive parts of the thesis: DR. GOTTFRIED HOHMANN, to whom I owe the most heartfelt thanks. Without him, I surely would not have endured the endless months far from any other social contact. Only he shares knowledge of the many puzzling aspects of bonobo life and for the unique, resulting, and often colourful discussions, I dedicate to him the "pseudo-nest", as evidence of our efforts at joint problem solving. DR. VOLKER SOMMER introduced me to scientific primatology, and discussions with him were always lively and inspiring. To

him, I dedicate the "taboo"-nest. I thank the club "Alternde Biologen am Wörthsee (AG)" for regularly training my "Zwerchfellmuskels" by providing many witty evenings. Special thanks are due to DR. HERIBERT HOFER who stopped me just in time from committing statistical crimes.

Many people helped during the field seasons and made enjoyable the time on the road and in the forest. I am most grateful to EMIL (DL9IW) and PAULA OTT (DF5RO). They were the abiding link through all these years, giving us the radio-connection to the outside world. Whenever we went to Kinshasa, many people made these stays pleasant. Most remain unnamed but three stand out: HEIKE DETTMANN was so kind as to provide housing in the first year of the project, and HANS-PETER and TRAUDL REICH gave us lodging in the other years, supporting us in countless ways. The MISSIONARIES OF HERZ JESU (Sacre Coeur), generously helped with regular contact, mail, and personal transport, and provided the first cool beers after months of abstinence. Without them, cargo, fuel transport, and shelter for us and our equipment would have been much harder in the interior of Equateur.

At Lomako, I thank the PEOPLE OF NDELE, LIFENGO, BOKOLI and BOFUA for accepting us in their forest and for providing food and insight into their lives. IKALA LOKULI, BONTAMBA LOKULI, BOKUA BOLESA and LOMBOTO ISOTUKU contributed either to domestic work or to data collection and deserve special thanks.

In the Zoological Institute, I thank the whole department (of Prof. Neuweiler) for their continuous interest in the project. MAIKE PÖTKE entered endless columns of numbers on the nests into a graphic program, ACAD11. She taught me how to use it and helped whenever it was necessary. For her untiring search for appropriate patterns, she deserves a First-Class-"Musternest". DIETER LEIPPERT was so kind as to write the software for intra- and inter-group analyses and voluntarily assisted whenever there was a computer problem. CLAUDIA SCHULTE helped on data entry in the first year. ERIKA YOUNG and BENEDIKT GROTHE stood out by creating the kind of

personal atmosphere needed to feel comfortable and settled. My "other" department, the Forschungsstelle für Humanethologie in der MPG (of Prof. Eibl-Eibesfeldt), has my most heartfelt appreciation: All members showed me that life in an institute can be warm and social, and the regular coffees, reunions, spontaneous and traditional feasts greatly impressed me: I hope to take this familiar atmosphere to all future institutions I will work with.

Finally, I thank the EYENGO COMMUNITY for their tolerance to us. They allowed us humans to experience their lives in ways no one has done before. They are the only beings mentioned here who will never read these lines, although I wished to get their opinion.

The government of Zaïre, Ministère de la Recherche Scientifique et Technologie, gave permission to do research at Lomako from September 1990 to October 1994 (Autorisation de Recherche N^o: ESURS/CABMIN/2360/90 and RST/CABMIN/03995/92); the Centre de Recherche en Sciences Naturelles (CRSN) provided travel permits for these periods (Ordre de Mission N^o: ESURS/CRSN/BL/KM/033/90 and RST/CRSN/BL/KM/1200/001/93), and the commissaire de zone de Befale issued residence cards (cartes de résidences). The German Embassy (Ambassade de l'Allemagne), Hanns-Seidel-Stiftung (Fondation Hanns-Seidel) and Gesellschaft für technische Zusammenarbeit (GTZ) in Kinshasa were most helpful in administrative and logistic way. Substantial financial aid was given by the German Academic Exchange Service (DAAD), Max-Planck-Society (MPG), University of Munich (LMU), and private donors.

- ADLER, J. 1991. The species of douc langurs - a first pictures demonstration. Paper given at the 2. Kongress der Gesellschaft für Primatologie (30.09.1991 - 02.10.1991) in Bochum, Germany.
- ALCOCK, J. 1972. The evolution of the use of tools by feeding animals. *Evolution*, **26**, 464-73.
- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.
- ANDERSON, J.R. & MCGREW, W.C. 1984. Guinea Baboons (*Papio papio*) at a sleeping site. *American Journal of Primatology*, **6**, 1-14.
- ANDERSON, J.R., WILLIAMSON, E.A. & CARTER, J. 1983. Chimpanzees of Sapo forest, Liberia: density, nests, tools and meat-eating. *Primates*, **24**, 594-601.
- BADRIAN, A. & BADRIAN, N. 1977. Pygmy chimpanzees. *Oryx*, **13**, 463-468.
- BADRIAN, A. & BADRIAN, N. 1978. Wild bonobos of Zaïre. *Wildlife News*, **13**, 12-16.
- BADRIAN, N. & BADRIAN, A. 1984. Social organization of *Pan paniscus* in the Lomako forest, Zaïre. In: *The Pygmy Chimpanzee*, ed. R.L. Susman, pp. 325-346. New York & London: Plenum Press.
- BADRIAN, N. & MALENKY, R.K. 1984. Feeding ecology of *Pan paniscus* in the Lomako Forest, Zaïre. In: *The Pygmy Chimpanzee*, ed. R.L. Susman, pp. 275-299. New York: Plenum Press.
- BALDWIN, P.J., MCGREW, W.C. & TUTIN, C.E.G. 1982. Wide ranging chimpanzees at Mt. Assirik, Senegal. *International Journal of Primatology*, **3**, 367-385.
- BALDWIN, P.J., SABATER PI, J., MCGREW, W.C. & TUTIN, C.E.G. 1981. Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). *Primates*, **22**, 474-486.
- BEARDER, S.K. 1987. Lorises, Bushbabies, and Tarsiers: Diverse Societies in Solitary Foragers. In: *Primate Societies*, ed. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker, pp. 11-24. Chicago: University of Chicago Press.
- BECK, B.B. 1980. *Animal Tool Behaviour*. New York: Garland STPM.
- BERNSTEIN, I.S. 1962. Response to nesting materials of wild born and captive born chimpanzees. *Animal Behaviour*, **10**, 1-6.
- BERNSTEIN, I.S. 1967. Age and experience in chimpanzee nest building. *Psychological Reports*, **20**, 1106.
- BLOWER, J. 1956. The mountain gorilla and its habitat in the Birunga Volcanoes. *Oryx*, **3**-6.
- BOESCH, C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, **117**, 220-242.
- BOESCH, C. 1995. Innovation in wild chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, **16**, 1-16.

- BOESCH, C. *in press*. Social grouping in Taï chimpanzees. In: *Great Ape Societies*. ed. W.C. McGrew, L.F. Marchant, & T. Nishida. New York: Cambridge University Press.
- BOESCH, C. & BOESCH, H. 1981. Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. *Journal of Human Evolution*, **13**, 415-585-593.
- BOESCH, C. & BOESCH, H. 1983. Optimization of nut cracking with natural hammers by wild chimpanzees. *Behaviour*, **83**, 265-286.
- BOESCH, C. & BOESCH, H. 1989. Hunting behaviour of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology*, **78**, 547-573.
- BOESCH, C., MARCHESI, P., MARCHESI, N., FRUTH, B. & JOULIAN, F. 1994. Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution*, **26**, 325-338.
- BOLWIG, N. 1959. A study of the nests built by mountain gorilla and chimpanzee. *South African Journal of Science*, 286-291.
- DE BOURNONVILLE, D. 1967. Contribution à l'étude du chimpanzé en République de Guinée. *Bulletin de l'Institut Fondamental d'Afrique Noire*, **29A**, 1188-1269.
- BROSIOUS, G. & BROSIOUS, F. 1995. *SPSS Base System and Professional Statistics*. Science.com
- CASIMIR, M.J. 1975. Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuzi region (République du Zaïre). *Folia primatologica*, **24**, 81-136.
- CASIMIR, M.J. 1979. An analysis of gorilla nesting sites of the Mt. Kahuzi region (Zaïre). *Folia primatologica*, **32**, 290-308.
- CHAPMAN, C.A., WHITE F.J. & WRANGHAM, R.W. 1994. Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In: *Chimpanzee Cultures*, ed. R.W. Wrangham, W.C. McGrew, F.B.M. de Waal & P.G. Heltne, pp. 109-128. Cambridge, MA: Harvard University Press.
- CHARLES-DOMINIQUE, P. 1977. *Ecology and Behaviour of Nocturnal Primates. Prosimians of Equatorial West Africa*. New York: Columbia University Press.
- CLARK, A.P. 1991. The Socioecology of Wild Chimpanzee Vocal Behavior in the Kibale Forest, Uganda. Ph.D. thesis: University of Michigan.
- CLIFF, A.D. & ORD, J.K. 1981. *Spatial Processes: Models & Applications*. London: Pion Limited.
- COOLIDGE, H.J. 1933. *Pan paniscus*, pigmy chimpanzee from south of the Congo river. *American Journal of Physical Anthropology*, **XVIII**, 2-59.
- CRAMER, D.L. & ZIHLMAN, A.L. 1978. Sexual dimorphism in the pygmy chimpanzee, *Pan paniscus*. In: *Recent Advances in Primatology, Volume 3, Evolution*. ed. D.J. Chivers and K.A. Joysey, pp. 487-490. London: Academic Press.

- DAVENPORT, R.K. 1967. The orang-utan in Sabah. *Folia primatologica*, **5**, 247-63.
- DONISTHORPE, J.H. 1958. A pilot study of the mountain gorilla (*Gorilla gorilla beringei*) in south west Uganda, February to September, 1957. *South African Journal of Science*, 195-217.
- DORAN, D.M. 1989. Chimpanzee and Pygmy Chimpanzee Positional Behavior: The influence of environment, body size, morphology, and ontogeny on locomotion and Posture. Ph.D. thesis: State University of New York at Stony Brook, Stony Brook, New York.
- DORAN, D. M. 1993. Comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. *American Journal of Physical Anthropology*, **91**, 83-98.
- DU CHAILLU, P. 1861. *Explorations and Adventures in Equatorial Africa*. London: John Murray.
- DUNBAR, R.I.M. 1988. *Primate Social Systems*. London: Croom Helm.
- ELLIOTT, R.C. 1976. Observations on a small group of mountain gorillas (*Gorilla gorilla beringei*). *Folia primatologica*, **25**, 12-24.
- EVARD, C. 1968. *Recherches Écologiques sur le Peuplement Forestier des Sols Hydromorphoses de la Cuvette Centrale Congolaise*. Bruxelles: INEAC, séries scientifiques, No. 110.
- FIEDLER, W., GEWALT, W., GRZIMEK, B. HEINEMANN, D. HERTER, K. & THENIUS E. (eds.). 1968. Spitzhörnchen und Halbaffen. In: *Grzimeks Tierleben: Säugetiere I* (Band 10). pp. 243-296. Zürich: Kindler Verlag.
- FOSSEY, D. 1974. Observations on the home range of one group of mountain gorillas (*Gorilla gorilla beringei*). *Animal Behaviour*, **22**, 568-581.
- FOSSEY, D. & HARCOURT, A.H. 1977. Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla beringei*). In: *Primate Ecology*, ed. T.H. Clutton-Brock, London: Academic Press.
- FRUTH, B. 1990. Nussknackplätze, Nester und Populationsdichte von Schimpansen: Untersuchungen zu regionalen Differenzen im Süd-Westen der Elfenbeinküste. Diplomarbeit: Ludwig-Maximilians-Universität München.
- FRUTH, B. & HOHMANN, G. 1993. Ecological and behavioral aspects of nest building in wild bonobos (*Pan paniscus*). *Ethology*, **94**, 113-126.
- FRUTH, B. & HOHMANN, G. 1994a. Comparative analyses of nest building behavior in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). In: *Chimpanzee Cultures*, ed. R.W. Wrangham, W.C. McGrew, F.B.M. de Waal and P.G. Heltne, pp. 109-128. Cambridge, MA: Harvard University Press.
- FRUTH, B. & HOHMANN, G. 1994b. Nests: Living artefacts in recent apes? *Current Anthropology*, **35**, 310-311.
- FRUTH, B. & HOHMANN, G. *in press*. Nest building behavior in the great apes: The great leap forward? In: *Great Ape Societies*. ed. W.C. McGrew, L.F. Marchant, and T. Nishida. New York: Cambridge University Press.

- FURUICHI, T. 1987. Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee females at Wamba, Zaire. *Primates*, **28**, 309-318.
- GARCIA, J.E. & BRAZA, F. 1993. Sleeping sites and lodge trees of the night monkey (*Aotus azarae*) in Bolivia. *International Journal of Primatology*, **14**, 467-477.
- GALDIKAS, B.M.F. 1975. Orangutans, Indonesia's "people of the forest". *National Geographic*, **148**, 444-73.
- GALDIKAS, B.M.F. 1979. Orang-utan adaptation at Tanjung Putin Reserve: mating and ecology. In: *The Great Apes*. ed. D.A. Hamburg and E.R. McCown, pp. 195-234. Menlo Park: Benjamin/Cummings.
- GALDIKAS, B.M.F. 1982. Orang-utan tool use at Tanjung Putin reserve, central Indonesian Borneo (Kalimantan Tengah). *Journal of Human Evolution*, **10**, 19-33.
- GANDINI, G. & BALDWIN, P.J. 1978. An encounter between chimpanzees and a leopard in Senegal. *Carnivore*, **1**, 107-109.
- GARNER, R.L. 1896. *Gorillas and chimpanzees*. London: Harpers.
- GHIGLIERI, M.P. 1979. The socio-ecology of chimpanzees in Kibale Forest, Uganda. Ph.D. thesis. Davis: University of California.
- GHIGLIERI, M.P. 1984. *The chimpanzees of Kibale forest: a field study of ecology and social structure*. New York: Columbia Press.
- GOODALL, J., V.L. 1962. Nest building behavior in the free ranging chimpanzee. *Annals of the New York Academy of Sciences*, **102**, 455-467.
- GOODALL, J., V.L. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monography*, **1**, 163-311.
- GOODALL, J., V.L. 1973. The behavior of chimpanzees in their natural habitat. *American Journal of Psychiatry*, **130**, 1-12.
- GOODALL, J., V.L. 1975. Chimpanzees of Gombe National Park: thirteen years of research. In: *Hominisation und Verhalten*. ed. Eibl-Eibesfeldt, pp. 74-136. Stuttgart: Gustav Fischer Verlag.
- GOODALL, J. 1977. Infant-killing and cannibalism in free living chimpanzees. *Folia primatologica*, **28**, 259-282.
- GOODALL, J. 1986. *The Chimpanzees of Gombe: Patterns of Behaviour*. Cambridge, MA: Harvard University Press.
- GOODALL, J. & ATHUMANI, J. 1980. An observed birth in a free-living chimpanzee (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania. *Primates*, **21**, 545-549.
- GOODALL, J., BANDORA, A., BERGMANN, E., BUSSE, C., HILALI, M., MPONGO, E., PEARCE, A. & RISS, D. 1979. Intercommunity interactions of the chimpanzee population of the Gombe National Park. In: *The Great Apes*, ed., D.A. Hamburg and E.R. McCown, pp. 13-53. Menlo Park, CA: Benjamin/Cummings.
- GROVES, C.P. & SABATER PI, J. 1985. From ape's nest to human fix-point. *Man*, **20**, 22-47.

- HAGGET, P., CLIFF, A.D. & FREY, A. 1977. *Locational Methods*. London: Edward Arnold.
- HALPERIN, S.D. 1979. Temporary association patterns in free ranging chimpanzees: an assessment of individual grouping preferences. In: *The Great Apes*. pp. 491-500. ed. D.A. Hamburg and E.R. McCown. Menlo Park: Benjamin Cummings.
- HAMILTON, W.D. 1964. The evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1-52.
- HARRISSON, B. 1960. A study of orang-utan behaviour in semi-wild state, 1956-1960. *Sarawak Museum Journal*, **IX**, 422-447.
- HARRISSON, B. 1962. *Orangutan*. London: Collins.
- HARRISSON, B. 1969. The nesting behaviour of semi-wild juvenile orang-utans. *Sarawak Museum Journal*, **XVII**, 336-384.
- HEDIGER, H. 1977. Nest and home. *Folia primatologica*, **28**, 170-187.
- HIRAIWA-HASEGAWA, M. 1989. Sex differences in the behavioral development of chimpanzees at Mahale. In: *Understanding Chimpanzees*, ed. P.G. Heltne and L.A. Marquardt, pp. 104-115. Cambridge, MA & London: Harvard University Press and Chicago Academy of Sciences.
- HLADIK, A. 1978. Phenology of leaf production in a rain forest of Gabon: distribution and composition of food for folivores. In: *The Ecology of Arboreal Folivores*. ed. G. G. Montgomery, pp. 51-71. Washington: Smithsonian Insitute Press.
- HOHMANN, G. & FRUTH, B. 1993. Field observations on meat sharing among bonobos (*Pan paniscus*). *Folia primatologica*, **60**, 225-229.
- HOHMANN, G. & FRUTH, B. 1994a. Structure and use of distance calls in wild bonobos (*Pan paniscus*). *International Journal of Primatology*, **15**, 767-782.
- HOHMANN, G. & FRUTH, B. *in press*. Food sharing and status in unprovisioned bonobos (*Pan paniscus*): preliminary results. In: *Food and the Status Quest*. ed. P. Wiessner and W. Schiefenhövel. Harvard: Marion Berghahn Press.
- HOPPE-DOMINIK, B. 1991. Distribution and status of chimpanzees (*Pan troglodytes verus*) on the Ivory Coast. *Primate Report*, **31**, 45-75.
- HORN, A.D. 1980. Some observations on the ecology of the bonobo chimpanzee (*Pan paniscus*, Schwarz 1929) near Lake Tumba, Zaire. *Folia primatologica*, **34**, 145-69.
- HORNADAY, W.T. 1879. On the species of Bornean orangs, with notes on their habits. *Proceedings of American Assotiation of Advanced Sciences*, **28**, 438-55.
- HORR, D.A. 1972. The Borneo orang-utan. *Borneo Research Bulletin*, **4**, 46-50.
- IHOBE, H. 1992. Observations on the meat-eating behavior of wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaire. *Primates*, **33**, 247-250.
- ISAAC, G. 1978. The food-sharing behavior of protohuman hominids. *Scientific American*, **238**, 90-108.

- ITANI, J. 1979. Distribution and adaptation of chimpanzees in an arid area. In: *The Great Apes*, ed. D.A. Hamburg and E.R. McCown, pp. 54-71. Menlo Park, CA: Benjamin/Cummings.
- JOHNSON, S.C. 1981. Bonobos: Generalized hominid prototypes or specialized insular dwarfs. *Current Anthropology*, **22**, 363-375.
- JONES, C. & SABATER PI, J. 1971. Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. *Bibliotheca Primatologica*, **13**, 1-96.
- JUNGERS, W.L. & SUSMAN, R.L. 1984. Body size and skeletal allometry in African apes. In: *The Pygmy Chimpanzee*. ed. R.L. Susman, pp. 131-177.
- KANO, T. 1979. A pilot study at the ecology of pygmy chimpanzees, *Pan paniscus*. In: *The Great Apes*. ed. D.A. Hamburg and E.R. McCown, pp. 123-135. Menlo Park, CA: Benjamin/Cummings.
- KANO, T. 1980. Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. *Journal of Human Evolution*, **9**, 243-260.
- KANO, T. 1982a. The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. *Primates*, **23**, 171-188.
- KANO, T. 1982b. The use of leafy twigs for rain cover by the pygmy chimpanzees of Wamba. *Primates*, **23**, 453-457.
- KANO, T. 1983. An ecological study of the pygmy chimpanzees (*Pan paniscus*) of Yalosidi, Rep. of Zaire. *International Journal of Primatology*, **4**, 1-31.
- KANO, T. 1992. *The Last Ape*. Stanford, CA: University Press.
- KANO, T. & MULAWWA, M. 1984. Feeding ecology of the pygmy chimpanzee (*Pan paniscus*) of Wamba. In: *The Pygmy Chimpanzee*. ed. R.L. Susman, pp. 233-274. New York & London: Plenum Press.
- KAWAI, M. & MIZUHARA, H. 1959. An ecological study on the wild mountain gorilla (*Gorilla gorilla beringei*). *Primates*, **2**, 1-42.
- KNAPP, R. 1973. *Die Vegetation von Afrika*. Stuttgart: Gustav Fischer Verlag.
- KORTLANDT, A. 1992. On chimpanzee dormitories and early hominid home sites. *Current Anthropology*, **33**, 399-401.
- KUMMER, H. 1968. *Social Organization of the Hamadryas Baboons*. Basel: Karger Verlag.
- KURODA, S. 1979. Grouping of pygmy chimpanzees. *Primates*, **20**, 161-183.
- KURODA, S. 1980. Social behaviour of the pygmy chimpanzees. *Primates*, **21**, 181-197.
- KURODA, S. 1984. Interactions over food among pygmy chimpanzees, *Pan paniscus*. In: *The Pygmy Chimpanzee*. ed. R.L. Susman, pp. 65-87. New York: Plenum Press.
- LEQUIME, M. 1959. Sur la piste du gorille. *La vie des Bêtes*, **14**, 7-8.
- LETHMATE, J. 1977. Nestbauverhalten eines isoliert aufgezogenen, jungen Orang-Utans. *Primates*, **18**, 545-554.

- LETOUZEY, R. 1982. *Manuel de Botanique Forestière. Afrique Tropicale*. Nogent s/Seine: Centre Technique Forestier Tropicale.
- MACKINNON, J. 1974. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour*, **22**, 3-74.
- MALENKY, R.K. 1990. Ecological factors affecting food choice and social organisation in *Pan paniscus*. Ph.D. thesis: State University of New York, Stony Brook.
- MALENKY, R.K. & STILES, E.W. 1991. Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako Forest, Zaire. *American Journal of Primatology*, **23**, 153-169.
- MALENKY, R.K. & WRANGHAM, R.W. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako forest, Zaire, and *Pan troglodytes* in the Kibale forest, Uganda. *American Journal of Primatology*, **32**, 1-12.
- MANSON, J.H. & WRANGHAM, R.W. 1991. Intergroup Aggression in Chimpanzees and Humans. *Current Anthropology*, **32**, 369-390.
- MARCHESE, P., MARCHESE, N., FRUTH, B. & BOESCH, C. *in press*. Census and distribution of chimpanzees in Côte d'Ivoire. *Primates*.
- MARTIN, R.D. 1973. A review of the behaviour and ecology of the lesser mouse lemur (*Microcebus murinus* J.F. Miller 1777). In: *Comparative Ecology and Behaviour of Primates*. ed. R.P. Michael and J.H. Crook, pp. 1-68. London & New York: Academic Press.
- MARTIN, R.D. 1975. The bearing of reproductive behavior and ontogeny on strepsirrhine phylogeny; In: *Phylogeny of the Primates*. ed. Lockett & Szalay. pp. New York: Plenum Press.
- MATSUZAWA, T. *in press*. Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use. In: *Great Ape Societies*. ed. W.C. McGrew, L.F. Marchant and T. Nishida. New York: Cambridge University Press
- Matthews, J. 1788. A voyage to the river Sierra Leone, on the coast of Africa ... pp. 41-42. London (cited in Yerkes & Yerkes 1929).
- MCGREW, W.C. 1979. Evolutionary implications of sex-differences in chimpanzee predation and tool-use. In: *The Great Apes*. ed. D.A. Hamburg and E.R. McCown. pp.440-463. Menlo Park: Benjamin/Cummings.
- MCGREW, W.C. 1991. Chimpanzee material culture: what are its limits and why? In: *The Origin of Human Behaviour*. ed. R.A. Foley, pp. 13-24. London: Unwin Hyman.
- MCGREW, W.C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. New York: Cambridge University Press.

- MITANI, J. 1992. Preliminary results of the studies on western lowland gorillas and other sympatric diurnal primates in the Ndoki Forest, northern Congo. In: *Topics in Primatology Vol. 2: Behavior, Ecology and Conservation*. ed. N. Itoigawa, Y. Sugiyama, G.P. Sackett, and R.K.R. Thompson. pp. 215-224. Tokyo: University of Tokyo Press.
- MORBECK, M.E. & ZIHLMAN, A.L. 1989. Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. *Primates*, **30**, 369-382.
- MWANZA, N., YAMAGIWA, J., YUMOTO, T. & MARUHASHI, T. 1992. Distribution and range utilization of eastern lowland gorillas. In: *Topics in Primatology Vol. 2, Behavior, Ecology and Conservation*, ed. N. Itoigawa, Y. Sugiyama, G.P. Sackett and R.K.R. Thompson, pp. 283-300. Tokyo: University of Tokyo Press.
- NISHIDA, T. 1972. Preliminary information of the pygmy chimpanzees (*Pan paniscus*) of the Congo Basin. *Primates*, **13**, 415-425.
- NISHIDA, T. 1979. The social structure of chimpanzees of the Mahale Mountains. In: *The Great Apes*. ed. D.A. Hamburg and E.R. McCown. pp. 73-121. Menlo Park: Benjamin Cummings.
- NISHIDA, T. (ed.). 1990. *The Chimpanzees of the Mahale Mountains*. Tokyo: University of Tokyo Press.
- NISHIDA, T. 1994. The politicking chimpanzees. Paper held in at Symposium 118 by Wenner-Gren Foundation at Cabo San Lucas 12.-19. Nov 1994.
- NISHIDA, T. & HIRAIWA-HASEGAWA, M. 1985. Responses to a stranger mother-son pair in the wild chimpanzee: A case report. *Primates*, **26**, 1-13.
- NISHIDA, T. & KAWANAKA, K. 1985. Within-group cannibalism by adult male chimpanzees. *Primates*, **26**, 274-284.
- NISHIDA, T. & HIRAIWA-HASEGAWA, M. 1987. Chimpanzees and Bonobos: Cooperative Relationships among males. In: *Primate Societies*. ed. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham and T.T. Struhsaker, pp. 165-177. Chicago: University of Chicago Press.
- NISHIDA, T., TAKASAKI, H. & TAKAHATA, Y. 1990. Demography and Reproductive Profiles. In: *The Chimpanzees of the Mahale Mountains. Sexual and Life History Strategies*, ed. T. Nishida, pp. 63-97. Tokyo: University of Tokyo Press.
- NISSEN, H.W. 1931. A field study of the chimpanzee. Observations of chimpanzee behavior and environment in Western French Guinea. *Comparative Psychology Monographs*, **8**, 1-122.
- OSBORN, R.M. 1957. Observations on the mountain gorilla. Mt. Muhavura, S.W. Uganda. unpublished manuscript. cited in Schaller 1963.
- PARISH, A.R. 1995. Sex and food control in the "uncommon chimpanzee": How bonobo females overcome a phylogenetic legacy of male dominance. *Ethology & Sociobiology*, **15**, 157-179.

- PARISH, A.R. *in press*. Sexual dimorphism, maturation, and female dominance in bonobos, (*Pan paniscus*). *American Journal of Physical Anthropology*.
- REMIS, M.J. 1993. Nesting behavior of lowland gorillas in the Dzanga-Sangha Reserve, Central African Republic: implications for population estimates and understandings of group dynamics. *Tropics*, **2**, 245-55.
- REYNOLDS, V. & REYNOLDS, F. 1965. Chimpanzees of the Budongo forest. In: *Primate Behavior*. ed. I. De Vore, pp. 368-424. New York: Holt, Rinehart and Winston
- RIJKSEN, H.D. 1978. *Sumatran Orang Utans (Pongo pygmaeus abelii Lesson 1827) Ecology, Behaviour and Conservation*. Wageningen: H.Veenman & Zonen B.V.
- RISS, D. & GOODALL, J. 1976. Sleeping behavior and associations in a group of captive chimpanzees. *Folia primatologica*, **25**, 1-11.
- RODMAN, P.S. 1979. Individual activity pattern and the solitary nature of orangutans. In: *The Great Apes*, ed. D.A. Hamburg and E.R. McCown, pp. 234-55. Menlo Park, CA: Benjamin/Cummings.
- ROHLF, F.J. & SOKAL, R.R. 1981. *Statistical Tables*, 2nd Ed. San Francisco: W.A. Freeman.
- SABATER PI, J. & VEA, J.J. 1990. Estudio Eto-Etológico del Chimpancé Bonobo (*Pan paniscus*) de la Región de Lokofe-Lilungu-Ikomaloki (Dist. de Ikela) Zaire. Informe Preliminar. Universidad de Barcelona.
- SABATER PI, J., BERMEJO, M., ILLERA, G. & VEA, J.J. 1993. Behavior of bonobos (*Pan paniscus*) following their capture of monkeys in Zaire. *International Journal of Primatology*, **14**, 797-804.
- SAVAGE, T.S. & WYMAN, J. 1843. Observations on the external characters and habits of the Troglodytes niger, Geoff. and on its organization. *Boston Journal of Natural History*, **4**, 362-86.
- VAN SCHAIK, C.P. 1983. Why are diurnal primates living in groups? *Behaviour*, **87**, 120-144.
- VAN SCHAIK, C.P. & VAN HOOFF, J.A.R.A.M. *in press*. Toward an understanding of the orangutan's social system. In: *Great Ape Societies*. ed. W.C. McGrew, L.F. Marchant and T. Nishida. New York: Cambridge University Press.
- SCHALLER, G.B. 1961. The orang-utan in Sarawak. *Zoologica*, **46**, 73-82.
- SCHALLER, G.B. 1963. *The Mountain Gorilla*. Chicago: University of Chicago Press.
- SCHWARZ, E. 1929. Das Vorkommen des Schimpansen auf dem linken Kongo-Ufer. *Revue de Zoologie et de Botanique Africaine*, **16**, 425-426.
- SMUTS, B. 1985. *Sex and Friendship in Baboons*. Hawthorne, N.Y: Aldine.
- SEPT, J.M. 1992. Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. *Current Anthropology*, **33**, 187-207.

- SOKAL, R.R. & ROHLF, F.J. 1981. *Biometry*. 2nd Ed. San Francisco: W.A. Freeman.
- SUGARDJITO, J. 1983. Selecting nest sites of Sumatran orang-utans, *Pongo pygmaeus abelii* in the Gunung Leuser national park, Indonesia. *Primates*, **24**, 467-74.
- SUGIYAMA, Y. 1989. Population dynamics of chimpanzees at Bossou, Guinea. In: *Understanding Chimpanzees*. ed. P. Heltne and L. Marquardt, pp. 134-145. Cambridge, MA: Harvard University Press.
- SUSMAN, R.L. 1984. *The Pygmy Chimpanzee*. New York and London: Plenum Press.
- SUZUKI, A. 1969. An ecological study of chimpanzees in a savanna woodland habitat. *Primates*, **10**, 103-148.
- THOMPSON-HANDLER, N. 1990. The Pygmy Chimpanzee: Sociosexual Behavior, Reproductive Biology and Life History Patterns. Ph.D. thesis: New Haven, Connecticut: Yale University.
- THOMPSON-HANDLER, N., MALENKY, R.K. & BADRIAN, N. 1984. Sexual behavior of *Pan paniscus* under natural conditions in the Lomako forest, Equateur, Zaire. In: *The Pygmy Chimpanzee*. ed. R.L. Susman, pp. 347-368. New York: Plenum Press
- THOMPSON-HANDLER, N., MALENKY, R.K. & REINARTZ, G.E. (ed.). 1995. *Action Plan for Pan paniscus: Report on free-ranging populations and proposals for their preservation*. Milwaukee, WC: Zoological Society of Milwaukee County.
- TRIVERS, R. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35-57.
- TUTIN, C.E.G. & FERNANDEZ, M. 1983. Recensement des Gorilles et des Chimpanzés du Gabon. Franceville/Gabon: CIRMF.
- TUTIN, C.E.G. & FERNANDEZ, M. 1984. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *American Journal of Primatology*, **6**, 313-336.
- TUTIN, C.E.G., MCGREW W.C. & BALDWIN, B.J. 1983. Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates*, **24**, 154-173.
- TUTIN, C.E.G., R.J. PARNELL, L.J.T. WHITE & FERNANDEZ, M. 1995. Nest building by lowland gorillas in the Lopé reserve, Gabon: environmental influences and implications for censusing. *International Journal of Primatology*, **16**, 53-76.
- VINCENT, F. 1968. La sociabilité du Galago de Demidoff. *La Terre et la Vie*, **22**, 51-56.
- VIVIEN, J. & FAURE, J.J. 1985. *Arbres des Forêts Denses d'Afrique Centrale*. Paris: Agence de Coopération Culturelle et Technique.

- DE WAAL, F. 1987. Tension regulation and nonreproductive functions of sex in captive bonobos (*Pan paniscus*). *Natural Geographic Research*, **3**, 318-335.
- DE WAAL, F. 1988. The communicative repertoire of captive bonobos (*Pan paniscus*), compared to that of chimpanzees. *Behaviour*, **106**, 183-251.
- DE WAAL, F. 1989. *Peacemaking among Primates*. Cambridge, MA: Harvard University Press.
- WARD, P. & ZAHAVI, A. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis*, **115**, 517-534.
- WHITE, F.J. 1986. Behavioral ecology of the pygmy chimpanzee. Ph.D. thesis. State University of New York at Stony Brook.
- WHITE, F.J. 1988. Party composition and dynamics in *Pan paniscus*. *International Journal of Primatology*, **9**, 179-193.
- WHITE, F.J. 1992a. Pygmy chimpanzee social organization: variation with party size and between study sites. *American Journal of Primatology*, **26**, 203-214.
- WHITE, F.J. 1992b. Activity budgets, feeding behavior and habitat use of pygmy chimpanzees at Lomako, Zaire. *American Journal of Primatology*, **26**, 215-223.
- WHITE, F.J. *in press*. Comparative socioecology of *Pan paniscus*. In: *Great Ape Societies*. ed. W.C. McGrew, L.F. Marchant, and T. Nishida. New York: Cambridge University Press.
- WHITE, F.J. & BURGMAN, M.A. 1990. Social organisation of the pygmy chimpanzee (*Pan paniscus*): multivariate analysis of intracommunity associations. *American Journal of Physical Anthropology*, **83**, 193-201.
- WHITE, F.J. & WRANGHAM, R.W. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour*, **105**, 148-163.
- WILLIAMSON, E.A. 1988. Behavioural Ecology of Western Lowland Gorillas in Gabon. Ph.D. thesis: University of Stirling.
- WIESE, B. 1980. *Zaire: Landesnatur, Bevölkerung, Wirtschaft*. Darmstadt: Wissenschaftliche Buchgesellschaft.
- WINA, E. 1989. Observations on the nesting of eastern lowland gorillas (*Gorilla gorilla graueri*) at the Kahuzi Biega National Park, Zaire. In: *Interspecific Relationships of Primates in the Tropical and Montane Forests* **1**, pp. 97-104. ed. Japan Zaire cooperative studies of Primates: Grant-in-Aid For Overseas Scientific Research Report.
- WRANGHAM, R.W. 1975. The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. thesis: University of Cambridge.
- WRANGHAM, R.W. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: *Primate Ecology*. ed. T.H. Clutton-Brock. pp. 504-538. London: Academic Press.

- WRANGHAM, R.W. 1979. Sex differences in chimpanzee dispersion. In: *The Great Apes*. ed. D.A. Hamburg and E.R. McCown. pp. 481-489. Menlo Park, CA: Benjamin/Cummings.
- WRANGHAM, R.W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262-300.
- WROGEMANN, D. 1992. Wild Chimpanzees in Lopé, Gabon: Census Method and Habitat Use. PhD thesis: University of Bremen.
- YAMAGIWA, J. 1983. Diachronic changes in two eastern lowland gorilla groups (*Gorilla gorilla graueri*) in the Mt. Kahuzi region, Zaire. *Primates*, **24**, 174-183.
- YERKES, R.M. & YERKES, A.W. 1929. *The Great Apes*. New Haven: Yale University Press.
- YOSHIBA, K. 1964. Report of the preliminary survey on the orang-utan in North-Borneo. *Primates*, **5**, 11-26.
- ZIETEMANN, V. 1995. Experimentelle Untersuchungen zur Nestort und Materialwahl an Bonobos (*Pan paniscus*) in Gefangenschaft (Zoo Planckendael, Belgien). Diplom: Ludwig-Maximilians-Universität München.
- ZÖFEL, P. 1988. *Statistik in der Praxis*. Stuttgart: Gustav Fischer Verlag.

Local Name	Scientific Name	Used for Nest Construction
Bentende	?	-
Boala	Pentaclethra macrophylla	+
Boembe	Lasiodiscus mannii	-
Bofafunga	?	-
Bofale	Parinari glabra	+
Bofili	Scorodophloeus zenkeri	+
Bofonge	Bosqueia angolensis	-
Bofumbo	Grewia luisii	+
Bofunga	?	-
Bokaka	Ouratea annoldiana	-
Boke	?	-
Bokolofe	Staudtia stipitalis	-
Bokotombolo	?	-
Bolafa	Gilbertiodendron dewevrei	+
Bolelembo	?	-
Bolemba(o)	Desplatsia dewvrei	-
Bolinda	Polyalthia suaveolans	+
Bolongo	Bolonge? Gambeya africana	-
Bomoto	Anthonotha macrophylla	-
Bompoma	Garcinia cola	+
Bompombo	Berlinia giorgii	-
Bondola	Trichoscyoha ferruginea	-
Bonenge	Anonidium mannii	+
Bonga	?	-
Bongolu	Beilschmiedia corbisicri	-
Boovo	?	-
Bosaake	Caloncoba welwitschii	-
Bosaw	Dacryodes edulis (Bosau?)	-
Bosefe	Garcinia punctata	+
Bosenga	Pycnanthus angolensis	-
Bosijo	?	-
Bosiyo	?	-
Botaka	Strombosiopsis tetrandra	-
Botakoko	?	-
Boteko	Panda oleosa	-
Botende	Pancovia laurentii	+
Booko	?	+
Boonga	Uapaca guinensis	-
Booso	Blighia welwitschii	+
Botondo	?	-
Botuna	?	-
Djofa	?	-
Djouwe	Strombosia glaucescens	+

Efombo	<i>Diogoia zenkeri</i>	+
Eele	<i>Napoleana imperialis</i>	-
Elelembo	?	-
Elimilimi	?	+
Engondo	<i>Fagara sp.</i>	-
Esenge	<i>Crudia harmsiana</i>	+
Eteko	?	+
Ilo gr. feuille	<i>Diospyros sp.</i>	+
Ilo pt. feuille	<i>Diospyros sp.</i>	+
Kutende	?	-
Lifake	<i>Entandrophragma sp.</i>	+
Liluku	?	-
Lintsilutsi	?	-
Lintsintsi	?	-
Lisaba	?	-
Lisala	?	+
Liteku	<i>Guarea laurentii</i>	-
Loambo	?	+
Lokumo	?	-
Lomba	?	-
Lonenja	?	-
Lonjama	<i>Cola griseiflora</i>	+
Loolo	?	-
Mbeko-moindo	?	-
Mpembe	?	-
Nsumbo-langi	<i>Thomandersia Laurifolia</i>	-
Oki	?	-
Samba	?	-
Waka	<i>Copaifera mildbraedii</i>	-
Weo	<i>Massularia aluminata</i>	-
Wanga	<i>Tridesmostemon omphalocarpoides</i>	-
Wendjeleke	<i>Monopetalunthus microphyllus</i>	-
Wenge	<i>Macaranga sp.</i>	-
Wengete	<i>Maesobotrya staudtii</i>	-
Windzindzi	?	+
Wingo	<i>Mondora angolensis</i>	+
Yese-yombola	?	-

CURRICULUM VITAE

Barbara Ingrid Fruth

Date of Birth: 28. November 1964

Place of Birth: Munich/ Germany

Father: Dr. Irmin Otto Fruth; Dipl. Geologist

Mother: Ingrid Lena Fruth, née Pühn; Chemical Technician

EDUCATION

1970-1974 Primary School in Planegg and Gauting.

1974-1983 High School: Otto-von-Taube Gymnasium Gauting; Abitur (June 1983).

1983-1986 University: Ludwig-Maximilians-Universität München: Basic studies in biology; Vordiplom.

1986-1990 Ludwig-Maximilians Universität München: Main studies, focussing on ecology, ethology and systematics; final examinations in zoology (ethology), systematical botanic and palaeontology; Diploma (M.S.) in Biology (March 1990)

1988-1989: Diploma Research: Field Study at Côte d'Ivoire on the project "Tradition in West African Chimpanzees (*Pan troglodytes*)". Title of the Diploma: "Nests, Nutcracking Sites and Population Density of Chimpanzees: Studies on Regional Differences in the South Western Part of Ivory Coast (Rép. de Côte d'Ivoire).

1990-1994 Ludwig-Maximilians Universität München & Forschungsstelle für Humanethologie in der Max-Planck-Gesellschaft;

1990-1994: Establishment of a long term research project on wild bonobos (*Pan paniscus*) at Lomako/ Zaïre together with Gottfried Hohmann under the auspices of the Forschungsstelle für Humanethologie in der Max-Planck-Gesellschaft. Dissertation Research; Research area: behavioural ecology and ethology of nonhuman primates.

1995 Ludwig-Maximilians Universität München & Max-Planck-Institut für Verhaltensphysiologie Seewiesen; Ph.D. Title: Nests and Nest Groups in Wild Bonobos (*Pan paniscus*): Ecological and Behavioural Correlates.

AWARDS AND FELLOWSHIPS

- 1988 (12 months) Research grant from the German Academic Exchange Service for conducting field work in the at Côte d'Ivoire in purpose of the Diploma
- 1990 (12 months) Research grant from the German Academic Exchange Service for conducting field work at Lomako/ Zaire; withdrawn in July because of the political instability in Zaire.
- 1990 (August - December) Inland fellowship from the Max-Planck-Society
- 1991 (July - November) Honorarium from the Max-Planck-Society for data analyses
- 1992 (12 months) Research fellowship from the Max-Planck-Society for etho-ecological investigations on wild bonobos
- 1993 (12 months) Research fellowship from the Max-Planck-Society for etho-ecological investigations on wild bonobos
- 1994 (January-July) Research fellowship from the Max-Planck-Society for etho-ecological investigations on wild bonobos
- 1994-1995 (12 months) Dissertation fellowship (HSP II) from Munich University.

PUBLICATIONS

- FRUTH, B. & HOHMANN, G. 1993. Ecological and behavioural aspects of nest building in wild bonobos (*Pan paniscus*). *Ethology*, **94**, 113-126.
- HOHMANN, G. & FRUTH, B. 1993. Field observations on meat sharing among bonobos (*Pan paniscus*). *Folia Primatologica*, **60**, 225-229.
- BOESCH, C., MARCHESI P., MARCHESI N., FRUTH B. & JOULIAN, F. 1994. Is nut cracking in wild chimpanzees a cultural behaviour? *Journal of Human Evolution*, **26**, 325-338.
- FRUTH, B. & HOHMANN, G. 1994a. Nests: living artefacts of recent apes?. *Current Anthropology*, **35**, 310-311.
- FRUTH, B. & HOHMANN, G. 1994b. Comparative analyses of nest building behavior in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). in: *Chimpanzee Cultures*. ed. R.W. Wrangham, W.C. McGrew, F.B.M. de Waal and P.G.Heltne, pp. 109-128. Harvard University Press, Cambridge, MA.
- HOHMANN, G. & FRUTH, B. 1994. Structure and use of distance calls in wild bonobos (*Pan paniscus*). *International Journal of Primatology*, **15**, 767-782.

- BERLE, A., FRUTH, B. & VAN ELSACKER, L. 1995. Nestbuilding behavior in captive bonobos (*Pan paniscus*). *Primate Report*, **42**, 43-45.
- FRUTH, B. & HOHMANN, G. *in press*. Nest Building in the Great Apes: The Great Leap Forward? in: *Great Ape Societies*. ed. W.C. McGrew, L. Marchant and T. Nishida. Cambridge University Press, NY.
- GERLOFF, U., SCHLÖTTERER, C., RASSMANN, K., RAMBOLD, I. HOHMANN, G. FRUTH, B. & TAUTZ, D. *in press*. Microsatellite amplification from excremental DNA of bonobos (*Pan paniscus*). *Molecular Ecology*.
- HOHMANN, G. & FRUTH, B. *in press*. Food sharing and status in unprovisioned bonobos (*Pan paniscus*): preliminary results. in: *Food and The Status Quest*. ed. P. Wiessner and W. Schiefenhövel. Harvard: Marion Berghahn Press.
- HOHMANN, G. & FRUTH, B. *in press*. Loud calls in great apes: sex-differences and social correlates. In: *Current Topics In Primate Vocal Communication*. ed. Zimmermann E., Newman J. & U. Jürgen. Plenum Press. London.
- MARCHESI, P., MARCHESI, N., FRUTH, B. & BOESCH, C. *in press*. Census and distribution of chimpanzees in Côte d'Ivoire. *Primates*.