

## Shadows on a Changing Landscape: Comparing Nesting Patterns of Hominids and Chimpanzees Since Their Last Common Ancestor

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Studying the evolution of nesting behavior within the human–chimpanzee clade is problematic because evidence is sparse and difficult to interpret. Lacking a fossil or archaeological record for proto-chimpanzees, reconstructions of the antecedents of modern chimp nesting patterns can be reconstructed only from careful studies of variation in current chimpanzee and bonobo nesting patterns within the context of spatial and temporal landscape parameters. The ethology of nesting also provides an important frame of reference for reconstructions of early hominid nesting behavior. If the contemporary contrast between human and chimpanzee nesting patterns is seen as an evolutionary dichotomy, then African prehistoric landmarks that mark the origin of this split might include bipedalism and the origins of the hominidae, the first stone tools and the origins of *Homo*, the developmental and behavioral adaptations of *Homo ergaster*, shifts in Late Acheulian settlement patterns, and the origins of anatomically modern humans and the Middle Stone Age. The issue of whether Early Stone Age archaeological sites were used for nesting is unresolved because potential markers of such behavior, such as hearths, structures, or bedding, are not unambiguously recognizable in the archaeological record until the Middle Stone Age. *Am. J. Primatol.* 46:85–101, 1998. © 1998 Wiley-Liss, Inc.

**Key words:** nest; archaeology; ethnoarchaeology; hominid; chimpanzee; Africa

### INTRODUCTION

How can we discern the evolutionary history of human “nesting” patterns? Like other historical scientists, paleoanthropologists must use a knowledge of the present to interpret direct evidence of the past that is often very different from extant examples. First, we must compare current examples of how humans live in the world within a broader ethological framework than traditionally used by socio-cultural anthropologists. As long-term field studies teach us more about the African apes, what were once considered clear contrasts between the ranging and nesting patterns of hominids and other hominoids have become less easily

Contract grant sponsor: L.S.B. Leakey Foundation; Contract grant sponsor: National Geographic Society; Contract grant sponsor: Jane Goodall Foundation; Contract grant sponsor: Wenner-Gren Foundation for Anthropological Research.

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Received 15 February 1997; revision accepted 2 February 1998

distinguishable. In turn, archaeologists must learn to recognize the potential archaeological signatures of nesting/resting behavior, and other behaviors associated with it, in the context of non-modern human behavior. The field of ethnoarchaeology needs to be broadened to become more consistent with behavioral ecology [O'Connell, 1995] and include systematic observations of non-human primate behaviors in a format designed to be partially comparable to archaeological evidence [e.g., Sept, 1992a, Joulian, 1994]. Only then can we examine prehistoric traces for direct evidence of such behavior—the material remains that make up the archaeological record—and consider the trajectory of how hominid nesting patterns evolved.

In this paper I will describe a comparative framework for such studies, acknowledging that work has barely begun, and focus on what archaeologists need to learn from primatologists to help them interpret the prehistoric record.

### COMPARATIVE BEHAVIORAL CONTEXT OF NESTING BEHAVIOR

Whether studying settled villagers and food producers, or people who traditionally foraged from temporary/seasonal camps, researchers have often recognized the “nesting” patterns of modern humans as fundamentally different from those of other hominoids. As the anthropologist Michael Jackson described in his recent book, *At Home in the World*, people may have a universal sense of home in which “person and place coalesce” in remembered landscapes or social traditions of space [Jackson, 1995, p. 125]. People gather at particular places on a landscape not merely from habit (historical contingency) or for protection, but also from perceived social valence. And in many cases residential camps or home bases are not mere resting/nesting sites, but hubs of activity, sharing and exchange [Kelly, 1995]. “Rest” is likely to be far down the list of social and economic activities that occur in most human camps.

On the other hand, convenient rest and refuge seem to be primary nest building goals of the apes most closely related to us, the chimpanzees [Horai et al., 1995; Mann and Weiss, 1996; Pilbeam, 1996]. In particular, chimpanzees often nest at sites adjacent to recent or anticipated feeding patches [e.g., Goodall, 1986] or travel paths [Fruth and Hohmann, 1994a; Fruth and Hohmann, 1994b; Fruth and Hohmann, 1994c]. Although chimpanzees and bonobos makes new nests every night, they do reuse nesting sites; some habitual nesting sites may likely be important habitat localities that are remembered in any “mental maps” [Milton, 1981; Boesch and Boesch, 1984a; Cheney and Seyfarth, 1990] of their ranging areas. I consider this to be emerging evidence that habitual nesting sites (such as those described by Kortlandt [1983], Goodall [1986], and Baldwin, et al. [1982]) are likely part of the learned landscape, along with other localized resources such as nut trees, seasonal fruiting patches and good termite mounds. Yet most authors would still be reluctant to equate a “nest site” with a “home” [Hediger, 1977]. If we want to understand the evolution of these different patterns, we need to focus on better defining the elements of similarity and difference and evaluating the types of evidence to search for that could elucidate prehistoric patterns of nesting behaviors.

### Landscape Context

From an evolutionary perspective, the last 20,000 years of human existence have culminated in a veneer of settled life that is atypical of most of our past. Growing populations of complex human societies have shaped their landscapes in ways that are fundamentally different from those of their predecessors. Ho-

locene food producers have had a significant anthropogenic impact on their environments, whether directly—for example, through frequent burning, forest clearance, or the propagation of wild economic species such as the oil palm—or indirectly, as when weeds invade the disturbed soils around settlements [Deacon et al., 1983; Hamilton et al., 1986; Stager, 1988; Marean et al., 1991; Elenga et al., 1994; Jolly et al., 1994; Marean et al., 1994]. In this context, it is intriguing to learn from the Lamako study [Fruth & Hohmann, 1994a,b] how bonobos may have also shaped their landscapes, albeit in incremental ways (branch damage, seed dispersal) that seem subtle to us.

It has become almost axiomatic to acknowledge that groups of traditional foragers in Africa have lived in the interstices of food producers' landscapes, participating in large-scale economic systems for thousands of years [Schrire, 1984; Wilmsen, 1989; Kelly, 1995]. So have our cousins, the African apes [Sept & Brooks, 1994]. The manner in which human foragers and great apes share the landscape has been partially recognized as an evolutionary issue [McGrew, 1992; Wrangham et al., 1994] but not directly studied apart from its implications for modern conservation [Goodall, 1994]. Of course, our species have historically been unequal partners on the landscape. Ape habitats are threatened by human land use, not the other way around. As an archaeologist, I think it is important for primatologists to consider the extent to which millennia of human land use pressures might have influenced chimpanzee ranging behavior and the local expressions of their nesting patterns.

In the longer term, there is little question that climatic changes have had a profound influence on the evolution of patterns of chimpanzee and hominid ranging and, by implication, nesting behavior. On a macroevolutionary scale, for example, Vrba's [Vrba, 1985, 1988, 1995a] influential turnover pulse hypothesis proposes that climatic change has had a causal effect on the origin, extinction, and dispersal of species. As summarized by Kimbel [1995], this hypothesis poses a causal chain in which large-scale environmental change (such as climatic fluctuations) triggers the fragmentation of habitats, causing a vicariance in species' ranges. Over time, such allopatric conditions could allow or encourage behavioral divergence in ranging, foraging, and nesting patterns as well as selection for the morphological change which ultimately could lead to speciation. A number of authors have suggested that hominid divergence from our last common ancestor with chimpanzees was either caused or encouraged by changing strategies of resource procurement and ranging in response to environmental changes [Laporte & Zihlman, 1983; deMenocal, 1995; Partridge et al., 1995; Vrba, 1995b]; but others have alternative views [Foley, 1994]. For example, Isbell and Young [1996] have argued that common chimps and hominids both responded to changing climate in different ways—hominids becoming more mobile to maintain large group sizes, chimpanzees splitting into smaller groups to exploit smaller patches of food.

Given that lineages of *Pan* also likely diverged during the Plio-Pleistocene [Morin et al., 1993, 1994; Ruvolo et al., 1994; Ruvolo, 1994, 1995; Horai et al., 1995], we should consider what influence the climatic changes had on the ranging and nesting behaviors of different populations of bonobos and chimpanzees in different habitats. DeMenocal [1995] has argued that the changing periodicity of climatic cycles beginning around 2.8 ma greatly amplified the intensity of the effects of increasingly cool/arid/seasonal conditions. Therefore, ape populations within forest refugia in western and central Africa would have adapted to more stable environmental settings than populations in the woodland/savanna belts of the Sahel margins or the topographically varied Rift [Partridge et al., 1995], where plant communities would have become more strongly mosaic and resources

patchier in space and time. Significant habitat change can occur swiftly in such semiarid settings; this was dramatically demonstrated by Western [Western & Van Praet, 1973] for the Amboseli region of Kenya, where cyclical rainfall fluctuations lowered the water table, decimating extensive woodlands in the basin in only 50–70 years. Syntheses by Nicholson and others [e.g., Fontes & Gass, 1991; Nicholson, 1993, 1996a] on the impact of climatic fluctuations across the African continent, coupled with high-resolution studies of pollen and wind-blown sediments from deep-sea cores [Fredoux, 1994; Leroy & Dupont, 1994, P. DeMenocal, personal communication] could help form the basis for regional models of the relative sensitivity of different chimpanzee habitats to degrees of climatic change. Coupled with habitat-by-habitat comparisons of current variation in nesting patterns [Baldwin et al., 1981, 1982; Fruth & Hohmann, 1994b], such an approach could help formulate hypotheses about the evolution of ranging and nesting behavior among chimpanzees that could potentially be evaluated with (yet to be discovered) fossil evidence.

While nesting/resting behavior may be a conservative element of the ancestral suite of behaviors recognized in living hominoids [Wrangham, 1987], given the currently known range of nesting site configurations in *Pan* [Fruth & Hohmann, 1994b], it is possible that the current patterns of chimpanzee and bonobo nesting and ranging behavior are as unrepresentative of their ancestral patterns as the modern land-use patterns of human foragers are atypical of prehistoric ones. In this context, living apes are cast as a surviving sample of a more diverse range of earlier populations whose behaviors must have changed/evolved through time in addition to their genes [Morin et al., 1993, 1994]. While there is a current consensus that the last common ancestor (LCA) of the human–chimp clade was relatively *Pan*-like [Wrangham, 1987; Berger & Tobias, 1996; Hunt, 1996; Moore, 1996; Pilbeam, 1996], the narrow living diversity emphasizes the need to avoid building models of early members of the chimp–human clade on the basis of single living populations, subspecies, or species [Tooby & DeVore, 1987; Moore, 1996]. Herein lies an important challenge raised by symposium organizers Fruth and McGrew: to begin phylogenetic comparisons and analysis of the variability and ecological convergence or divergence in the characteristics of nesting and ranging patterns within the chimpanzee–human clade in a way that allows comparisons with the paleoanthropological record.

### Nesting Behavior Proxies

What types of evidence for nesting behavior are likely to be preserved through time? This question can be answered only through comparative studies of the anatomy and material culture of living populations.

Comparative anatomy can be used to deduce basic information about the physiological adaptations that potentially influence nesting behavior. For example, body size and climbing ability could constrain the placement of nests but might prove less relevant than sexual dimorphism (as an indicator of social group structure) or craniodental anatomy (as an indicator of dietary adaptations) for predicting general patterns of nest site location. Anatomical differences between common chimpanzees and bonobos [Cramer, 1977; Kinzey, 1984; Doran, 1993; Doran & Hunt, 1994] seem to relate to consistent differences in diet, grouping, and locomotor behavior and thus have the potential to be correlated with differences in nest height and clustering as they become better understood [Fruth & Hohmann, 1994a,c].

Ethnoarchaeology has been described as a study of the relationships between modern human behavior and its material consequences with a goal of interpreting archaeological evidence of past human behavior [O'Connell, 1995]. Ethno-

archaeological research allows archaeologists to examine how behavioral processes such as creating, using, and discarding artifacts and other traces of behavior can contribute to the archaeological record. In a comparable way, paleoanthropologists need to expand on classic primatological studies to document variability in the natural (wild) material culture and other behavioral traces of apes in a way that can help evaluate the processes of archaeological site formation from a nonhuman perspective. For example, with a few exceptions [e.g., Boesch & Boesch, 1983, 1984a; Boesch et al., 1994], primatologists have not documented artifact use and discard patterns among wild chimpanzees with the appropriate detail to be useful for ethnoarchaeological study. As a result, archaeologists themselves have begun such studies [Sept, 1992a; Joulain, 1994, 1995, 1996; Joulain & Roulon-Doko, 1994] but have only scratched the surface of the rich repertoire of artifact use present in surviving chimpanzee and bonobo populations. In this context, nest locations can be studied ethoarchaeologically (ethological–archaeologically) as artifacts of ape behavior and site formation processes, even though nests themselves will never be preserved as part of the archaeological record. Although preliminary, even the first ethoarchaeological study of chimpanzee nesting [Sept, 1992a] was able to reveal important attributes of chimpanzee nest location that had been previously overlooked or misunderstood by archaeologists, as described below.

One key to such actualistic studies is to control for environmental variables, such as vegetation type and sedimentary environment. Thus, it is important to investigate ape behavior in habitats that are at least partially comparable to paleoenvironmental settings frequented by prehistoric hominids. Studies of chimpanzee behavior in living dry, deciduous woodlands provide useful comparative data for the earliest known hominids [Moore, 1996], while studies of chimps in open, savanna environments [McGrew et al., 1981; Baldwin et al., 1982; Kortlandt, 1983; Tutin et al., 1983; Moore, 1992, 1996] and/or semiarid riparian habitats [Sept, 1992a, 1994] provide useful comparisons for Plio-Pleistocene hominid tool-makers. At the same time, just as savanna environments represent only a fraction of the ecological range of living chimpanzees, so too the paleoanthropological record of early hominid fossils and archaeological site locations is a strongly biased sample of semiarid sedimentary basins and undoubtedly not representative of the biogeographical and ecological range of early hominid ecological variation [White, 1988; Sept, 1992b; Schrent et al., 1993].

#### **EVALUATING PREHISTORIC EVIDENCE FOR NESTING/RESTING BEHAVIOR**

Tracing the antiquity of the contrast between human and chimpanzee nesting/resting behavior back into time has proven problematic, in part because so little direct evidence of such behaviors is preserved and in part because what is preserved is difficult to interpret. The limited fossil evidence for Late Miocene, Pliocene, and Pleistocene apes [Andrews, 1992; Pilbeam, 1996] provides little evidence for the anatomy of the antecedents of living African apes, let alone ranging or nesting behavior. No artifactual record of prehistoric apes has yet been recognized, although it could theoretically exist for the West African chimpanzee populations [Joulain, 1994, 1995, 1996] which have been cracking nuts with stone tools at least since the sixteenth century [Sept & Brooks, 1994]. The antiquity of their stone tool use is unknown, but, given its cultural variation, it may postdate the isolation of these far-western chimpanzee populations (*P.t. verus*) from other subspecies of chimps which do not crack nuts in this way [McGrew, 1992; Boesch et al., 1994; Wrangham et al., 1994].

The hominid fossil record, in contrast, has had significant new discoveries in recent years which add to the evidence that the anatomy of the earliest hominids (and, by implication, the Last Common Ancestor of chimps and humans) was *Pan*-like in terms of cranial anatomy [White et al., 1995a,b] and included riverine forest and dry woodland settings in its range [Kingston et al., 1994; Wolde Gabriel et al., 1994; Leakey et al., 1995]. However, the archaeological record for early hominid behavior does not appear until the halfway point of the 5–6 million years of hominid evolution (approximately 2.6 ma) [Harris, 1983; Howell et al., 1987; Kimbel et al., 1996; Semaw et al., 1997]. If we assume, based on anatomical clues, that the earliest hominids were bipedal when terrestrial but also accomplished tree climbers with chimp-like feeding preferences [Pilbeam, 1996], this leaves a wide range of possibilities open for the possible nesting/resting patterns of such creatures. Perhaps a profound shift in ranging behavior and nesting patterns had already occurred with the initial bipedal adaptation, and the origins of “home” can be traced back to the origins of the lineage? There is no way to test this hypothesis with currently available data.

The earliest archaeological sites currently known are late Pliocene in age, approximately 2.6 ma [Harris, 1983; Howell et al., 1987; Kibunjia et al., 1992; Rogers et al., 1994; Kimbel et al., 1996; Semaw et al., 1997], but have proven to be an ambiguous record at best of early hominid ranging and nesting behavior [Isaac, 1982, 1984; Binford, 1987]. A short history of the great “Home Base Debate” illustrates both the interpretive challenge and the promise of a broad ethological approach to questions of the evolution of human nesting. The question of when and how protohuman hominids first started down the road to more human-like behavior was first articulated in an effective synthesis by Glynn Isaac, who proposed the “home base hypothesis” to suggest that Plio-Pleistocene archaeological sites in East Africa had been central places to which hominids returned from foraging to share food and presumably rest, relax, and socialize [Isaac, 1978, 1981, 1984]. In effect, Isaac used two main arguments to support his interpretation of these sites. First, these sites were originally recognized by archaeologists because they were anomalous concentrations of stone artifacts on an otherwise relatively uncluttered, natural landscape, suggesting that the sites had been a focus of hominid debris-producing activity. Secondly, most of the stones and associated fossil bones that made up these clusters of debris had been imported to the sites, leaving an image of the sites as prehistoric social magnets that somehow attracted repeated episodes of debris-producing behaviors by hominids. Isaac suggested food sharing as a compelling explanation for how repeated transport could lead to a dense concentration of remains.

Since Isaac first formulated his home base hypothesis, a number of archaeologists have suggested alternative explanations to account for the patterns of debris [for summaries see Isaac, 1984; Sept, 1992a,b] including taphonomic concentration [Binford, 1981, 1987] repeated uses of the site locality which did not invoke food sharing but only temporary, localized activity patterns related to tool use and food extraction, such as a cache of stones used for butchery [Potts, 1988, 1991], an attractive site near shade or water used independently for diverse activities [Kroll & Isaac, 1984; Schick, 1987; Bunn, 1991; Kroll, 1994], and activity sites abandoned due to predator avoidance butchery [Potts, 1988, 1991]. From a behavioral perspective, evolutionary ecologists and primatologists have reminded paleoanthropologists that many animals, including chimpanzees, frequently engage in “reciprocity-based cooperation” [Winterhalder, 1996a:55] and food-sharing behaviors that take diverse forms and follow a variety of spatial patterns [e.g., Blurton-Jones, 1987; de Waal, 1989; Winterhalder, 1996b; Stanford, 1996];

food sharing is neither distinctly human nor necessarily home-based. Also, subsequent fieldwork by researchers such as Boesch and Boesch [1983, 1984a], Boesch et al. [1994], Frederick Joulain [1994, 1995, 1996], and others [for summary see McGrew, 1992] have shown that the localization of tool use by chimpanzees is not random but is related to food distribution (localities of nut trees, termite mounds, bee hives, etc). To my knowledge, formal analyses of the spatial relationships between chimpanzee localities of tool manufacture, use and discard, feeding localities, cooperative localities, and nesting localities have not yet been undertaken for any study site.

However, Isaac's [1978] underlying assumption that the patterns of concentrated debris were fundamentally human and un-ape went unchallenged until I undertook a systematic ethoarchaeological study to map the debris patterns of living chimps along the Ishasha River in the semiarid Parc National des Virunga, eastern Zaire [Sept, 1992a]. Thirty-five belt transects were placed perpendicular to the river to traverse all vegetation types found between the river margin gallery forest and the savanna. The transects were spaced randomly, at least 200 m apart, and sampled a total length of 6.6 km. All nests within 25 m on either side of the transect were recorded during two field seasons in July 1989 and July and August 1990. The average nest density for all transects sampled was five nests/hectare, with ten of 35 transects recording above average nest densities and 14 transects remaining empty during the study. The heights of the nests and nesting trees were measured by clinometer in 1989 and estimated by eye and calibrated with a clinometer in 1990. Nest heights observed during the two field seasons did not differ significantly, although the height of the trees in which the nests were built varied slightly. A frequency distribution of nest heights ( $n = 101$ ) revealed a skewed distribution, with a median nest height (11.5 m) less than the total mean of 13.5 m. Ninety-seven of the observed nests were built in a closed canopy gallery forest zone, and attributes of the trees in which they were built are included in Table I. Although nest height is obviously constrained by maximum tree height, it was only weakly dependent upon tree height in this sample ( $r = 0.67$ ,  $P < .001$ ), and no significant relationship was evident between nest height and either tree dbh ( $r = 0.44$ ) or crown diameter ( $r = 0.35$ ). No tendency was observed for the chimpanzees to select fruit-bearing trees for nesting.

At that time archaeologists were relatively uninformed about patterns of great ape nesting behavior and the fact that chimpanzees would often revisit nesting sites. Now such nesting patterns are receiving the systematic study that they deserve (e.g., this symposium issue). Therefore, while the early archaeological record is unique to early hominids—the visibility of the Plio-Pleistocene sites and the types of stone tools and large animal remains do not match the behavior patterns of any living primate, including humans—archaeologists can no longer claim that repeated episodes of feeding and tool use that create concentrations of debris at a site are evidence of home-base behavior and fundamentally human.

The archaeological visibility of most chimpanzees is very low, because the nests and organic tools they make and discard rot away during their lifetimes. The exceptions are chimpanzees which use stone tools; they are creating a potential archaeological record [Joulain, 1994, 1995, 1996]. However, when mapped for several seasons, the riparian debris patterns of the Ishasha chimpanzees mimicked the patchy distribution patterns of debris that can lead to site formation in comparable sedimentary situations. This problem of equifinality [Gifford-Gonzalez, 1991] is common to any archaeological interpretation; there are often several behavioral and natural processes that can create similar patterns of material culture or debris. From an ethnoarchaeological perspective, despite their very

**TABLE I. Attributes of Ishasha Forest Trees Containing Nests Observed During 1989 and 1990\***

	Primary forest			Dry forest			Savanna					
	NN	NT	Range	Mean $\pm$ s.d.	NN	NT	Range	Mean $\pm$ s.d.	NN	NT	Range	Mean $\pm$ s.d.
DBH (cm)	89	67	11-301	54 $\pm$ 49	4	4	17-42	28 $\pm$ 12	4	1	123	123
Tree height (m)	89	67	7-40	20 $\pm$ 9	4	4	8-37	23 $\pm$ 13	4	1	26	26
D crown (m)	88	66	2-40	13 $\pm$ 11	3	3	2-5	4 $\pm$ 2	4	1	12	12

\*NN, number of nests; NT, number of nesting trees; DBH, diameter at breast height; D, diameter.



different ranging and economic patterns, both chimpanzees and human foragers use the landscape in a patchy, redundant way, leaving palimpsests of debris in their wake. In both cases, evidence of the nests/beds themselves generally rots away, leaving circumstantial evidence at best of other activities that occurred at the site (e.g., durable tools, broken animal bones). Therefore, whether or not early hominids reused nesting sites/camps must be evaluated independently of the fact that they started butchering animal carcasses with stone tools (and creating concentrations of debris that archaeologists could see).

In fact, archaeologists have yet to demonstrate that hominids actually rested or slept at any of the early archaeological sites. The stone circle site at DK (Bed I, Olduvai Gorge, Tanzania) [Leakey, 1971] has often been cited as evidence for a structure, but this interpretation has been seriously questioned from a taphonomic perspective [Potts, 1988]. Lacking the direct types of evidence for resting behavior that occur at younger sites (such as artificial shelters, hearths, or remains of bedding materials), Plio-Pleistocene archaeologists have tried to analyze the spatial distribution patterns of artifacts [Kroll & Isaac, 1984; Kroll, 1994], to look for traces of the controlled use of fire [Clark & Harris, 1985; Brain & Sillen, 1988; Brain, 1993; Bellamo, 1994], and to look for evidence of food sharing in the faunal assemblages associated with tool concentrations [Bunn & Kroll, 1986; Bunn, 1991]. However, a number of ethnoarchaeological studies of modern human foragers [Bunn et al., 1988; O'Connell and Hawkes, 1988; O'Connell et al., 1990, 1991; Marshall, 1994] have demonstrated that bone assemblages get so mixed up that skeletal evidence of food sharing is difficult to recognize even in modern human camp settings. Compounded with taphonomic biases and bioturbation, the problems of recognizing archaeological signatures of food sharing or resting sites may be insurmountable for the remote past. We may never know whether the first appearance of "stone age visiting cards" [Isaac, 1981] also marked the beginnings of home and central place foraging.

Rogers et al. [1994] have described evidence for a development of site size and complexity in the Turkana Basin that seems to be correlated with longer average transport distances for artifact raw materials. For example, the earliest sites like Hadar and the Omo have small assemblages with artifacts made from local pebbles, whereas by 1.8 ma sites like FxJj1 (KBS) (or FLK-Zinj from the same time period at Olduvai Gorge) encompass much larger areas, with denser concentrations of bones and stones and artifacts over 10 km from their original stone source. Such patterns may be evidence of the increased frequency/duration of site use or a greater diversity/intensity of activities at the sites and are suggestive of shifts in the ranging patterns of the early hominid toolmakers. Perhaps this quantitative change in Oldowan site structure is associated, behaviorally, with the evolution of early *Homo*? Certainly by 1.6 ma the anatomy of the Nariokotome hominid *Homo ergaster/H. erectus* [Walker, 1993] had evolved a modern aspect, including body size and limb proportions adapted to terrestrial life in hot, dry habitats, a relatively larger brain, and smaller teeth, suggesting a high-quality diet and likely prolonged gestation associated with more altricial infants and increased parental investment [Stanley, 1992; Walker, 1993; Aiello & Wheeler, 1995]. All these physiological traits suggest that socioeconomic cooperation, such as food sharing, would have been strongly selected for in these populations. However, discerning archaeological evidence for food sharing at well-preserved 1.6 ma open air sites such as FxJj20 or FxJj50, Lake Turkana [Bunn et al., 1980; Isaac & Isaac, 1997], is no less problematic than for the earlier East African sites.

Hearths are a social focus for later hominids, and their position in a site can influence the accumulation of camp debris patterns [Yellen, 1977; Binford, 1978]

so recognizing the use of fire at a site can help determine the activities that took place there. Sites such as FxJ20 and Chesowanja preserved anomalous patches of earth burnt in antiquity, associated with concentrations of artifacts and animal bones, and studies of their sedimentology and archaeomagnetism suggest that these fires were used and controlled by hominids [Clark & Harris, 1985; Bellomo, 1994; Bellomo, 1997]. Evidence that tools and food remains were repeatedly carried into early Pleistocene caves in South Africa such as Swartkrans [Brain, 1993] and that some of these bones were burned in the caves [Brain & Sillen, 1988] may be the best current evidence that hominids deliberately used fire in these caves and used the caves as habitual shelters.

The addition of large cutting tools (handaxes) to the hominid toolkit before 1.6 ma provides clear evidence for tool curation—carrying and reuse—but most of the primary context handaxe localities seem to be butchery sites rather than multiple activity sites or camps [Asfaw et al., 1992; Clark, 1994; Leakey, 1994]. As a result, by Acheulian times, hominid ranging, subsistence, and tool-using patterns had clearly diverged from ape-like patterns, but that does not imply that *Homo ergaster*/early *Homo erectus* had nesting/camping behavior similar to that of modern human foragers. The unique settlement patterns of Acheulian hominids are still poorly understood because so few in situ sites have been studied in detail but appear opportunistic and probably transient compared to later time periods [Klein, 1994; Leakey, 1994; Potts, 1994]. The first direct evidence for nesting/camping behavior in Africa comes from middle Pleistocene Late Acheulian sites such as Kalambo Falls [Clark, 1969], where artifacts are associated with burnt logs and other botanical remains, and sites such as Cave of Hearths [Mason, 1988], where artifacts and faunal remains are stratified with ashy cave deposits, which may or may not have been humanly induced. Middle Pleistocene sites in Eurasia seem to have similar evidence of stratified occupation debris associated with hearths, although none of the Acheulian evidence for hearths is undisputed [Clark & Harris, 1985].

Many authors now assert, however, that the first signs of what could be called modern human behavior patterns and a logistical use of camps as social foci analogous to modern human forager camps can first be found in African Middle Stone Age (MSA) sites [e.g., Clark, 1988; Deacon, 1989]. Sites such as Dire Dawa in Ethiopia [Clark et al., 1984], Mumbwa Cave in Tanzania [Mehlman, 1991], and Boomplaas and Klasies River Mouth Cave in South Africa [Deacon, 1989] preserve dense occupation deposits with a diversity of food remains, exotic raw materials, and stratified hearths that document a deliberate use of space and long-term foraging strategies calibrated to the local landscape. Such MSA sites are contemporary with the earliest evidence for anatomically modern humans in Africa [Stringer, 1995]. Comparable patterns of logistic site use do not appear until much later in Europe and the Near East [Mellars, 1996]. It may prove that the first modern home-base strategies in the human lineage are also associated with the emergence of language and symbolic representation—communication skills that can lead to the symbolic importance of home in the land-use strategies of people today.

## CONCLUSIONS AND SUMMARY

During his descriptions of the Home Base Hypothesis, Glynn Isaac often used the metaphor of archaeologists stepping back through time, from recent towards the more remote, encountering traces of human behavior that were increasingly unfamiliar [Isaac, 1984]. After this brief review of the types of evidence that exist for the evolution of human nesting/resting behavior, we can ask if the evidence of

“unfamiliar” increases gradually, as we step back through time, or if there are thresholds/steps which mark periods of rapid change/transition from one behavioral system to another. If one sees the contemporary contrast between human and chimpanzee nesting behaviors as a dichotomy, then any one of the prehistoric landmarks I have described could be treated as the turning point, the evolutionary moment that marked/caused a nesting transition from ape to human: bipedalism and the first hominid; stone tools, archaeological sites, and the first *Homo*; a developmental and behavioral transition with *Homo ergaster*/early *H. erectus*; Late Acheulian settlement patterns; or MSA and the origins of modern human communication and logistic strategies. On the other hand, if one attends to the variation in nesting behavior in living apes and humans and recognizes the difficulty of finding archaeological signatures of nesting and resting behavior, the evidence could just as easily support a relatively slow, even gradual divergence of hominid nesting patterns away from the behavior of the Last Common Ancestor. The record is too unfocused to be able to answer the fundamental question of the tempo and mode of human divergence from ape-like patterns of nesting and resting.

Let me summarize several points in relation to key questions the symposium organizers posed. What do archaeological nesting/resting places look like? What are the determinants of site location? Alas, these are fine-grained questions that are difficult or impossible to answer given the resolution of the early archaeological record for proto-human behavior.

1. The issue of whether Early Stone Age archaeological sites were actually used for nesting or resting is unresolved, because potential markers of such behavior, such as hearths, structures, or bedding, are not unambiguously recognizable in the archaeological record until Middle Stone Age times. For earlier times, “nests” are only indirectly implied shadows of inferred behavior patterns.
2. If sites were resting places, archaeological evidence in East Africa is biased to open-air localities in semiarid sedimentary environments (lake and river margins) until the Middle Pleistocene, when caves and rockshelters become repositories of layered debris and possibly hearths. South African caves begin to accumulate archaeological debris in the early Pleistocene, but there is some debate about whether they were used as shelters or merely acted as sediment traps.
3. Hypotheses about ESA site location attributes that might have attracted hominid activities include arboreal shade, predator refuge, and riparian food patches (e.g., fruits, tubers, or scavenging opportunities). However, these vegetation features are commonly associated with riparian forest in sedimentary environments as well as openings to karstic caverns and thus may just be associated with sites as a consequence of taphonomic biases in site preservation rather than any factor of hominid selection.
4. Selectivity in site location may first be evident in Late Acheulean and MSA times, but these sites may have functioned as hunting blinds or ambush stations rather than residential camps.
5. Frequency of site use cannot be easily resolved with the limitations of the sedimentary record, the nature of time-averaged accumulations in some depositional environments, and the long-term dynamics of changing landscapes. However, it is clear that even the earliest sites were palimpsests of debris which accumulated through multiple activities and at least several episodes of transport. We can study the formation of some sites as short-term spatial foci of debris accumulation. But were they nests?

Overall, substantial progress has been described at this symposium in documenting the variability in primate nesting patterns. As an archaeologist, I hope that these research initiatives can continue with particular attention to spatial dimensions of habitat variables and the temporal dynamics of spatial patterning at longer-term scales. Archaeologists would benefit if primatologists could begin to document how the behavioral variation they are able to demonstrate in nesting patterns may relate to long-term changes or fluctuations in those patterns through time, whether due to habitat shifts induced by humans, changing natural environment, or both. Finally, I think that field studies of the spatial and temporal patterns of chimpanzees and bonobo material culture manufacture, use, and discard will have much more to contribute to the field of ethoarchaeology and will help Plio-Pleistocene archaeologists develop a more effective basis for interpreting prehistoric evidence for early hominid behavior. As archaeologists pursue the questions of which hominids slept where they ate, fed where they slept, or neither, it will be useful to have the analogous range of living ape and other primate nesting and discard behaviors described, mapped, and ready for comparative analysis.

#### ACKNOWLEDGMENTS

I thank Barbara Fruth and Bill McGrew for the invitation to participate in this symposium. The Ishasha research project was done in collaboration with H.D. Steklis and the generous collaboration of members of our interdisciplinary research team, including Leonard Mubalama Kakira, Nyakabwa Mutabana, Paluku Mutakirwa Alexis, Martha Holder, Netzin Gerald, Leah Gardner, Susan Cachel, and Cheryl Fimbel, with permission from the Delegation Générale of the Institut Zairois pour la Conservation de la Nature, Ministère de l'Environnement Conservation de la Nature et Tourisme, République de Zaire. It was supported by grants from the L.S.B. Leakey Foundation, the National Geographic Society, and the Jane Goodall Foundation, and my continuing research on chimpanzee ethoarchaeology has been supported by the Wenner-Gren Foundation for Anthropological Research.

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