

## FROM APE'S NEST TO HUMAN FIX-POINT

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Nests of gorillas, chimpanzees and orang utans show similarities in basic construction, but also characteristic differences in use of material, site and location preference, and so on, the behaviour of the different ape species in and around nests also differs from species to species. The campsites of human nomads, and by extension the fix-points of humans in general, have the same basic plan as those of apes, and the social organisation that lies at the base of the 'nest' and campsite organisation is derivable from the common denominator of the apes' societies. The peculiarly human aspects of 'nesting' are no less remarkable for being essentially elaborations on the generalised ape pattern.

### *Introduction*

Anyone however slightly familiar with Great Apes in their natural environment will have been struck by their elaborate nests: their ubiquity, the regularity of their construction, the skill required to make them, and in many cases their apparent incongruity. This is especially the case for the gorilla, the only ape to construct its nest usually on the ground. One of us (J.S.P.) has collected a mass of data on gorilla nests in Equatorial Guinea, and has made comparative observations on nests of the same species in Rwanda, in quite a different habitat; observations on gorilla nests in Rwanda have also been made by C.P.G. A large number of chimpanzee nests were observed by J.S.P., but more cursorily mainly for conservation reasons (Jones & Sabater Pi 1971; Baldwin *et al.* 1982). We feel that the full data on these nests should be published, with a survey of published data on nesting patterns across the Hominoidea, taking advantage at the same time of recent theoretical advances (Hediger 1977; Isaac 1978; P. C. Reynolds 1981) to draw conclusions as to the functional and pattern regularities across species.

The Great Apes—*Pongo*, *Pan*, *Gorilla*—are the only 'higher' non-human primates (Anthropoidea = Simiiformes) which construct nests. At first sight such behaviour links them to certain Strepsirhini (specifically, members of the genera *Galago*, *Microcebus*, *Cherogaleus*, *Hapalennus*, *Varecia*, *Lepilemur* and *Daventonina*). As Hediger has pointed out, however, the nests of the two groups are quite different functionally. The strepsirhine nest would be a 'fix-point' in a territory: it is a place of maximum security, a sleeping place, and a place for rearing young (more especially the last), although, in the light of the finding of

Bearder and Martin (1980) of multiple nest sites per home range in *Galago senegalensis*, the designation 'fix-point' seems not always strictly appropriate. The hominoid nest, however, is made afresh each evening and abandoned the next morning, there being no fix-point; it is a sleeping-place only. In Hediger's terminology, the strepsirhine nest is a Home; that of the apes is not—indeed is it a true Nest, but something new and unprecedented in mammalian evolution.

The human home-base would seem at first sight to have aspects of the strepsirhine Home. Or does it? We shall examine this proposition below.

### *Nests of apes*

Briefly, we may make the following generalisations about nest-making in each of the three Great Apes: a nest is built each evening by each animal above about three years of age. Nests are not shared, except by females and their infants, except as an anomaly; but co-bedding would seem to be much less anomalous in *Pan paniscus* than in other apes, involving a male and an oestrous female, or two females (Kuroda 1980). The nest is made of vegetation which is pulled towards the maker, held down with some twisting into place, pieces being also broken off and inserted. A cup and a rim can commonly be differentiated. Nest-building takes one to five minutes. The nest is slept in for one night only; the following day it is abandoned and left to disintegrate, and a new one is constructed the following night, even if the maker has not travelled very far that day.

Nests are not uncommonly left unused, by both gorillas and chimpanzees, but under what circumstances is not known. On rare occasions nests may be re-used; such a case is recorded by Sabater Pi and de Lassaletta (1958), and Fang assistants assured one of us (J.S.P.) that re-use occurs. Dyce Sharp (1927) records a case where (in the Cross River District of Cameroon) a troop were bottled up in a small area by floods yet went to some pains to build new nests each night only a few yards from the previous night's, or in the same tree.

Bernstein (1967) found that wild-born chimpanzees will make nests from an early age in captivity if given suitable material, whereas captive-born adults will not, even if caged with wild-born chimpanzees who are able to make them. Even chimpanzees caught at about one year of age will make some kind of nest. Later (1969) the same author found that all three species of Great Ape will make nests if given the opportunity, when still immature; the quality of the nest improves with age, up to maturity—to some extent, at least, independent of practice. He found differences between the three species: chimpanzees would make the 'standard' ape nest, and sleep entirely within it; gorillas were less elaborate, and often slept partly draped over the rim; orangs made the best nests, and not only slept within them but even (in most cases) covered themselves up inside it. All three species would transport material to the nest-building site if none was available in the vicinity; they would use synthetic material, such as hosepipe and sacking, as well as vegetation; they would sometimes sit alert, or eat food, in the nest, as well as sleeping in it.

From the wild it is clear that chimpanzees, at least, learn not only how to make

sturdier nests, but even where to make them for best results (Goodall 1968). There is both maturation and learning involved, as one of us (J.S.P.) has observed additionally in the Barcelona Zoological Gardens.

#### Nests of gorillas and chimpanzees

(1) *Size and shape.* In the Equatorial Guinea sample, the nests of gorillas were nearly always oval, but sometimes round. The greatest diameter of nests made by silverback males was 1.3 to 1.35 m; by adult females and blackback males, 1.1 to 1.2 m; by juveniles, 0.7 to 0.8 m. These figures agree well with those published by Casimir (1979) and Schaller (1963) for mountainous areas (table 1); Dyce Sharp (1927) is alone in giving figures as much as 9 ft by 6 ft (2.75 × 1.8 m) for the male's nest, though this could be an estimate rather than a measurement.

Chimpanzee nests are also oval, in Equatorial Guinea and in Senegal (data courtesy P. J. Baldwin; see Baldwin *et al.* 1981) the mean sizes are somewhat less than those of juvenile gorillas, while in the Kasakati basin (Izawa & Itani 1966) the mean values are larger (table 1). There are unfortunately no data on the sizes of the 'double beds' reported for *Pan paniscus* (though one was described as 'large' (Kuroda 1980)), nor is it stated whether one or both occupants constructed them—i.e. whether the structure was planned as such, or simply became a bed for two when a second bonobo climbed in.

(2) *Pattern of nest site (a) Size of nesting site.* As the whole troop nests together each night in all known populations of gorillas, the number of nests at a site is the number in the troop minus the number of infants, except that a few infants make tentative nests even in their first year. The site may be long and the nests strung out, but more usually there is an oval plane to the site. The greatest diameter of the site is approximately 10–30 m (Schaller 1963) though both larger and smaller diameters were recorded in Rio Muni; the site area is of the order of 160–170 m<sup>2</sup> (table 1). Elliott (1976) found that a small group nested within 20 m, reducing to about 13 m when the group lost a juvenile, and remaining at 13 m or so even when joined by another female. Casimir (1979) states that the area of the nest site increases according to the size of the group; inspection of his fig. 6 suggests that any such correlation is very weak. It might appear that only when a peripheral male is in temporary association with the troop is the nest site area much expanded (C.P.G., personal observations; and inference from Schaller 1963).

Three nest sites (containing 10, 4 and 11 nests respectively) were surveyed by Burtler (1980) near Mouloundou, S. E. Cameroun. The greatest diameter of the site in both the first two cases was about 10 m (measured from his fig. 4); in the third case, 16 m, one of the nests being well apart from the others, which were together in an oval space some 9 m across. This evidence, too, suggests little correlation between size of group and that of nesting area.

(b) *Spacing of nests.* Within the site, a nest could be from 1.5 to 1.5 m from its nearest neighbour (C. P. G.'s observations). Schaller (1963) finds that most of the troop nest 1.5 m apart from each other, the medium-sized nests being never

TABLE 1. Sizes of nests in African apes.

Locality	Source	n	Mean Diameter of individual nests (m)			Mean Diameter of nest site (m)	
			Adult male	Adult female	Juvenile		
<i>Gorilla</i>							
G.g. gorilla	Rio Muni	J.S.P., this paper	23	1.32	1.15	0.75	16.3 × 11.5
	Cross River	Dyce Sharp (1927)	1	2.75 × 1.80	—	—	—
G.g. graueri	Mt Kahuzi	Casimir (1979)	63	1.25	1.05	0.79	19.4 × 10.1
G.g. beringei	Kabara	Schaller (1963)	?	1.50	—	0.60	20?
		Elliot (1976)					
<i>Chimpanzee</i>							
P.t. verus	Assirik	Baldwin <i>et al.</i> (1981)	157		0.80 × 0.60		—
P.t. troglodytes	Okorobiko	J.S.P., this paper	8		0.80 × 0.62		22.7 × 9.7
P.t. schweinfurthii	Kasakati	Izawa & Itani (1966)	9		1.12 × 0.89		—

more than 6 m apart; but silverbacks nest an average of 4 m from other troop members, and 10 m from each other if there are more than one. Juveniles' nests are some 3.8 m from each other. Jones & Sabater Pi (1971) agree that nearly all nests are less than 10 m from their nearest neighbour. Casimir (1979) gives very much greater mean distances between nests than other authors. The data suggest a regularity of a sort in the pattern of nesting found at any given site; Elliott's data suggest, too, that there might be traditions within a single troop for such patterns, which we agree is very plausible.

Chimpanzees' nests average a minimum of 4 m apart in two regions (Baldwin *et al.*, 1983); clustering seems to vary slightly according to habitat, there being less distance between nests in secondary forest (Rio Muni) and in woodland or grassland (Senegal), but more in gallery forest (Senegal). Fifty per cent. of chimpanzee nests in Rio Muni are 3–4 m apart, but 30 per cent. are over 10 m from their nearest neighbours (Jones & Sabater Pi 1971). The greater dispersal of the nests may simply reflect the nature of the substrate, or may relate to the less cohesive nature of the society. In Rio Muni there is nearly always one nest only per tree, but in Senegal two—but a median of 5 nests per tree in woodland in Senegal. Baldwin *et al.* (1983) note that despite this the similar absolute spacing of nests suggests that there is an optimal distance effect at work.

(c) *Other factors.* It has been suggested from time to time (Blower 1956; Osborn 1957; Sabater Pi 1960) that there is a certain element of organisation in the nest site, relating to the location of the nest of the silverback. Neither Schaller (1963) nor Casimir (1979) are in agreement with this proposition, although the latter does note a tendency for the silverback to bed down at the base of a large tree, where, surprisingly, he makes only the most rudimentary of nests; but such is not the case in Rio Muni.

For the present study, we have accepted that the silverback's nest is in a 'special position' if it is in the most elevated position, or central, or peripheral, or with a clear view of the total group. Out of 40 nest sites the silverback's position is 'special' in 21, not 'special' in 19. However, in the medium-sized groups (5–8 nests) there was such a 'special' position in 13 out of 14 cases; more data would be needed, and perhaps the different kinds of 'special position' should be taken separately. In Butzler's (1980) study, in his two large groups (10 and 11 nests), one of the nests in each case was larger and stood apart from the rest (very markedly so in one case, as noted earlier). Dyce Sharp (1927) notes that in his experience the nests of all other troop members are visible from the male's.

Some nest sites are divided into two or more units by bushes or by *Aframomum* stands. This was recorded for 52 nest sites (26 each for wet and dry seasons); the group was divided in such a way in 15 cases of which 10 were for the rainy season. This initially promising finding, with its small sample size, fails to attain 5% significance.

(3) *Structure and techniques of construction.* The nests are really very simple structures, whose method of construction can be deduced from analysis of their components. Those of chimpanzees are more complex than those of gorillas; Dyce Sharp (1927) seems to be alone in describing gorilla beds as the most

elaborate of the two, this being in the isolated (as far as gorillas are concerned) Cross River region.

The commonest type of bed made by gorillas in Equatorial Guinea is made on flat ground in patches of *Aframomum* sp. The stalks of the plant are bent and arranged around the body, while sitting or standing, to make the rim; the centre is then filled with branches pulled in or broken off from all round. The most leafy plants are used, providing a springy, comfortable platform. The next commonest type of bed is made on steeply sloping ground, again in *Aframomum*. There is here a barrier of stems of the plant, preventing the body from sliding down the slope during the night; the structure is finally levelled all over with more branches and leaves, to give the usual circular shape. Despite these precautions, gorillas do sometimes slide down the slope at night. Casimir (1979) also notes that nests are 'propped up' when made on slopes; he reports that silverbacks nest more often on slopes than do other troop members, juveniles less so. The third type of bed is constructed in bushes (*Haringana* sp., *Vernonia* sp., etc) one to two metres above the ground. The smaller branches are bent, the larger ones forcefully split, to make a solid platform; the centre is then filled in with fine, soft, leafy branches. The resulting bed is very good and springy. A few nests are made in trees, especially *Musanga cecropioides*. In these cases branches are bent over to fill in a platform made by the branching of the major forks to form the canopy. In all cases, there may be some interweaving as well as simple bending into place. The cup-and-rim shape is generally evident. Chimpanzee nests in general resemble those of gorillas that are made in trees, though more elaborate.

In 37 cases the number of leaves was roughly estimated for the first type of gorilla bed (J.S.P.), with the intention of investigating whether there were any differences in insulation between wet and dry season nests. The results seemed promising: of 18 dry season nests, 10 had under 200 leaves, while of 19 rainy season beds only 3 had under 200 leaves, while 12 had over 400 (in one case, over 600). This is significant at  $p < 0.05$ , but should be taken cautiously nonetheless because of the small sample size. It does suggest, then, that the gorilla gives some attention to climatic factors in nest-building; it is of course possible that there are simply more leaves available during the wet season, though we do not think this the probable explanation given the nature of the vegetation in the two seasons.

Day nests, commonly constructed during the inactive hours of the day, are simple structures, sometimes limited to only two or three stems of *Aframomum* (in the case of gorillas), bent and arranged on the ground in the basic plan of the first night-nest type described above.

1.

(4) *Materials used in construction.* Table 2 shows the plants identified in 448 gorilla beds studied by J.S.P. Of the main plants utilised, *Aframomum* (5 species), *Sarcophyllum* and *Cosus* are grasses, *Musanga* and *Haringana* are trees; of the rest there are one shrub, three trees and three lianes, the rest being grasses.

Among the five *Aframomum* species, *A. giganteum* and *A. sanguineum* were by far the most utilised, occurring in 366 beds. They and the two grasses that are never more than all tall species growing at the forest edge and in secondary

TABLE 2. Plants used for construction of gorilla nests in Rio Muni.

Plant	No. of nests	Plant	No. of nests
<i>Aframomum</i>	366	Branches (indet.)	5
<i>Sarcophyllum</i>	66	<i>Hypelodaphys</i>	4
<i>Cosus</i>	26	Leaves (indet.)	4
<i>Mucanga</i>	24	<i>Halopogia</i>	3
<i>Hannangana</i>	22	<i>Oncoctalamus</i>	2
<i>Hannannia</i>	12	<i>Cissus</i>	2
<i>Ptiliosa</i>	12	<i>Cyathia</i>	1
<i>Manihot</i>	11	<i>Anodinium</i>	1
<i>Grewia</i>	10	<i>Scleria</i>	1
<i>Veronia</i>	6	<i>Mussaenda</i>	1
<i>Lophira</i>	5	<i>Macaranga</i>	1

growth, and are eaten by gorillas. 'Two species of *Aframomum*' were the exclusive material utilised in the nests studied by Butzler (1980).

Table 3 shows the percentages of plants among those (305 out of 488) beds in whose construction only a single plant type was used. Here again *Aframomum* predominates, followed by *Sarcophyllum*; but here the order changes, and it appears that some plants (*Cosus*) are never used alone in construction, while others (*Lophira*) are never used in conjunction with any others. Most beds are made with a single species, or only two; only 3.7 per cent. of the total contain as many as 5 or 6 different plant species.

Table 4 gives the distribution of nests in different biotopes. From table 4a can be seen the extraordinary dependence of gorillas on regenerating fallow land, or tertiary forest (in which, of course, *Aframomum* predominates), and the contrasting dependence of chimpanzees on dense forest. Table 4b shows that these dependences are more marked in the dry season ( $p < 0.005$ ). During the rainy season the gorilla is more often in dense forest and in secondary forest, taking advantage of the fruiting abundance, while chimpanzees by contrast nest more in secondary and agrological areas at this time. Of 11 day nests, 5 were in tertiary or regrowth forest, 4 in secondary forest, 2 in dense forest. Twelve examples of nests being used twice were found; but these were *not* on consecutive nights.

Gorillas in Rio Muni are, therefore, rather discriminating in their use of plants to make nests: they appear not simply to nest beside their latest meal, but to choose among the plants growing nearby those which experience has shown to

TABLE 3. Gorilla nests in Rio Muni constructed with only one plant species.

Plant	No. of nests using that plant alone	Plant	No. of nests using that plant alone
<i>Aframomum</i>	243	Green leaves,	
<i>Sarcophyllum</i>	15	sp. indet.	4
<i>Hannangana</i>	15	Dry leaves,	
<i>Lophira</i>	5	sp. indet.	3
<i>Mucanga</i>	5	<i>Veronia</i>	2
Flexible branches,		<i>Oncoctalamus</i>	1
sp. indet.	4	<i>Artocarpium</i>	1
<i>Grewia</i>	4	<i>Ampelocissus</i>	1
<i>Cyathia</i>	1	<i>Scleria</i>	1

TABLE 4. Biotopes of ape nests in Rio Muni.

	Gorilla				Chimpanzee	
	No. of nests	Percent	No. of nests	Percent		
<b>(a) General figures</b>						
Forest regrowth	316	70.53	23	11.79		
Secondary forest	88	19.04	38	19.48		
Dense or primary forest	36	8.03	134	68.71		
Plantations	8	1.78	0	0.00		
	448	99.98	195	99.98		
<b>(b) Relation between biotope and season</b>						
	Forest regrowth	Secondary forest	Dense forest	Plantations	Total	
<b>Gorilla</b>						
Dry season	233	20	3	8	264	
Rainy season	83	68	33	0	184	
	316	88	36	8	448	
						$p < 0.05, d.f. = 3$
<b>Chimpanzee</b>						
Dry season	1	14	70	0	85	
Rainy season	22	24	64	0	110	
	23	38	134	0	195	
						$p < 0.005, d.f. = 2$

make the most satisfactory nests. What they are feeding on towards dusk will of course influence where they nest in so far as it may itself provide suitable bedding, or is growing in an area suitable for nest-making, or is growing in association with other suitable materials. The food itself may be the commonest plant in the given region, or a rare plant but favoured by gorillas, and so on. Thus, the nesting site choice involves the presence of food supply, but does not depend on it.

Casimir (1979) states that in Kahuzi the frequency of use of a plant species for a nest is a pure reflection of its frequency in the biotope; inspection of his table 1 suggests, however, that this is not the whole story: for example, the commonest tree in the area is only half as much utilised in nest building as the next commonest, while food plants are not predominant in nest building at all.

(5) *Siting of nests: (a) Height above ground.* Table 5 (a, b) shows the height above the ground of nests found in Equatorial Guinea. Overwhelmingly, gorillas nest on the ground. Nests that are not on the ground may be on tree stumps or on fallen trees ( $n = 13$ ), over the branches of fallen trees (14), or on rocks (2), as well as in trees or bushes as described above; two were on a very large trunk at the very edge of a river bank—an anomaly considering that gorillas are supposed to be much afraid of water, though in Barcelona and other zoos the gorillas make regular use of a pool in summer, and Fang guides maintained to J. S. P. that they have many times seen gorillas bathing in forest streams.

Casimir (1979) has summarised everything published about the height of gorilla nests. In different areas, 43.5 to 97.1 per cent. of beds are directly on the

TABLE 5a. Height above ground of gorilla nests (n = 448) in Rio Muni.

Approx. height (metres)	Number of nests
<1	349
1	50
2	24
3	5
4	7
5	4
6	1
7	4
8	2
15	2

very important effect from simple ecological factors; but, as Goodall & Groves (1977) have emphasised, there are also behavioural factors with cultural connotations. Gorillas make their beds at nightfall, more or less wherever they happen to be feeding. Stinging of nests, like material utilised, will therefore depend on a variety of factors mainly related to food supply.

In sharp contrast to gorillas, chimpanzees nest high in the trees (table 5b). In Equatorial Guinea (Jones & Sabater PI 1971) they are rarely below 3 metres above the ground, though relatively few were above 11 m, and the mode is 5-6 m; in other localities they tend to be above this level—between 4 and 14 m in Guinea (Bournonville 1967), usually 4 to 24 m with a mode of 9-10 m, in Senegal (Baldwin *et al.* 1981), between 4.5 and 25 m in Gombe (Goodall 1968), and commonly even above 30 m in the Budongo Forest (Reynolds & Reynolds 1965). Mean heights are greater in the wet season than in the dry, in both Rio Muni and Senegal; and in Senegal higher in gallery forest than in woodland (Baldwin *et al.* 1981). There is also the curious finding that in Senegal nests are

TABLE 5b. Height above ground of chimpanzee nests (n = 195) in Rio Muni.

Approx. height (metres)	Number of nests	Approx. height (metres)	Number of nests
0	8	15	21
1	3	16	1
2	3	17	3
3	5	18	6
4	11	19	0
5	18	20	10
6	16	21	2
7	11	22	0
8	17	23	1
9	8	24	1
10	18	25	1
11	2		
12	18	30	1
13	4		
14	5		

built in the crowns of trees, but in Rio Muni generally in the first fork; Baldwin *et al.* (1981) speculate that the abundance of leopards at the Senegal site may influence this. Day nests may however be made on the ground; Goodall (1971) also records that a wounded young female made a ground nest to lie in and dab her wounds with leaves.

The nests may take up to 30 minutes to make but usually only 1 to 5 minutes (Goodall 1962); in Senegal, the mean time is 4 minutes (Baldwin 1979). Like gorillas' tree nests, they are mainly in tree forks (82 per cent.), or sometimes where two horizontal branches cross. Smaller branches are bent over and held in place with the feet, then leafy twigs are pushed in round the rim. A further handful of leafy twigs may be placed under the head or body after the nest has been tried out.

(b) *Use of overhead cover.* In the Equatorial Guinea study, 25 per cent. of gorilla (but 83 per cent. of chimpanzee) nests were made beneath tree foliage which provided the users with a certain amount of protection from the rain and the night dew. The remainder were in the open with no protective cover. Casimir (1979) found that on Mt Kahuzi only 5.5 per cent. of gorilla nests were under cover. The gorilla seems deliberately to seek open areas for nest-building; the chimpanzee closed areas.

When the data are split up by season, however, a different picture emerges (table 6): the gorilla does build under cover rather more in the wet season. Such a finding is in conflict with both Casimir (1979) and Kawai & Mizuhara (1959), both of whom report no correlation. One solution could be the nature of the habitat: the more open nature of the forest as a whole, and the rarity of cultivated land and consequent regrowth, in the eastern areas, and the more closed nature of the forest—the gorilla's prime wet season refuge—in west Africa. As the

TABLE 6. Incidence of cover over ape nests in Rio Muni.

(a) General figures		Gorilla	Chimpanzee
Cover		113	162
Absence of cover		335	33
		448	195

(b) Relationship between cover and season		Gorilla:	Chimpanzee:
		$p < 0.01$ , d.f. = 1	$p < 0.001$ , d.f. = 1
	Cover	Absence of Cover	Total
Gorilla			
Dry season	53	211	264
Rainy season	60	124	184
	113	335	448
Chimpanzee			
Dry season	81	4	85
Rainy season	81	29	110
	162	33	195

$p < 0.05$ , d.f. = 1

$p < 0.005$ , d.f. = 1

gorilla tends actually to remove overhead cover as a by-product of the bed-making activity (Jones & Sabater Pi 1971), there is a possibility that a choice to leave some intact under certain circumstances could be involved.

In nests observed by C. P. G. in the open-canopy *Hagenia* woodlands of the Virunga Volcanoes, Rwanda, there appeared to have been attempts in a few cases to construct the nests under banks or tree-root formations, but most remarkable was the case of a juvenile female of Group 5 who on at least four occasions (over a 2-week period) had obviously pulled down overhead vegetation to form a kind of roof. This, as far as we know, remains the only record of a covered nest in the gorillas.

Unlike gorillas, chimpanzees do not remove overhead plant cover when nest-building, so they are generally protected to some extent from the weather. There was much less overhead cover to nests in Senegal than in Rio Muni, perhaps simply because of the nature of the vegetation; and they are built less undercover in the rainy season (see discussion in Baldwin *et al.* 1981). Day nests are most usually made in response to rain (Goodall 1971). Like gorillas, chimpanzees almost never re-use old nests, but construct a new one each night. Goodall (1968) reports the case of one juvenile female chimpanzee who appeared deliberately to construct a 'roof' over her nest during the rains. Partial body covering appears to be common in at least some groups of Bonobos (Kano 1982): a specialised use of leafy twigs, generally in day nests, in contact with the body (a raincoat more than a roof) and, in Kano's opinion, not in fact very effective in keeping the rain off!

(c) *Orientation of nest site.* Jones & Sabater Pi (1971) claimed in an early study that there was a significant tendency for gorilla and chimpanzee nests in Equatorial Guinea, if constructed on slopes, to be on east and south facing slopes (gorilla 46

TABLE 7. Orientation of ape nests in Rio Muni.

(a) General figures		Flat ground	Sloping ground	Total
Gorilla		222	226	448
Chimpanzee		68	127	195
	Gorilla: $p < 0.05$ , d.f. = 1			
	Chimpanzee: $p < 0.05$ , d.f. = 1			
(b) Relationship between orientation and season				
Gorilla	Flat	Facing		Total
		SE, SW, S, W	NE, N, E	
Dry season	143	66	55	264
Rainy season	79	53	52	184
	222	119	107	448
	$p < 0.05$ , d.f. = 2			
Chimpanzee				
Dry season	Flat	Facing		Total
		SE, SW, S, W	NE, N, E	
	27	33	25	85
Rainy season	41	42	27	110
	68	75	52	195
	$p > 0.05$ , d.f. = 2			

per cent., chimpanzee 62 per cent.) rather than north and west facing (21 per cent., 15 per cent.), the remainder being on flat ground. In view of the failure of other authors to find such a tendency (see, for example, Goodall & Groves 1977), we feel that it is time to examine the question again, using more extensive data and a  $X^2$  test (table 7). It appears that the correlation does not survive this new test; separating the data by season, the probability is above 5 per cent. of the null hypothesis for gorillas (but only just), but below this level for chimpanzees. There may still, therefore, be some element of foreknowledge of possible thermal benefit in orientation. Casimir (1979) found a similarly equivocal result. Jones & Sabater Pi (1971) reported that 22 per cent. of chimpanzee nests are constructed where the terrain is flat, 63 per cent. where the slope faces east or south, and only 15 per cent. facing west and north. In view of the modifications which become necessary to similar conclusions for gorillas (see above), this proposition needs to be re-tested for chimpanzees also. In chimpanzees, of course, the overhead cover will diminish any thermal benefit of orientation.

(6) *Faeces in nest.* The presence of faeces in the gorilla's nest at night has been much discussed. Schaller (1963) found that 73 per cent. of nests in the Virunga Volcanoes contained faeces, contrasting somewhat with the findings of A. Goodall (1974), who found only 14.2 per cent. and 2.4 per cent. in two regions of Mt Kahuzi. Goodall suggests that gorillas in colder climates deliberately defaecate in their nests to insulate the beds against freezing or near-freezing night temperatures. In Equatorial Guinea, 316 out of 395 nests contained faeces (80 per cent.). There is no correlation with season, although in Goodall's hypothesis one might expect some. It was not always clear, however, whether the faeces had been in the nests most of the night, or were emitted at dawn; in the latter case they would, of course, afford no thermal advantage.

The explanation we now think most probable would be the following: the gorilla is a large mammal whose whole lifestyle is characterised by an economy of energy expenditure. Its largely herbivorous diet is at once low in nutrient content and heavily fibrous; defaecation takes place about five times per 24 hours (Schaller 1963). Faeces are not messy and adherent like those of most other primates, but of the consistency of horse dung. Gorillas defaecate frequently; considering that they are likely to do so at least once during the night, the energetic cost of waking up and unrolling (with loss of heat) in order to defaecate might well exceed the disadvantages of lying on the faeces, which would not be great given the nature of the gorilla's dung balls. In simple terms, it is just not worth the gorilla doing it! As for chimpanzees, the position of their nests, high in the trees, and perhaps the smaller size of the nest, makes it much easier to eliminate over the side with just a slight movement. One of us (J.S.P.) has, however, a few records of faeces within the chimpanzee nest.

(7) *Size of nest groups.* As noted above, the size of the nest group in gorillas is the same as the size of the troop, except that infants below about 3 years of age share their mothers' beds, and solitary males may nest on the periphery of the troop. For Equatorial Guinea the size of gorilla groups varies between 2 and 16

that a nest group larger than 7 beds corresponds to two or more groups nesting conjointly where their home ranges coincide; an aspect of gorilla life noted also by Schaller, and made the subject of speculations as to the nature of the social group by Goodall & Groves (1977).

In chimpanzees, the size of the nest group is not that of the 'troop', which only rarely comes together. From 1 to 12 chimpanzees may nest together. In Rio Muni there is no seasonal difference (mean of rainy season 2.8, of dry 3.1), but in Senegal, where the seasons are more marked, the respective means are 2 and 7—that is, foraging groups, hence nesting groups, are considerably larger in the dry season corresponding, presumably, to either a coarser-grained environment or reduced predation or both.

(8) *Relation to human settlements.* Returning to the positioning of the nest groups, the distance from the nearest human habitation was examined, with relation to the size of the group (table 8a). It appears that among gorillas the smaller nest

TABLE 8. Distance of gorilla nest sites from human habitation.

Gorilla Size of groups	Distance to settlement (m)					Total
	0-2000	2000-4000	4000-6000	6000-8000		
1-4	2	7	5	7	7	21
5-8	1	6	3	3	3	13
9-12	2	8	1	1	1	12
13-16	0	3	0	0	0	3
	5	24	9	11	11	49

$p < 0.05$

Chimpanzee Size of groups	Distance to settlement (m)					Total
	0-2000	2000-4000	4000-6000	6000-8000		
1-2	15	2	10	1	1	28
3-4	4	5	1	1	0	10
5-6	5	0	2	0	0	7
7-8	0	1	1	0	0	2
9-10	1	0	0	0	0	1
11-12	1	0	1	1	0	2
	26	8	15	1	1	50

$p = 0.01$

(b) *According to season*

Distance to Settlement (m)	Total			
	0-100	101-1000	1001-4000	4001-8000

Gorilla Dry Season Wet Season	Distance to Settlement (m)				Total
	0-100	101-1000	1001-4000	4001-8000	
Dry Season	15	96	29	16	156
Wet Season	19	71	11	38	139
	34	167	40	54	295

$p < 0.05$ , d.f. = 3

Chimpanzee Dry Season Wet Season	Distance to Settlement (m)				Total
	0-100	101-1000	1001-4000	4001-8000	
Dry Season	0	28	34	18	80
Wet Season	0	38	11	33	82
	0	66	45	51	162

$p < 0.05$ , d.f. = 2

groups are located further from human settlements. Perhaps the larger groups are less frightened to sleep in proximity to human habitation. For chimpanzees, there is no correlation between size of nesting group and distance from human habitation. The distance from settlements for both species is greater in the wet season (table 8b).

(9) *Timing of nest construction and abandonment.* Nests are made at nightfall. They are often constructed in great haste because of falling light, and nests are made earlier when the sky is darkened with cloud. The activity begins some time between 1726 and 1834 hrs (mean 1800 hrs), but is normally complete by 1835 (fig. 1). It takes longer in groups that are larger: up to 14 minutes, while in smaller groups it can be as little as 4 minutes. The silverback is usually the first to begin nesting. Individual nests take from under a minute to 5 minutes to make.

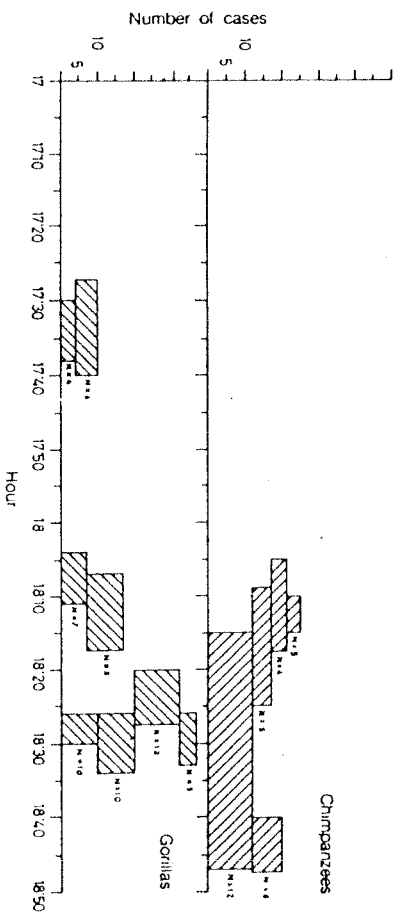


FIGURE 1. Timing of nest construction in chimpanzees and gorillas in Rio Muni.

Gorillas rise from their beds when there is light enough to permit easy movement and feeding, between 0555 and 0650 hrs (fig. 2); the later times correspond to days of morning fog or cloudiness. The first up is usually a juvenile, but the nest site is not abandoned until the silverback or an old female leaves the place.

There appears to be no moving around at night, but vocalisations and (in gorillas) chest-beating do occur. As fig. 3 shows, there is much chest-beating up till 2000 hrs. Odd vocalisations recommence after 0400, and chest-beating begins to be heard again after 0600 hrs.

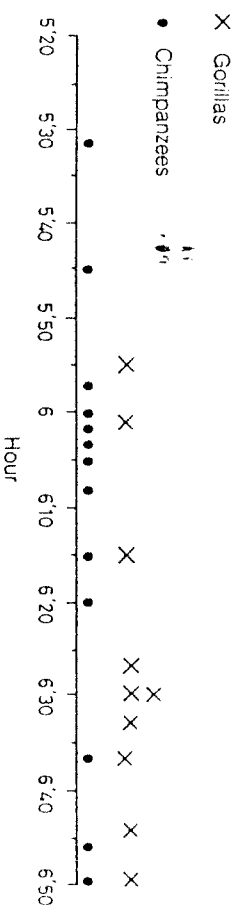


FIGURE 2. Timing of morning abandonment of nests by gorillas and chimpanzees in

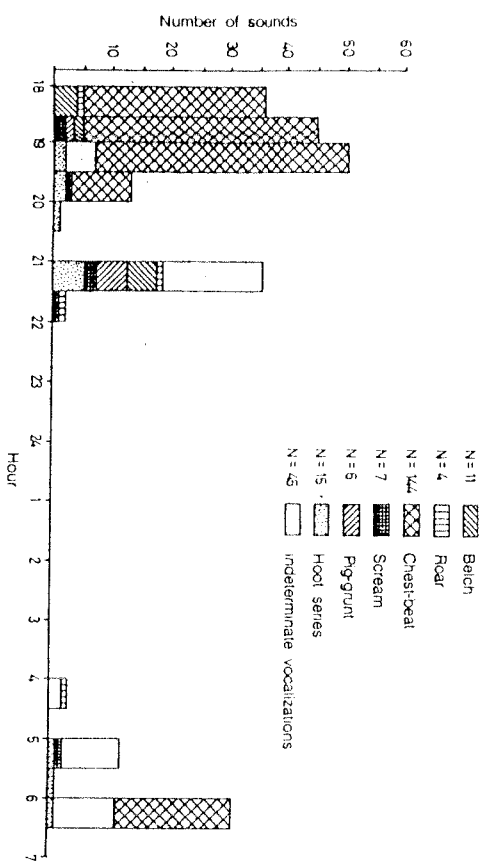


Figure 3a. Nocturnal vocalisations and chest-beats by gorillas in Rio Muni.

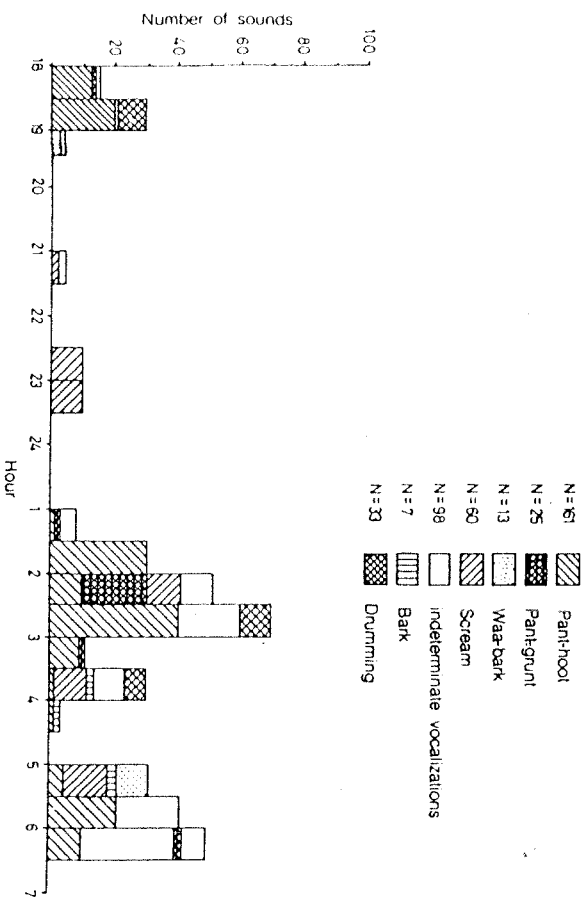


Figure 3b. Nocturnal vocalisations and drumming by chimpanzees in Rio Muni.

In chimpanzees, the nest area falls quiet after about 1930 hrs, with a few scream vocalisations heard up to about 0100, after which there is an increasing noise level—predominantly pant-hoots—up to 0330 or 0400; a further hour of quiet gives place, after 0500, to further, more varied, vocalisations as the day's activity begins.

(often, food plants), in a fairly tight group especially the adult females, and with some seasonal variation. These generalities can be used as a basis for comparison with the less ample data for chimpanzees and orang utans.

Chimpanzee nests were first reported in the literature by Du Chailu (1861), whose account of them, however, is a veritable goldmine of misinformation. He attributes nests to a special species, *Troglodytes calvus*, known to the Fang as *Nshigo mbouvé*. The nests he reports as usually 15 to 20 ft above the ground, invariably on a tree standing a little apart from the others, with no limbs below the one bearing the nest. The male and female cooperate in gathering leafy branches, and vines with which they tie them to the tree: the female brings the vines to the male, who does the actual building, one nest for each of them but in different trees. The nest is interpreted not as a platform but as a roof (in fact, it is rounded at the top to throw off the rain); the animal sits on the branch below, its head reaching into the domed roof, its arms clasped about the trunk. The nest is said in one place to be inhabited for 8 to 10 days, in another for 10 to 15 days—as long as the nearby supply of wild berries lasts.

#### Orang utan nests

Orang utan nests are made at heights of 19.5 m (Mackinnon 1971, for Sabah), 13–15 m (Rijksen 1978, for Aceh), or thereabouts. Unlike chimpanzees and gorillas, the nests are not necessarily made at or near the evening feeding site: they may travel considerable distances to suitable nesting areas, and indeed Rijksen states that only day-nests are made in food trees. Again unlike the African apes, nests are re-used on occasion: but the inner lining is always reconstructed according to Rijksen (1978). As in captivity, so in the wild, the orang frequently covers itself up in its nest, holding or balancing loose branches above its head as a roof (Mackinnon 1971), or covering itself with loose branches and twigs, which it may leave the nest to go and collect (Rijksen 1978). And in captivity too, orang utans cover their head with sacks when sleeping or the whole body with straw or material when available.

Mackinnon's (1971) detailed description of nest-building gives the distinct impression that the finished affair is much more sturdily made than a chimpanzee's, despite taking only 2–3 minutes. There is much more use of branches from above or below, tucked in to give extra stability ('hanging' and 'pillaring' in Mackinnon's terminology). Nests are often built in vantage points, as on slopes or ridges, according to both Mackinnon and Rijksen. A drizzle during the day sends an orang back to the previous night's nest, or else a new one is made; day nests are often made to process awkward fruits, like durian and mango, in comfort. Females with young may build several nests in a day. As oranges are 'solitary' (with all the social complexity that that in fact implies), a single nest generally makes up the whole nest site.

Just as the greater arboreality of the orang utan cannot by itself explain the greater elaboration of its nest-building activity compared to the chimpanzee, neither can the additional dexterity of its prehensile feet. The same intellectual attributes are reflected in Parker's (1974) finding that, in manipulations of a rope,

behaviours—using the rope in reference to another object or to the animal's own body. For the moment we simply draw attention to what appear to be the facts of the matter, and will not speculate further.

#### Human nests

We must be perfectly clear why we feel justified in searching for a common origin of human and great ape nesting/camping patterns. First of all there is Bernstein's demonstration that there is an unlearned component to nest-making in apes; in what sense this might be true for humans as well is something we cannot be sure of. More important, however, is the matter of continuity. If four species—orang utan, chimpanzee, gorilla, human—perform a certain activity whose motor components and end result are similar, parsimony suggests that their last common ancestor was itself doing something of the kind, and that its descendants have been so doing ever since, the practice having been maintained from generation to generation because it was somehow advantageous. We cannot be sure, naturally, that at some point during the evolution of, say, the chimpanzee the activity ceased to be advantageous and so was discontinued, only to be reinvented later—because, after all, chimpanzees are intelligent and inventive—when it became advantageous again. Put like this, the loss-and-reinvention scenario sounds cumbersome and unnecessary. Substitute 'human' for 'chimpanzee', and to some readers the same idea would be more plausible; though one cannot think of any cogent reason why.

Baldwin *et al.* (1981) note that there is a common pattern in the way all apes build their nests, and that it is not the only conceivable way in which it might be done. 'Since', they write, 'all species of Great Apes build nests in the same manner, it seems likely that the behaviour evolved millions of years ago in their common ancestor and that it was already a stable and consistent pattern before the different pongid lines diverged'. Since the orang utan is less closely related to the gorilla and chimpanzee than are humans, this behaviour would have been present in the proto-human stock as well.

We propose that the most fruitful comparison in this context is likely to be hunter-gatherer camps. This is not because we suppose that these are somehow unchanged from a proto-hominid type, but because being those of nomads such camps will be subject to many of the same environmental constraints as the nest sites of the great apes. Data on such camps, as given by Yellen (1977) for the Dobe !Kung, by Harako (1976) and Tanno (1976) for the Mbuti, and by Gould (1977) for the Pitjantjajara, are summarised in table 9.

Among all hunter-gatherers there seem to be favoured spots, even to the extent that there may be occupation there most of the time, and there are casual encampments for a day or two. The big differences from all great apes are that (1) it is not anomalous for a group to stay more than one night running at a camp, and (2) good sites are often known about, and made for, rather than 'ad hoc', though the Mbuti do seem to be unusual among hunter-gatherers in that all their camps are at known sites, which are occupied in turn (Harako 1976; Tanno 1976).

It has been seen that any variation according to season is hard to find in apes

TABLE 9. Comparisons of 'nests' of Hominidae.

	Orang Utan	Gorilla	Chimpanzee	Human (Nomadic)
Existence of permanent sites	No	No	No	Yes
Duration of occupancy	1 night	1 night	1 night	1 night to 1 month
Re-use of nests	Occasional	No	Occasional	Yes
Occupancy of a nest	Individual	Individual	Individual (rare 'co-bedding' in Bonobo)	Social group or individual
Usual diameter of a 'nest'	?	1.3 m (adult) 1.1 m (medium) 0.7 m (juvenile)	0.7 m	2 m
Area available per individual	?	15 m <sup>2</sup>	38 m <sup>2</sup>	6.5 m <sup>2</sup>
Area of nest (camp) site	?	160–170 m <sup>2</sup>	210 m <sup>2</sup>	120 m <sup>2</sup> (!Kung)
Distance between nests	Not applicable	1.5 m	4 m	4 m
No. occupying a nest site	1	About 12	rainy 2–3 dry 3–7	ca. 17 (!Kung) ca. 45 (Mbuti) ca. 45 (Pitjantjajara)
Overhead cover as part of nest	Usual	Very rare	Very rare	Usual
Use of natural overhead cover	Yes	Rare: but esp. when wet	Common: esp. in dry season	Yes
Location of nests	15–20 m up tree	Ground	5–6 m up tree	Ground
Deliberate selection of suitable nest site	Yes?	No	No?	Yes
Relation to natural vegetation	Part of it	Part of it	Part of it	Free-standing

(except for chimpanzees in a woodland habitat in Senegal); but it has constantly been noted in humans. The camps of the !Kung were larger in the dry season, and people would stay in one place longer, providing greater continuity of occupation (Yellen 1977); dry-season camps have huts that are better made and more evenly arranged. Dry-season camps also tend to be larger in the Hadza (Woodburn 1966). Among the Mbuti on the other hand, it is the rainy season camp which is occupied for longest and by the largest number of people (Harako 1976). Among the Pigiangara winter camps are significantly larger in area than summer camps, but tend to be occupied by fewer people (Gould 1977).

In the rainy-season camps of the Dobe !Kung the huts are for storing possessions in, not for sleeping in, unless it is raining, but are also used for shade during the day; a hut and the associated area is occupied by a nuclear family and averages 4.9 m in diameter (range 2.2 to 8.2) (Yellen 1977). The camps of !Kung, Mbuti and Pigiangara are generally circular, with the huts (or other dwelling places) on the circumference, their entrances facing towards the centre of the camp. The !Kung camp has an area of 26–326 m<sup>2</sup> (mean 122), and is 7.0 to 25.2 m in diameter (mean 15.6); a single social unit occupies 2.2–8.2 (mean 4.9). Hut-to-hut distances around the circumference vary from 2 to 15.3 m, with a mode of 4–5 m (Yellen 1977). Pigiangara camps are much smaller than this.

The myth of the patrilineal, patrilocal horde in hunter-gatherers has died hard; but the essential flexibility of the social group is now clear. The number of people occupying a campsite varies from day to day, so that figures can be given on average only. Yellen gives a mean of 4.6 social units per site (these being more or less nuclear family groups), or 16.7 people, making 3.7 people occupying an individual area. Within each campsite, therefore, there is a theoretical area of 24.8 m<sup>2</sup> available to each social unit (range 11.3 to 47.8), and 6.5 m<sup>2</sup> (range 2.4 to 13.6) available to each individual. Mbuti camps would seem to contain 30–62 people, in 5–12 social units (broadly, families); camps of net-hunting bands were larger (37–62, mean 49, n=3), and the social units were larger (mean 7.2 people, n=21), than those of archers (30–45, mean 36, n=3; 3.9 people per unit, n=28) (calculated from data in Harako 1976). The Pigiangara campsite has 3 to 17 social units in summer, 2 to 6 in winter; 14 to 107 individuals in summer, 9 to 54 in winter. A social unit consists of 3.6 people: almost exactly the same as among the !Kung. The Gielli or Bayele camp (pygmoids of Rio Muni) has 5 to 20 social units year round, showing no difference between rainy and dry seasons (J.S.P. personal data).

What has been claimed as the earliest trace of a human habitation has been discovered at Olduvai (Leakey 1971). The famous Stone Circle at DK 1A, discovered in 1962, is a structure of blocks of basalt, piled loosely to nearly one foot (30 cm) in places, enclosing a space of 3.6 × 4.2 metres diameter, i.e. about 12.5 m<sup>2</sup> (calculated as the area of a circle 4 m diameter). There are small stones scattered over the enclosed surface; and on one side a number of small stone heaps spaced at intervals of 60–75 cm 'as if supports for branches or poles supporting a windbreak'. The circle is on a gentle slope; the ground inside is slightly lower than that outside. Careful excavation of the surrounding area failed to reveal any similar structure.

It must be admitted that the dimensions of the Olduvai Stone Circle fit neither

well in the !Kung data for individual camps. Such a small area could not possibly accommodate multiple social units. Yet its elaborateness suggests it was more than a temporary shelter or hunting blind, such as Gould (1977) describes. It was, apparently, on its own. Can this be taken as evidence for a stage in human evolution when social units were independent of one another? We will return to this topic below.

Isaac (1980) has thoroughly considered all the data on human social organisation and 'nesting' behaviour, and concluded that the following features are characteristic of the human pattern:

1. The sleeping place is a home base. Each day, the members of the social group move radially from it.
2. Males and females have separate trajectories; there may be more than one party of each sex.
3. On any given day, some individuals will stay at the home base.
4. Many (not all) foodstuffs are transported back to the home base, there to be shared out.
5. The whole group shifts its home base at intervals.
6. The group may undergo reversible fission or fusion.

Of these characteristics, the most fundamental from our point of view, as from Isaac's, is the first: the Home Base. As Hediger (1977) and P. C. Reynolds (1981) note, a 'fix-point'—even an artificially modified one—is nothing exceptional in the animal kingdom; but its evolution among the Hominoidea is unexpected. The question to be asked is surely, why did nests become re-usable and long-lasting? The answer given, implicitly, by Isaac, is that there were ecological/economic reasons, based on the division of labour.

Isaac considers what could be archaeological traces of home bases, and suggests they might be what he calls 'Type-C' sites, characterised by an accumulation of discarded tools and broken bones. These include the bones of large mammals, which are one type of food not utilised by other savannah or savannah-woodland primates (e.g. chimpanzees)—the others being deep tanners, scavenged meat and, unexpectedly, tortoiseshell. Binford (1977) has strongly criticised the basis on which an early big-game hunting culture is based: if this is justified, it rather knocks away the putative archaeological basis of Isaac, and leaves us back with the Olduvai Stone Circle.

We have noted the sort of argument that can be advanced for homologising nest-making behaviour in humans and apes; we must now examine possible origins for human social organisation, to see who might be expected to occupy a common 'nest site'.

1.

#### *The social organisation of early hominines*

The evidence to date of the bases of social organisation in the apes has been set out in a recent book (Hamburg & McCown 1980). The orang utan has a system of widely overlapping female home ranges overlain by a shifting network of male ranges; according to the state of the food supply, a prime male will either establish a temporary territory, from which rivals are excluded by vocal display

backed up by actual aggression where necessary, or become nomadic, returning to his familiar area when conditions are right. MacKinnon (1980) notes that old males become sterile but continue to behave territorially, and hypothesises that each is maintaining an exclusive area on behalf of a younger male relative (son?).

Understanding of chimpanzee social organisation has been in a state of flux ever since the early studies (Goodall 1963; V. & F. Reynolds 1963) described it as 'flexible'. Wrangham (1980) reviews the evidence, and proposes that the reality is not of a social community of males and females occupying a community range, and forming and dissolving daily subgroups of different composition, but one of two models:

1. The females within each community do not range throughout the community range, but each tends to stay within her own relatively restricted, but not exclusive, area.
2. The females are not strictly affiliated to a community at all, but occupy their own ranges as under (1) above, irrespective of where the communities of males are located.

In effect, the two models do not differ greatly in their practical consequences. Females are certainly associated more with one community of males than with another, and can be looked on as 'belonging' to a community. A female will generally shift her range—transferring between communities—on achieving her first oestrus, and sometimes again during subsequent oestrus periods. A male, on the other hand, may emigrate (alone or with other males) but does not transfer between communities.

Gorilla social organisation is more rigid than that of the other apes. A troop generally has a single mature (silverback) male and several females; younger silverbacks may emigrate and try to kidnap females from other troops, or may stay in the troop and mate with specific females (those not mates of the old male, and not their full sisters). It may be specifically the sons of the troop male who stay in the troop, and the sons of passing wanderers who emigrate (Harcourt *et al.* 1978). Females tend to transfer as do chimpanzees.

It is easy to see potential homologies between orang and chimpanzee social organisation, especially under Wrangham's second model: all we need is to have the males travelling in groups and associating for longer periods with female groups. To associate gorillas with such a scheme is more difficult. Goodall & Groves (1978) suggest that gorillas, too, may have local communities, and that their troops are simply the chimpanzee's flexible subgroups made permanent.

The social organisation of human nomadic peoples is thoroughly flexible: the composition of camps, as we have seen above, changes from day to day. There is however the vexed question of the nuclear family. Make the polygynous family more independent, and you have the gorilla troop; or dissociate the male-female pairs and you have the chimpanzee community. How, then, to explain the separating out of human male-female couples, or of one-male harem units?

The male-female unit in the human nuclear family has been called a pair-bond. It is not, for the following reasons:

1. It is potentially polygynous. The fact that, even in societies where polygyny

pair-bond-living species is ever polygamous in any sense (see P. C. Reynolds 1981: 245).

2. It does not exclude other kin, or indeed other, unrelated individuals. The pair-bond of birds, gibbons, etc. is the highest unit of social organisation. The nuclear family of human society, even where—as in twentieth-century industrial countries—it is neolocal and an independent entity for purposes of day-to-day subsistence, is never free of ties to other kin, and preserves a complex network of rights and obligations with respect to them. In most societies, of course, including our nomadic hunter-gatherers, the nuclear family is neither neolocal nor economically independent.

3. It is not permanent. Divorce and adultery 'give every indication of being as venerable as marriage' (P. C. Reynolds 1981). Woodburn (1966) emphasises this for the hunter-gatherer Hadza: the divorce rate is 49 per 1000 years of marriage, higher than in the typical industrial society. Splitting up and re-pairing is not known for certain under natural conditions, and extremely difficult to organise experimentally, in pair-bonded species.

4. The presence and degree of sexual dimorphism in the human species is much more consistent with the idea that male-female bonds have arisen within a multi-male group, with its concomitant dominance relationships (Martin & May 1981).

Chimpanzees form consorships, lasting sometimes for weeks, resulting in fertilisation (Tutin 1975). Troop-leader silverback gorillas mate only with certain females, leaving others to be mates to their sons or to the wandering silverbacks (Veit 1982); but mating is a rare event among gorillas in any case. The human nuclear family is clearly derived from a long extension of a consorship, and has retained many of the same characteristics (dissolubility, existence within a wider social group, etc.). Chimpanzee consort pairs—and orang consort pairs, when they occur—separate from the social group for long periods. Human consort pairs do likewise, for still longer periods.

It is interesting that Imani (1977) has argued that the basic social organisation of the Hominoidea is what he calls 'pair type'. If this viewpoint is acceptable, our argument above still makes it most unlikely that human social structure is of this type; a partial reversion, on a very superficial level, is 'all that can be said for it'.

#### Discussion

If we are correct in deriving the human social organisation from the common denominator of apes, the human camps from ape nest sites, then we must be clear about exactly what factors are in common and what the differences are. Human social groups are of the same general size (20–80) as those of chimpanzees and the hypothesised ones of gorillas: in theory, at least, they would be derivable from the dispersed organisation of orang utans (see, for example, the model of Calhoun 1966). Within the social group, subgrouping takes place with much of the same flexibility as the chimpanzee exhibits, with this one exception: that consorships are longer-lasting and tend to form a consistent basic mini-

know), a male forms multiple concurrent consortships (polygyny): rarely, though not in apes, a female does the same (polyandry). A consortship, in all cases, is a potentially reproductive relationship in that it is the usual way infants are conceived, and the male partner claims social paternity even if not the biological father; and so is to be distinguished from the promiscuous sex that is such a misleadingly conspicuous feature of chimpanzee social life, and some human societies, but does not normally result in the birth of infants.

In a subsistence system in which sharing, while it occurs, is not pervasive, the major resources being available to all, a lengthening of consort bonds could easily result in the spatial separation of the consort pair for longer periods than occur in chimpanzees, whether this is total separation from other groups or merely remaining together during travel from one camp to another. As a bush/savannah ape, the early human ancestor would require an enormous memory store, a highly developed reasoning ability to follow the fluctuation of environmental vicissitudes, and enhanced learning ability: not new capabilities for a new set of requirements, but an elaboration of the same skills as are already highly developed in apes (Menzel 1970; Rodman 1975), and for the same reasons magnified—to be able to predict the location of resources in a fluctuating environment and so save crucial energy. The further reduced predictability of relevant causal processes, in a still less productive environment than inhabited by apes, demands a much wider home range and so selects the more intensely for learning ability and for the continued distalward expansion of iconic manipulation, as P. C. Reynolds (1981) expresses it. And so learning becomes supplemented by teaching, and intensified by rearing in an extended consortship.

A study of table 9, with due acknowledgement of the slenderness of the human data, shows that the campsites/nest sites of Hominiidae (here used to cover humans and great apes) are similar. The number of individuals occupying the site varies, but the size and shape (though not necessarily the internal organisation) of the site are similar, the spacing of the individual nests/camps is alike. In their social ordering, the major differences are two: the individual camps are arranged around the periphery in the human case, with a communal area and perhaps also an area for adolescents in the middle; and, still more strikingly, the individual camps are occupied by an entire nuclear family, not as in apes by a single individual or, at most, a mother-infant pair. Consort pairs nest close together in chimpanzees, but do not share a common nest, except, it would seem, in *Pan paniscus* in some instances (Kuroda 1980); otherwise only extreme peer-dependence has resulted in nest-sharing: and this concerned not consorts but brothers (Riss & Goodall 1976).

Functionally, the nest of apes has taken on aspects of the Home but for only one night. The human 'nest' is a place for reconvening, both of the consort pair and of different social units. No ape nest-site is definitely known about and re-used, although there is a possibility that orang utans may in fact select in this way; whereas good sites are deliberately made for by human nomadic bands, and in many cases there is even a major base-camp. It is a place of maximal security, a fit-point. No doubt, the elaboration of food-sharing and division of labour (Isaac 1980) intensified these aspects of the nest. What is noteworthy, as

functions of a breeding-place: this had to await the coming of permanent dwellings.

Structurally, too, the individual 'nests' have much in common between all species, but there are characteristic differences. In their simplest form, a scraping away of substrate to form a depression for the body is a shared feature. The more usual, more complex structure involves skilful interlacing and tying together of sticks and flexible plant material; there are very decided preferences, based presumably on experience, perhaps on tradition as well, for particular plant species from which to make the nest. Yet the ape uses material at hand or nearby always, as far as we know; the human collects it from a distance. Related to this, the ape makes its nest around it; the human may do this, but as frequently constructs it first, then enters it. Finally, the ape's nest is anchored to the growing vegetation structure, while the human's is a new structure; even such a superficially simple construction as a windbreak involves breaking off sticks and inserting them in the ground, supporting them if necessary with stones moved into place for the purpose—which is exactly what is supposed to have happened 1¼ million years ago to create the Olduvai Stone Circle.

P. Reynolds (1981) proposes nest-construction as a test of his 'distalward migration of conscious control' hypothesis. Apes, he observes, consciously control their hand movements in such a way as to place their hands in planned configurations, as for example in the gestures of sign-language. They can also manipulate and alter objects on an *ad hoc* basis, as in termite-fishing or other food-getting activities. No cercopithecoid monkey has anything like these activities. What apes do not do, however, is plan object configurations: they do not collect sticks for later use in termite-fishing, nor use objects to manipulate other objects. Nor, he surmises, does the ape work to a consciously controlled blueprint in nest-building: only in the human case has the distalward migration of conscious control reached so far.

All the evidence summarised above supports Reynolds's hypothesis. An ape does not collect suitable materials before beginning construction. It does not break off sticks, move them to a new location, and use them as supports for a superstructure. It does not construct a nest, then enter it. It does not, as far as can be deduced, design a structure capable of containing two bodies (though here we may be going beyond the evidence). It does not coordinate its building activities with all other troop members in such a way as to stamp a regular pattern on the nest site. It does not choose a site for its camping possibilities, and return to it again and again (orang utans perhaps excepted). The human, with its fully developed ability to visualise objects in new configurations, and to bring these configurations into being on the basis of that mental picture, does all these things.

By examining closely the regularities of nesting patterns in apes, especially gorillas, we believe that a groundwork can be laid from which it is possible to argue more securely to the origins of human camps. Both structure and function

the nest sites of apes to the camps of modern hunter-gatherers; but analysis of those aspects of structure which have changed, and of the differences in function, offers clues for the origins and selective advantages of human social organisation, and places in focus the cognitive similarities and differences between ape and human.

## NOTES

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