

Taphonomic perspectives on hominid site use and foraging strategies during Bed II times at Olduvai Gorge, Tanzania

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Abstract:

The faunal assemblages excavated by Mary Leakey in Bed II of Olduvai Gorge, Tanzania, have, like the more well-known Bed I assemblages, traditionally been interpreted as the result of hominid butchering activities in the lake margin and riverine settings of the paleo-Olduvai Basin. A reexamination of all of Leakey's Bed I sites has shown that hominids played little or no role in the formation of all but one of those faunal assemblages, a finding that prompted the reanalysis of the Bed II sites presented here. We expand upon a previous taphonomic study that provided systematic data for HWK East Levels 1–2, MNK Main, and BK. In addition to these assemblages, we provide data on HWK East Levels 3–5, FC West, TK, and SHK. Our data contradict previous interpretations of MNK Main as a hominid accumulation but uphold the contention that BK represents a primarily hominid accumulation reflecting early access to carcasses. The small and poorly preserved assemblages from FC West and TK are difficult to link un-ambiguously to either hominids or carnivores. Site MNK Main and HWK East Levels 3–5 appear to be death arenas where carcasses accumulated via natural deaths and/or serial predation. Site SHK is severely biased by selective retention and therefore little can be said of its formational history. Nevertheless, no hominid modifications were documented in this assemblage. Comparisons with other Olduvai sites indicate a more conspicuous hyena taphonomic signal during Bed II times than Bed I times, which appears to mirror the changing configuration of the large carnivore guild. These findings also beg the question of what activities were being carried out by hominids with the stone tools discarded at these sites. Although it seems clear that hominids were utilizing stone tools to carry out subsistence activities unrelated to carcass butchery, more excavation and techniques such as phytolith analysis should be employed to explore alternative explanations.

Keywords: Bone surface modifications, Breakage patterns, Cutmarks, Taphonomy, Tooth marks

Article:

Introduction

Mary Leakey's (1971) well-known claims for the existence of hominid "living floors" were based primarily on the large, well-preserved Bed I faunas from Olduvai Gorge, such as FLK 22, DK 3, and FLKNN 3. Building largely on the important taphonomic work of Bunn (e.g., 1982, 1986; Bunn and Kroll, 1986) and Potts (e.g., 1982, 1988), a recent reanalysis of all the Bed I sites from Leakey's (1971) excavations in the 1960s has demonstrated that, with the exception of FLK 22, hominids contributed little or not at all to the formation of the faunal assemblages (Dominguez-Rodrigo et al., 2007a,b; Egeland, 2007). Given that a number of the Bed II sites were also thought to be the focus of hominid subsistence and social activities, the findings from Bed I highlight the need to continuously reexamine excavated assemblages in order to provide more refined interpretations of hominid behavior during the Plio-Pleistocene. Monahan's (1996a,b) in-depth taphonomic analysis was an important step towards such an understanding of the formation of the Bed II sites from Olduvai, and we expand upon his foundation in this study.

Bed II at Olduvai Gorge is interesting for a number of reasons. In contrast to the Bed I archaeological occurrences, which are restricted to lake-margin zones, evidence for hominid activity in Bed II is preserved in a

variety of ecological settings, from lake margins to fluvial contexts well inland of the paleolake (Hay, 1976). A diversification in the stone toolkit also occurs, as Oldowan, Developed Oldowan, and Acheulean industries are all represented during Bed II times (Leakey, 1971). Bed II is contemporaneous with the appearance and spread of *Homo erectus*, which was the first hominid species to approach more or less modern body size and limb proportions (Walker and Leakey, 1993; McHenry and Coffing, 2000; Antón, 2003). Therefore, the Bed II sites can provide important information on behavioral variability during a dynamic phase of hominid bio-behavioral evolution.

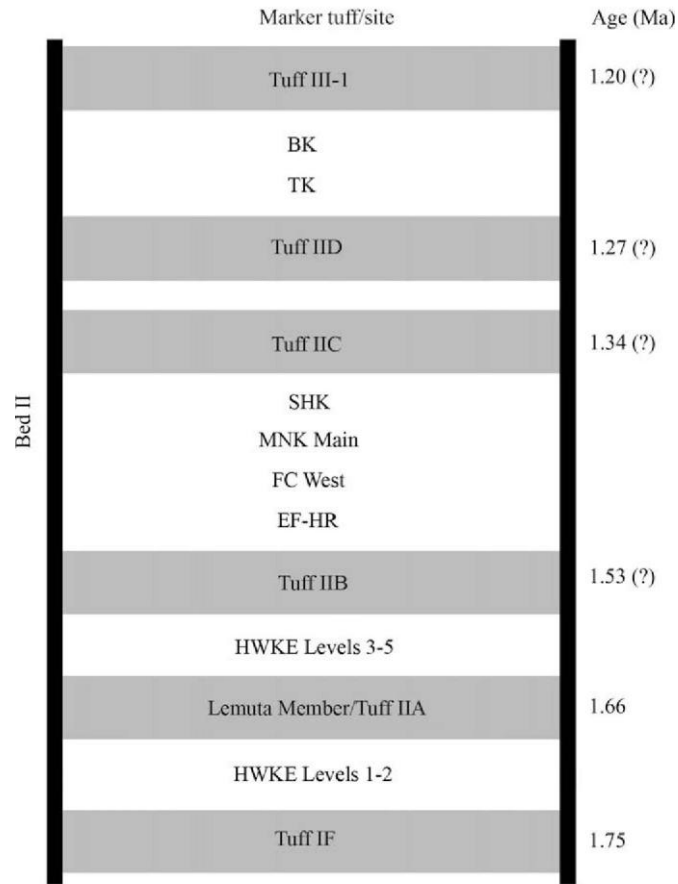


Fig. 1. Simplified composite stratigraphic sequence and radiometric dates for Bed II.

Materials and methods

In an earlier taphonomic study of the Bed II material, Monahan (1996a,b) examined the faunas from HWK East, MNK, EF-HR, FC West, TK, and BK, although systematic data were provided for only three of these assemblages (HWK East Levels 1–2, MNK Main Site, and BK). The scope of this study differs slightly from Monahan's (1996a,b) and considers the faunal assemblages from HWK East Levels 3–5, MNK Main, FC West, SHK, TK, and BK. Figure 1 summarizes the stratigraphic location and dating of each Bed II site. The chronostratigraphy of Bed II is less well understood than the underlying Bed I deposits due to the reworked nature of many of the marker tuffs. Nevertheless, radiometric dates from the bottom and top of Bed II indicate that the deposits date between 1.75 and 1.20 million years ago (Walter et al., 1991,1992; Manega, 1993). Although higher-energy fluvio-lacustrine deposits are common in Bed II, sediments laid down in lake, lake-margin, and alluvial fan environments also occur (Hay, 1976). Paleogeographic reconstructions indicate that, during lower and middle Bed II times, the Olduvai Basin contained a saline and alkaline lake of fluctuating size (Hay, 1976). By upper Bed II times, the perennial lake had disappeared to be replaced by small ponds and marshlands (Hay, 1976). Figure 2 shows the paleogeographic evolution of the basin during middle and upper Bed II times in addition to the location of each of the study sites.

The study sites

Levels 3–5 of HWK East (HWKE 3–5) are located in the lower part of middle Bed II and overlie the 2-m-thick clay deposit containing Levels 1–2. The HWKE excavation as a whole covered approximately 100 m².

Described by Leakey (1971: 96) as a horizon composed of coarse sand and gravel, Levels 3–5 contained stone artifacts and bones scattered throughout approximately 60 cm, which, based on Leakey’s (1971: 258) system, classifies the site as a “vertically dispersed deposit.” Sediments appear to have been deposited by streams flowing westward into the lake (Hay, 1976). During excavation, levels were differentiated based on a combination of find density and lithology. Therefore, the sandy gray tuff of Level 3 was denser in finds than the coarse sand and sandy tuff, respectively, of Levels 4 and 5. Leakey (1971: 97) noted that “fossil bones were rare and always in a fragmentary condition” in Levels 3–5, which contrasts with the more abundant and less fragmentary fauna from Levels 1–2 (Monahan, 1996a,b). However, lithic material, which was attributed to the Developed Oldowan, is much more common in Levels 3–5 than in Levels 1–2 (Leakey, 1971). Given the low frequency and nearly continuous distribution of faunal material throughout all three levels and the fact that several specimens lacked clear level provenience information, the assemblages were lumped together for the analysis.

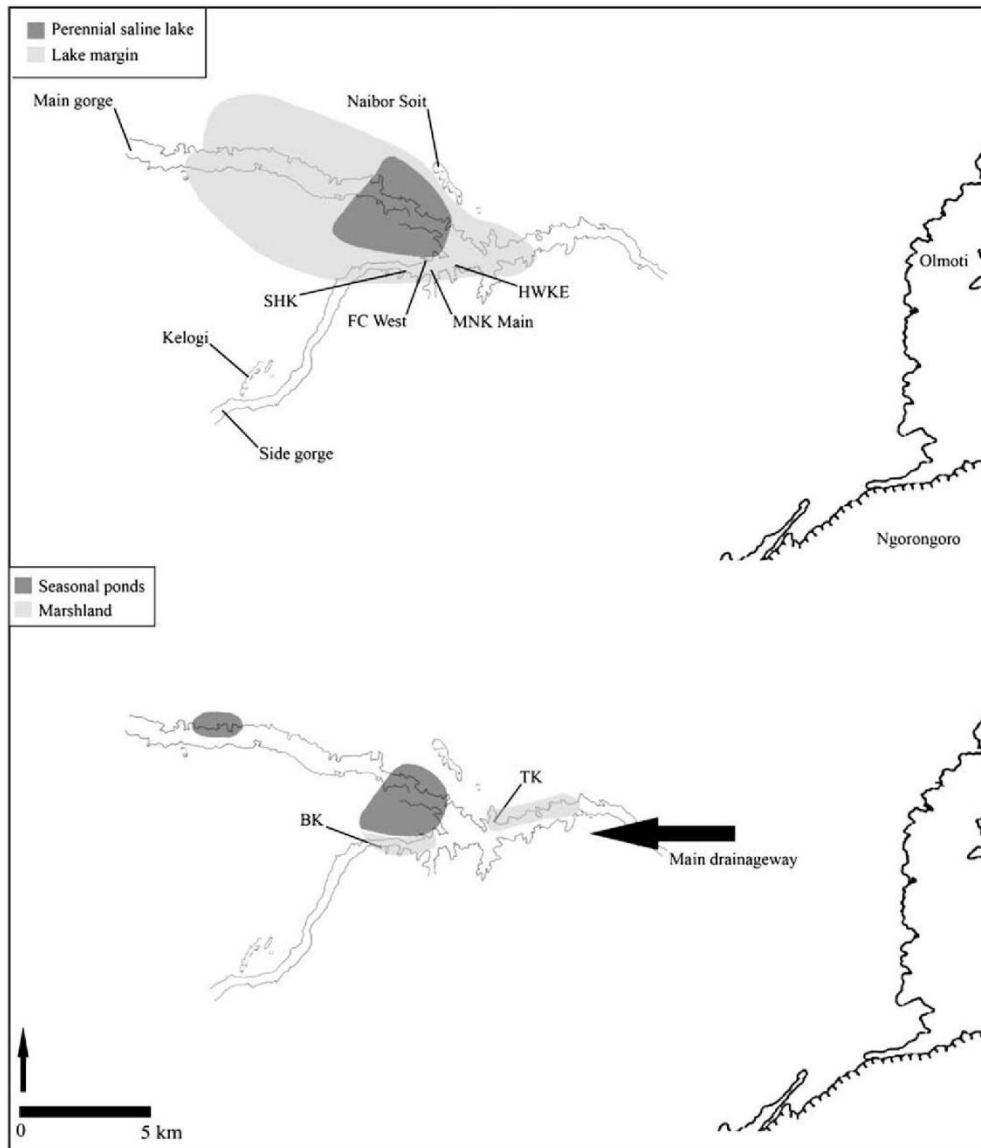


Fig. 2. Paleogeographic reconstructions of the paleo-Olduvai Basin based on Hay (1976). Top: middle Bed II (ca. 1.5 Ma); bottom upper Bed II (ca. 1.2 Ma). Base map modified from Hay (1976: Figure 18) and Peters and Blumenschine (1995: Figure 4).

The excavations at the MNK Main Site (MNK Main) were situated in middle Bed II and encompassed a little over 90 m². The approximately 1.4-m-thick deposit was divided by Leakey (1971) into six levels (1–6 from oldest to youngest), all of which were composed of a fine-grained, reworked tuff. Faunal and lithic material was distributed almost continuously throughout the entire MNK Main sequence. Given the homogeneity of the sediments and the absence of paleosols or any other evidence for stable landscape formation, levels were defined largely by density criteria. The site formed on the south/southeast margin of the Bed II paleolake (Hay,

1976). The lithic industry was characterized by [Leakey \(1971\)](#) as Developed Oldowan. Some of the fauna from the lowest occupation level was left in situ as an exhibit ([Leakey, 1971: 138](#)).

At FC West, [Leakey \(1971\)](#) uncovered an exceptionally dense collection of lithics and bones from an excavation covering approximately 21 m². Although a reworked tuff layer was documented at the locality, this analysis focuses only on the “living floor” assemblage that rested atop a 9-cm-thick, weathered light-brown clay paleosol. The lake had shrunk significantly in size by upper middle Bed II times, and FC West was located in the south-east lake-margin zone ([Hay, 1976](#)). The presence of bifaces and bi-face fragments indicates a Developed Oldowan affinity for the lithic assemblage.

The deposits at SHK are located in the lower part of upper Bed II. Fossil recovery at SHK began upon the site’s discovery in 1935, although systematic excavations were not carried out until 1953, 1955, and 1957. These excavations were conducted in two areas: the Main Site and the Annex. The brown clay that occurs at the base of the SHK sequence is overlain by an 80-cm-thick conglomerate channel deposit at the Main Site and a clay occupation floor at the Annex. Systematic screening was not carried out at the site, which severely biased the assemblage towards identifiable skeletal elements. Therefore, analyses were conducted only in hopes of identifying hominid surface modifications. Because of its biased nature, the SHK fauna is not included in every aspect of the analysis and discussion.

The TK sequence is found in upper Bed II, and [Leakey \(1971\)](#) identified a channel fill, an intermediate level, an upper tuff, and two occupation floors. Only the data from the two occupation floors, both of which occurred atop weathered paleosols, are presented in this analysis. Find density in the 87 m² excavation was relatively high. The perennial lake had disappeared by the time the TK deposits were laid down, and the site itself was located on the north side of a large east-west drainage that contained small streams and some marshland ([Hay, 1976](#)). Based on the presence of crude bifaces in the lithic assemblage, an affiliation with the Developed Oldowan was proposed by [Leakey \(1971\)](#).

Site BK is also located in upper Bed II, slightly higher in the stratigraphic sequence than TK. Although systematic excavations were carried out by Louis [Leakey \(1957\)](#), the selective retention of faunal material from the 1950s excavations is obvious; therefore, this analysis focuses only on Mary [Leakey’s \(1971\)](#) excavations from 1963, which covered an area of approximately 100 m². In her excavations, [Leakey \(1971: 199\)](#) noted the presence of both coarse sands and gravels and fine-grained silts and clays at BK. However, extensive cross-bedding prevented a reliable distinction of individual levels within the excavation trenches. Therefore, the material from all seven trenches (which varied greatly in depth) was necessarily lumped together in the analysis. In upper Bed II times, the site was located just south of seasonal ponds ([Hay, 1976](#)), although most of the material derives from the channel fill of a small stream that cut through the middle of the site.

Zooarchaeological and taphonomic variables

Four zooarchaeological measures of abundance were employed in this study: number of identified specimens (NISP), minimum number of elements (MNE), minimum number of animal units (MAU), and minimum number of individuals (MNI) (see [Lyman, 1994](#)). The maximum length of each specimen was measured to the nearest millimeter with digital calipers. The majority of analyses were based on a maximally inclusive level of identification by the Body-Size class scheme of [Brain \(1974, 1981\)](#) and [Bunn \(1982\)](#) (see also [Lyman, 1979](#)). Data were further divided into small (Size Class 1 and 2), medium (Size Class 3), and large (Size Class 4 and larger) groupings. The MNE estimates took into account the size, side, and ontogenetic age of each skeletally identifiable specimen, and the resulting counts were derived using a manual overlap approach ([Bunn, 1982, 1986; Bunn and Kroll, 1986](#)). All specimens identified to a specific skeletal element were placed together on a table and visually inspected for potential overlap. Following [Bunn \(1982, 1986; Bunn and Kroll, 1986\)](#) and others (e.g., [Todd and Rapson, 1988; Marean and Spencer, 1991; Morlan, 1994; Marean, 1998; Pickering et al., 2003; Assefa, 2006](#)), all limb bone (here ungulate humeri, femora, radii, tibiae, and metapodials; [Pickering et al., 2003](#)) MNEs are based on the systematic inclusion of shaft specimens.

Table 1
Minimum number of large mammal individuals (MNI) represented at the Bed II sites

Taxon	HWKE 3–5	MNK Main	FC West	SHK	TK LF	TK UF	BK
Alcelaphini							
<i>Connochaetes</i> sp.	—	2	—	3	—	—	—
<i>Damaliscus niro</i>	—	—	—	1	—	—	—
<i>Parmularius altidens</i>	2	2	—	—	—	—	—
<i>P. angusticornis</i>	—	—	—	3	—	—	—
<i>Megalotragus kattwinkeli</i>	—	1	—	2	—	—	—
Size 2/3a Alcelaphini	—	1	—	—	—	—	19
Size 3 Alcelaphini	—	—	2	—	—	—	—
Size 3a Alcelaphini	2	—	—	1	2	4	—
Size 3b Alcelaphini	1	—	—	—	—	1	—
Size 3b/4 Alcelaphini	—	—	—	—	—	—	10
Size 4 Alcelaphini	—	—	1	—	—	—	—
Antilopini							
<i>Antidorcas recki</i>	—	—	—	1	—	—	—
<i>Gazella</i> sp.	—	—	—	1	—	—	—
Size 1 Antilopini	4	1	—	—	—	—	2
Bovini							
<i>Pelorovis oldowayensis</i>	1	1	—	1	—	1	3
<i>Syncerus</i> sp.	—	—	—	1	—	—	—
Size 4 Bovini	—	1	—	—	—	—	4
Hippotragini							
<i>Hippotragus</i> sp.	1	—	—	—	—	—	—
<i>H. gigas</i>	—	—	—	1	—	1	2
<i>H. niger</i>	—	1	—	—	—	—	—
Reduncini							
<i>Kobus</i> sp.	—	—	—	1	—	—	—
<i>K. aff. kob</i>	—	1	—	—	—	—	—
Size 3 Reduncini	—	1	—	—	—	—	—
Tragelaphini							
<i>Tragelaphus strepsiceros</i>	—	2	—	1	—	—	—
Size 3b Tragelaphini	—	—	—	—	—	—	1
Size 4 Tragelaphini	—	—	—	—	—	—	1
Suidae							
Size 3 Suidae	—	—	—	—	1	—	—
Rhinocerotidae							
Rhinocerotidae indet.	—	—	—	—	—	1	1
Hippopotamidae							
<i>Hippopotamus</i> sp.	2	—	—	—	1	1	—
<i>H. gorgops</i>	—	1	1	—	—	—	1
Giraffidae							
<i>Giraffa jumae</i>	1	1	—	1	—	—	—
<i>Libytherium</i> sp.	—	—	—	—	—	—	1
<i>Sivatherium</i> sp.	—	—	—	—	—	—	2
Giraffidae indet.	—	—	1	—	—	1	—
Total	14	16	5	18	4	10	47

Skeletal element frequencies were further quantified using the Shannon evenness index as proposed by Faith and Gordon (2007). This value, which scales from 0.0 (lowest evenness) to 1.0 (highest evenness), is meant to measure the evenness of the distribution of skeletal elements in relation to a complete carcass and can be calculated using the formula:

$$-\left(\sum p_i \times \ln p_i\right) / \ln S$$

where p_i is the proportional representation of a particular skeletal element (measured by MAU) and S is the number of element types. This statistic provides a less subjective assessment of skeletal element frequencies and thus facilitates intersite comparisons. Element representation (measured by %MAU) was also examined in relation to a meat utility index (Metcalf and Jones, 1988), a marrow utility index (Blumenschine and Madrigal, 1993), and a combined food utility index (Metcalf and Jones, 1988) through regression and Spearman's rank-order correlation. Because one goal of evenness and economic analyses is to understand transport decisions (e.g., Binford, 1978; Faith and Gordon, 2007), it is important to control for density-mediated destructive processes such as carnivore ravaging, which tend to delete or at least depress the frequency of less dense axial bones and limb bone epiphyses (e.g., Brain, 1967, 1969; Marean and Spencer, 1991; Marean et al., 1992; Capaldo, 1998; Pickering et al., 2003). The effect of attrition on the composition of the bone assemblages was investigated through regression and Spearman's rank-order correlation between Lam et al.'s (1999) bulk mineral density (BMD) values for wilde-beest and %MAU. For limb bones, internal shape-corrected data were used. These data are more accurate because they take into account the empty medullary cavities of limb bones in measures of cross-sectional area. Given the evidence for density-mediated destruction (see results below), the

evenness and economic analyses focused on “high survival” bones [i.e., elements whose original representation can be reconstructed even in the wake of attrition (Marean et al., 2000; Marean and Cleghorn, 2003; Cleghorn and Marean, 2004)]. This “high survival” set includes the cranium, mandible, and limb bones (when shaft fragments are included in MNE estimates), while the “low survival” set is made up of axial elements and small compact bones [which, although relatively dense, are often consumed completely by carnivores (Marean et al., 1992; Capaldo, 1998; Pickering, 2001a,b)].

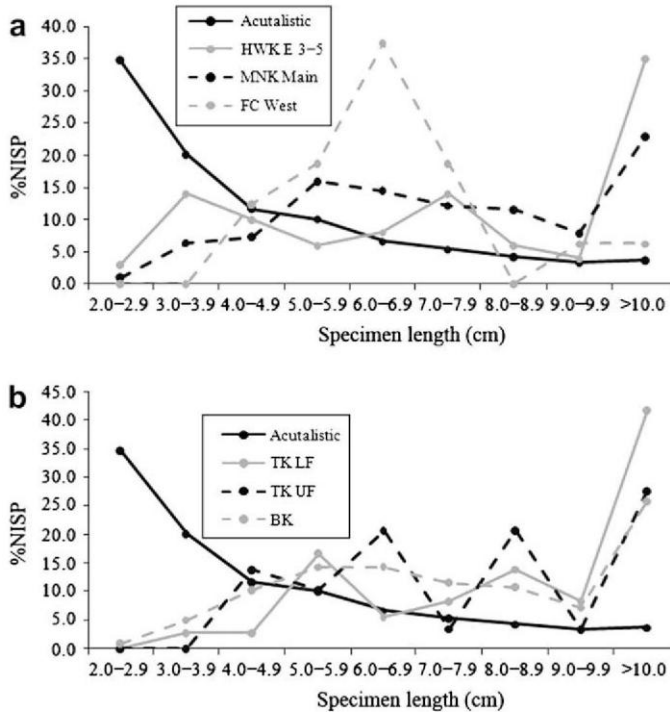


Fig. 3. Distribution of limb bone fragment sizes from (a) HWKE 3-5, MNK Main, FC West and (b) TK LF, TK UF, BK. All fossil data are compared to an actualistic control assemblage from Pickering and Egeland (2006).

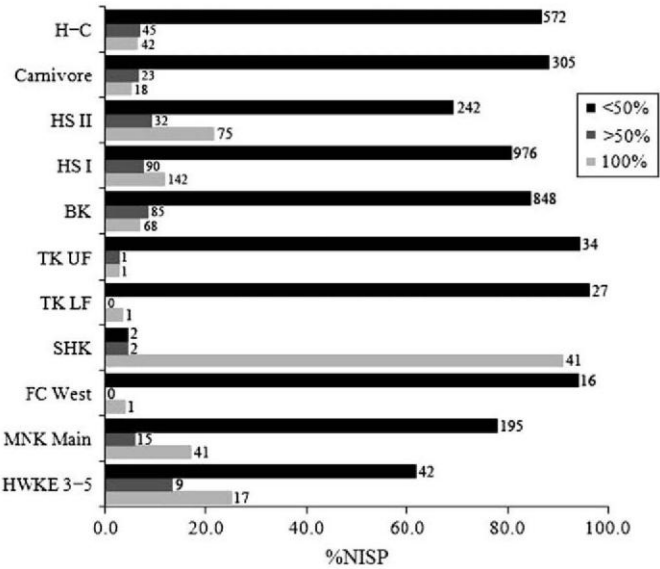


Fig. 4. Percentage of Bunn's (1982) circumference types from the Bed II sites and several actualistic controls. Note: fossil data include only green-broken specimens. Abbreviations: HS-C = hammerstone-to-carnivore; carnivore = carnivore-only; HS = hammerstone-only, HS-C, HS I, and carnivore data are from Marean et al. (2004); HS II data are from Pickering and Egeland (2006).



Fig. 5. Examples of heavily rolled specimens from BK. Scale bar = 1 cm.

A systematic search for bone surface modifications was also carried out on the Bed II faunas. All fragments were examined with the aid of 10× magnification and a strong oblique light source (Bunn, 1981; Blumenschine et al., 1996). Cutmarks, percussion marks, and carnivore tooth marks were identified following criteria outlined in Blumenschine et al. (1996, and references therein). Surface marks were tallied by skeletal element (e.g., cranium, humerus) or skeletal region (e.g., vertebrae, upper limb bones). For limb bones in particular, surface marks were also quantified by bone segment and bone section. Bone segment attributions were modified from Blumenschine's (1988: 467) epiphysis/near-epiphysis/midshaft system, where epiphyseal fragments preserve all or part of an articular surface, near-epiphyseal fragments lack an articular surface but preserve cancellous bone indicating proximity to an articular surface, and midshaft fragments lack an articular surface and have little or

no cancellous bone. Although this system can be successful at determining the order of carnivore access to carcasses (Blumenschine, 1988, 1995; Capaldo, 1997; Selvaggio, 1998), it can be insensitive to the actual location of a particular mark. For example, an epiphyseal specimen with a portion of attached shaft may have surface marks on the articular surface or at any location along the shaft. Therefore, following Dominguez-Rodrigo (1997) and Bunn (2001), surface marks on limb bones were also recorded by bone section. This system, which tracks the actual location of a particular surface mark, divides limb bones into three major anatomical sections: (1) proximal or distal epiphysis; (2) proximal or distal shaft; and (3) midshaft. However, surface mark frequencies quantified by bone section can be affected by differential fragmentation, which must be kept in mind during analysis.

Other surface modifications, including rounding (Shipman, 1981), sediment abrasion (Behrensmeyer et al., 1986; Fiorillo, 1989; Oliver, 1989), subaerial weathering (Behrensmeyer, 1978), and gastric etching (Lyman, 1994), were also recorded. In order to maximize comparability between the Bed II collections and the growing body of actualistic assemblages, it is important to control for cortical-surface degradation and diagenetic breakage. Therefore, in all comparisons with modern control assemblages, only those fossil specimens with good cortical preservation and green breakage were considered. In assessments of cortical preservation, a subjective score of “poor” or “good” was assigned to each specimen. This is meant to reflect the chances that current cortical surfaces continue to preserve prehistoric surface modifications (see also Pickering et al., 2007, 2008).

Table 2
Number of identified specimens (NISP) by skeletal element for small (Size Classes 1 and 2), medium (Size Class 3), and large (Size Class 4 and larger carcasses) for the Bed II sites

Element	HWKE 3-5			MNK Main			FC West			SHK			TK LF			TK UF		BK		
	S	M	L	S	M	L	S	M	L	S	M	L	S	M	L	M	L	S	M	L
Cranium	7	29	—	11	71	19	—	2	3	6	60	—	—	—	—	14	2	26	63	53
Mandible	15	26	—	6	67	15	—	2	2	5	42	20	—	4	—	8	1	32	84	33
Vertebrae	6	7	13	7	21	23	—	2	—	1	5	4	—	1	3	—	2	15	46	21
Innominate	1	2	—	1	2	7	—	1	1	—	1	—	—	—	1	3	1	6	21	6
Ribs	—	5	6	5	19	18	—	1	1	—	—	—	—	—	—	1	3	18	71	95
Scapula	5	1	1	5	19	3	—	1	1	—	1	—	—	—	1	2	1	3	20	10
Humerus	1	4	3	6	46	12	—	3	—	—	8	—	1	1	—	3	1	29	82	24
Radius	2	3	—	4	38	10	—	1	—	—	12	—	—	3	2	3	1	18	58	28
Ulna	—	—	—	—	2	2	—	—	—	—	2	—	—	—	—	—	—	4	12	4
Carpals	3	6	—	2	17	5	—	1	1	2	17	1	—	—	—	—	2	3	10	4
Metacarpal	3	6	—	3	30	10	—	3	—	—	20	—	—	1	—	—	—	18	35	8
Femur	1	6	—	10	33	34	—	1	1	—	—	—	1	—	1	4	1	38	61	27
Patella	2	2	—	2	6	2	—	—	—	2	—	—	—	1	—	—	—	3	2	2
Tibia	2	14	2	6	58	13	—	1	—	—	2	—	—	4	3	4	—	38	100	32
Tarsals	1	6	—	3	19	2	1	1	1	2	18	1	—	1	—	—	1	12	20	18
Metatarsal	1	5	—	6	27	3	—	2	2	—	—	—	—	2	—	1	—	23	53	11
Phalanges	5	3	—	11	11	4	—	—	1	1	31	—	—	—	—	—	—	8	12	7
Sesamoids	2	5	—	5	3	2	—	—	1	—	16	2	—	—	—	—	—	3	17	2
Total	57	130	25	93	489	184	1	22	15	19	235	28	2	18	11	43	16	297	767	385

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses; cranium and mandible counts include isolated teeth and tooth fragments.

Table 3
Minimum number of elements (MNE) by skeletal element for small (Size Classes 1 and 2), medium (Size Class 3), and large (Size Class 4 and larger) carcasses for the Bed II sites

Element	HWKE 3-5			MNK Main			FC West			SHK			TK LF			TK UF		BK		
	S	M	L	S	M	L	S	M	L	S	M	L	S	M	L	M	L	S	M	L
Cranium	3	7	—	2	6	7	—	1	2	2	12	4	—	—	—	5	2	8	13	11
Mandible	4	6	—	2	9	6	—	1	2	2	7	2	—	2	—	5	1	9	21	9
Vertebrae	5	7	6	7	16	14	—	2	—	1	5	4	—	1	3	—	2	9	29	16
Innominate	1	1	—	1	2	7	—	1	1	—	1	—	—	—	1	3	1	6	11	3
Ribs	—	3	3	4	15	3	—	1	1	—	—	—	—	—	—	1	3	4	13	20
Scapula	3	1	1	4	15	18	—	1	1	—	1	—	—	—	1	1	1	1	11	5
Humerus	1	3	2	2	12	2	—	3	—	—	7	—	1	1	—	3	1	21	35	10
Radius	1	2	—	2	12	4	—	1	—	—	10	—	—	2	1	2	1	13	28	16
Ulna	—	—	—	—	2	2	—	—	—	—	2	—	—	—	—	—	—	4	7	3
Carpals	3	6	—	2	17	5	—	1	1	2	17	1	—	—	—	—	2	3	10	4
Metacarpal	2	4	—	2	8	2	—	1	—	—	13	—	—	1	—	—	—	8	13	6
Femur	2	1	—	4	9	6	—	1	1	—	—	—	1	—	1	4	1	22	23	11
Patella	2	2	—	2	6	2	—	—	—	2	—	—	—	1	—	—	—	3	2	2
Tibia	2	6	1	3	13	5	—	1	—	—	2	—	—	2	2	3	—	18	34	12
Tarsals	1	6	—	3	19	2	1	1	1	2	18	1	—	1	—	—	1	10	18	19
Metatarsal	2	4	—	5	10	3	—	2	1	—	—	—	—	1	—	1	—	12	13	3
Phalanges	5	3	—	8	11	4	—	—	1	1	2	1	—	—	—	—	—	8	9	4
Sesamoids	2	5	—	5	3	2	—	—	1	—	16	2	—	—	—	—	—	3	16	2
Total	39	67	13	58	185	94	1	18	13	12	113	15	2	12	9	28	16	162	306	156

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses.

In order to help identify the type(s) of carnivores responsible for modifying carcasses at the Bed II sites, the length and breadth maxima of tooth pits occurring on limb bone diaphyses were measured with digital calipers on polyvinylsiloxane molds to the nearest 0.01 mm (see also Andrews and Fernández-Jalvo, 1997; Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Pickering et al., 2004a). Only those tooth pits with clearly delineated borders were measured.

When possible, specimens were coded as green- or dry-broken. Green breakage (or “nutritive phase” breakage; Blumenschine, 1986; Capaldo, 1995,1997) is usually the result of nutrient extraction by biological agents and was identified on limb bones by the presence of smooth release surfaces, obliquely oriented (in relation to the long axis of the specimen) fracture outlines, and obtuse or acute fracture angles. Other elements, such as ribs, pelves, and scapulae, will also exhibit some or all of these features when green-broken. Dry breakage was recognized by a combination of straight or stepped fracture outlines, ragged release surfaces, and 90, fracture angles (see Morlan, 1984; Johnson, 1985; Villa and Mathieu, 1991).

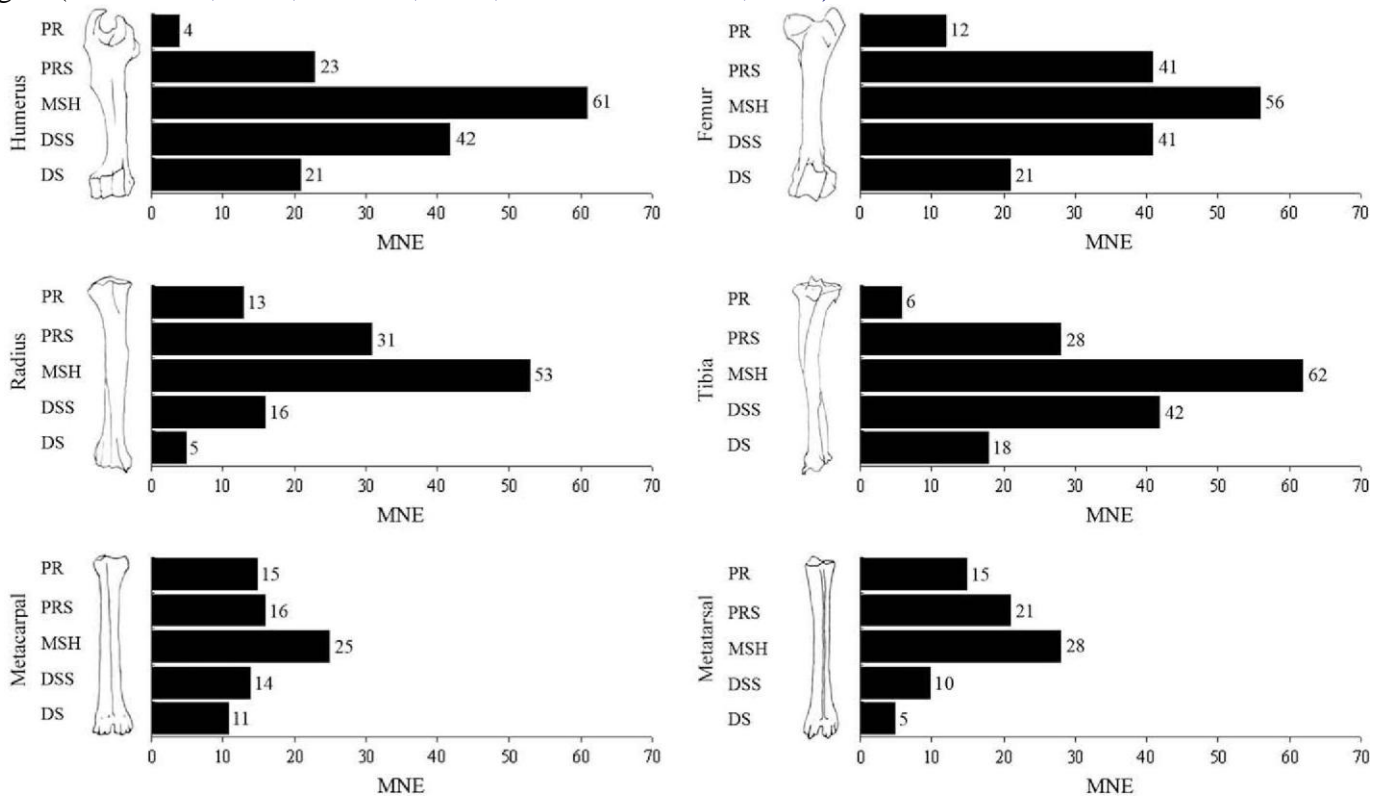


Fig. 6. Limb-bone MNEs (all size classes combined) by portion for BK. Abbreviations: PR = proximal; PRS = proximal shaft; MSH = midshaft; DSS = distal shaft; DS = distal.

Green bone breakage was analyzed using three complementary procedures, all of which helped to distinguish the dynamic loading that is characteristic of hammerstone-wielding hominids from the static loading employed by large carnivores (Johnson, 1985). First, the shape of all complete notches (i.e., those notches with two inflection points and nonoverlapping flake scars) was quantified using the ratios developed by Capaldo and Blumenschine (1994), which show that percussion notches tend to be shallower and broader in cortical view than carnivore-created notches (see also Bunn, 1981,1989; Blumenschine and Selvaggio, 1991). In addition, all notches were categorized to type [modified from Capaldo and Blumenschine (1994)], as hominid- and carnivore-broken assemblages result in different frequencies of notch types (Dominguez-Rodrigo et al., 2007a,b; Egeland, 2007). Second, all limb bone fragments were characterized according to Bunn’s (1982) circumference system as preserving <50%, >50%, or 100% of the original diaphyseal circumference. In addition to providing clues as to the breakage agent, the relative frequencies of circumference types can measure the severity of bias in a faunal assemblage. Marean et al. (2004) showed that assemblages biased by selective retention are deficient in specimens with <50% of the diaphyseal circumference preserved. Finally, because it has been shown that carnivore-induced fragmentation tends towards right-angled breaks while hammerstone fragmentation creates higher frequencies of obtuse and acute breaks (Pickering et al., 2005;

Alcántara Garcia et al., 2006), the angle of all longitudinal and oblique fracture planes greater than 4 cm in length was measured to the nearest degree using a goniometer. In calculating fragmentation ratios (NISP-to-MNE and epiphysis-to-shaft ratios), the number of dry- and recently broken specimens was divided by two (because at least two fragments will result when a single specimen is broken) and the resulting value added to the number of green-broken specimens. Fragmentation ratios were used to identify the bone-modifying agent in addition to providing estimates of competition. A more detailed description of the zooarchaeological and taphonomic methods summarized here can be found in Egeland (2007: 36–64).

Table 4
Limb bone MNEs based on epiphyses only and epiphyses and shaft fragments combined for the Bed II sites

Element	HWKE 3-5			MNK Main			FC West	TK LF	TK UF	BK		
	S	M	L	S	M	L	M	M	M	S	M	L
Humerus												
Epiphyses only	0	1	1	0	5	2	1	0	0	6	12	3
Epiphyses + shafts	1	3	2	2	12	2	2	1	3	18	34	9
Radius												
Epiphyses only	1	1	0	1	5	2	1	0	1	4	6	3
Epiphyses + shafts	1	2	0	2	12	4	1	2	2	11	27	15
Metacarpal												
Epiphyses only	2	4	0	2	8	1	0	1	0	4	6	5
Epiphyses + shafts	2	4	0	2	8	2	1	1	0	8	13	4
Femur												
Epiphyses only	1	1	0	1	2	1	0	0	2	3	7	4
Epiphyses + shafts	2	1	0	4	9	6	1	0	2	22	23	11
Tibia												
Epiphyses only	2	2	0	2	3	3	0	1	0	3	15	1
Epiphyses + shafts	2	6	1	3	13	5	1	2	3	18	33	11
Metatarsal												
Epiphyses only	2	3	0	5	10	3	1	1	0	7	7	1
Epiphyses + shafts	2	4	0	5	10	3	2	1	1	12	13	3

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses.

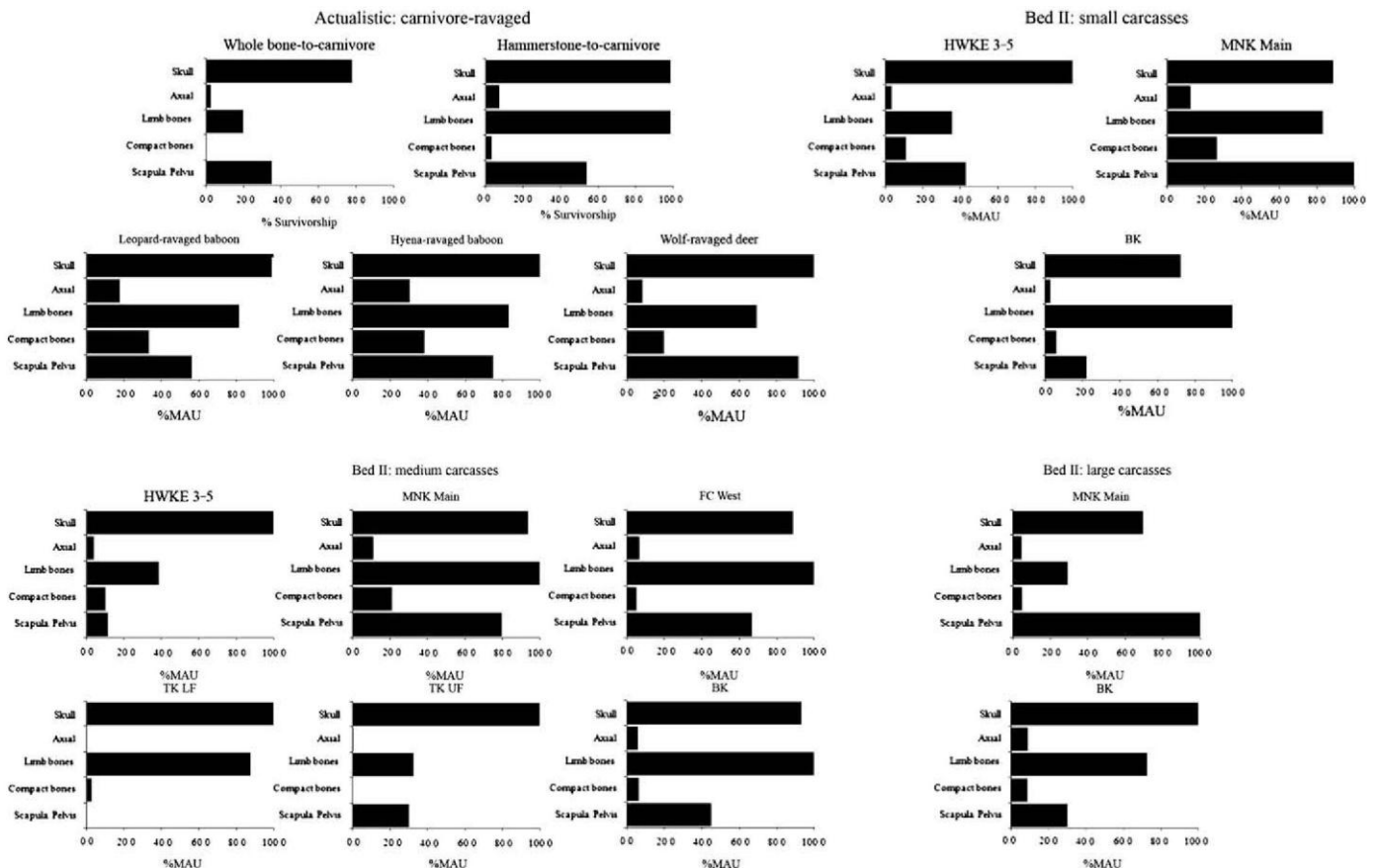


Fig. 7. Body-part representation by skeletal region for the Bed II sites and several actualistic controls. Whole bone-to-carnivore and hammerstone-to-carnivore data are from Capaldo (1998); leopard- and hyena-ravaged baboon data are from Pickering (2001a,b); wolf-ravaged deer data are from Snyder (1988).

Table 5
Regression and Spearman's statistics for the relationship between %MAU and density for the Bed II sites

	HWKE 3–5			MNK Main			FC West		TK LF		TK UF		BK		
	S	M	L	S	M	L	M	L	M	L	M	L	S	M	L
Regression															
r^2	0.26	0.36	0.10	0.45	0.65	0.33	0.62	0.53	0.42	0.30	0.53	0.33	0.77	0.72	0.67
F	6.93	11.44	0.22	4.95	14.78	2.48	12.55	7.62	4.33	1.96	7.95	2.49	28.74	20.97	16.22
p	<0.05	<0.05	0.64	<0.05	<0.05	0.13	<0.05	<0.05	0.05	0.18	<0.05	0.13	<0.05	<0.05	<0.05
Spearman's															
r_s	0.42	0.37	−0.02	0.44	0.59	0.46	0.56	0.57	0.29	0.21	0.42	0.14	0.66	0.61	0.53
p	<0.05	0.09	0.91	<0.05	<0.05	<0.05	<0.05	<0.05	0.19	0.35	<0.05	0.55	<0.05	<0.05	<0.05

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses. For limb bones, both the midshaft density value and the higher of the two epiphyseal values were used; for all other elements, the highest density value was used. Significant values are in bold.

Results

General assemblage composition

A total of 4,078 specimens (207 from HWKE 3–5, 814 from MNK Main, 95 from FC West, 268 from SHK, 215 from TK, and 2,479 from BK) were analyzed in this analysis. Table 1 provides MNI estimates for each of the assemblages (excluding primates, carnivores, and equids, the last of which were not available for study), which range from a minimum of four large mammalian individuals at TK LF to a maximum of 47 at BK. The FC West and TK assemblages are composed exclusively of medium- and large-sized animals, while the other assemblages show a variety of small, medium and large animals. With a few exceptions (hippopotamids at TK UF; giraffids and suids at BK), the non-bovid taxa are represented only by isolated skull material (mostly teeth), which contrasts with the more complete representation of bovids in the assemblages.

Table 6
Regression and Spearman's statistics for the relationship between %MAU and several measures of economic utility for the Bed II sites

	HWKE 3–5			MNK Main			FC West		TK LF		TK UF		BK		
	S	M	L	S	M	L	M	L	M	L	M	L	S	M	L
Meat index															
Regression															
r^2	0.26	0.36	0.10	0.45	0.65	0.33	0.04	0.01	0.19	0.09	0.53	0.33	0.77	0.72	0.67
F	6.93	11.44	0.22	4.95	14.78	2.48	0.23	0.01	1.41	0.62	7.95	2.49	28.74	20.97	16.22
p	<0.05	<0.05	0.64	<0.05	<0.05	0.13	0.65	0.92	0.28	0.46	<0.05	0.13	<0.05	<0.05	<0.05
Spearman's															
r_s	0.42	0.37	−0.02	0.44	0.59	0.46	−0.08	0.29	0.29	0.21	0.42	0.14	0.66	0.61	0.53
p	<0.05	>0.05	>0.10	<0.05	<0.05	<0.05	>0.10	>0.10	>0.10	>0.10	<0.05	>0.10	<0.05	<0.05	<0.05
Marrow index															
Regression															
r^2	0.03	0.14	0.06	0.01	0.33	0.34	0.17	0.02	0.45	0.87	0.86	0.01	0.80	0.30	0.49
F	0.14	0.67	0.28	0.02	1.94	2.01	0.12	0.06	1.02	27.16	11.00	0.03	7.14	0.39	1.24
p	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	0.75	>0.10	>0.10	<0.05	<0.05	>0.10	<0.05	>0.10	>0.10
Spearman's															
r_s	0.00	0.28	—	0.65	0.32	0.75	−0.37	—	0.28	0.86	0.81	—	0.71	0.58	0.77
p	>0.10	>0.10	—	>0.10	>0.10	>0.05	>0.10	—	>0.10	>0.05	>0.05	—	>0.05	>0.05	>0.05
Food index															
Regression															
r^2	0.06	0.23	0.03	0.15	0.01	0.04	0.02	0.08	0.06	0.40	0.01	0.07	0.56	0.08	0.01
F	0.38	1.82	0.17	1.06	0.03	0.25	0.12	0.54	0.37	4.00	0.07	0.45	7.74	0.49	0.06
p	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.05	>0.10	>0.10	<0.05	>0.10	>0.10
Spearman's															
r_s	−0.11	0.45	0.34	0.47	0.31	−0.12	−0.03	−0.14	−0.03	0.63	0.05	−0.21	0.71	0.30	0.02
p	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.05	>0.10	>0.10	>0.05	>0.10	>0.10

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses. All economic values are standardized to 100%, and only "high survival" elements were used in calculations. The marrow index with 93% marrow fat content was used (see Blumenschine and Madrigal, 1993). Significant values are in bold.

Site integrity

All of the Bed II sites are deficient in specimens less than 4 cm in size (Fig. 3). Limb bone fragments preserving <50% circumference dominate all the Bed II assemblages except SHK (Fig. 4), indicating that preferential discard of taxonomically non-diagnostic material is not a major source of bias. Polishing damage indicative of long-distance water transport is present on a total of three (1.4% of total NISP) specimens from HWKE 3–5, eight (1.0%) from MNK Main, six (6.3%) from FC West, two (0.7%) from SHK, three (3.8%) from TK LF, and seventy-four (3.0%) from BK. Lateral variation in the degree of polishing damage is evident at BK, as highly rounded pieces are more common in Excavation Unit 7 (Fig. 5; see also Monahan, 1996b: 87). Extensive efforts resulted in no bone fragment refits from HWKE 3–5, FC West, SHK, or TK, while no new refitting sets were added to those previously documented by Monahan (1996b: 221–222) from MNK Main and BK.

Skeletal element frequencies

Tables 2 and 3 summarize, respectively, the NISP data and MNE estimates by skeletal element and carcass size for each of the Bed II sites. Figure 6 presents limb bone MNEs by portion (following Marean and Spencer, 1991) for BK, which is the largest data set, and Table 4 provides limb bone MNEs based on epiphyses only, and on epiphyses and shaft fragments combined, for all the Bed II assemblages (except the selectively collected SHK assemblage). In every case, shaft-inclusive MNE estimates are equal to or greater than those derived using epiphyses only. Tibiae appear to be most affected by shaft fragment inclusion, followed by the upper limb bones, radii and, finally, metapodials. Overall, the skeletal part data show assemblages dominated by skulls and limbs, with axial elements and compact bones very rare, and scapulae and pelvis variably represented. This general pattern compares favorably to actualistic samples where carnivores ravaged carcasses (Fig. 7). Linear regression and Spearman's rank-order statistics show that, for most of the assemblages, a strong and significant relationship exists between density and skeletal part representation (Table 5).

Table 7
Shannon evenness index for the Bed II sites and several modern samples

Bed II	HWKE 3-5		MNK Main			FC West	TK LF	TK UF	BK		
	S	M	S	M	L	M	M	M	S	M	L
n	17	33	19	79	34	11	11	23	101	180	78
Evenness	0.916	0.882	0.899	0.994	0.770	0.952	0.875	0.980	0.973	0.973	0.941
Modern	Hadza-transported						Hadza-blind				
	S		M		L	S		M			
n	257		205		74	23		13			
Evenness	0.995		0.998		0.955	0.919		0.770			

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses. Evenness values calculated using only "high survival" elements. Only assemblages with MNE sample sizes above nine are presented. Hadza-transported data are from Monahan (1998); Hadza-blind data are from Lupo (2001).

The representation of high survival elements is significantly correlated with meat utility for small- and medium-sized carcasses at HWKE 3-5, MNK Main, and BK, for medium-sized carcasses at TK UF, and for large-sized carcasses at BK (Table 6). Overall food utility is significantly correlated with high survival element representation only for small-sized carcasses at BK. Table 7 provides evenness values for the Bed II assemblages and two ethnoarchaeological samples from the Hadza of Tanzania. Simulation experiments indicate that at MNE sample sizes of 50 and 100, evenness values below 0.925 and 0.961, respectively, reflect incomplete carcass representation (Faith and Gordon, 2007: 876). It therefore appears that more-or-less complete carcasses are represented at BK and among medium-sized animals at MNK Main. Although FC West and TK UF are also suggestive of complete carcass deposition, small sample sizes preclude definitive interpretations.

Table 8
Tooth mark frequencies by skeletal element and carcass size for the Bed II sites

Element	HWKE 3-5		MNK Main			SHK		BK		
	S	M	S	M	L	S	M	S	M	L
Mandible	1/3 (33.3)	1/1 (100.0)	0/1 (0.0)	6/10 (60.0)	1/8 (12.5)	0/5 (0)	0/0 (0)	0/16 (0.0)	1/41 (2.4)	1/20 (5.0)
Vertebrae	1/6 (16.6)	4/7 (57.1)	2/7 (28.5)	6/21 (28.5)	2/8 (25.0)	0/1 (0)	0/5 (0)	1/15 (6.7)	8/46 (17.4)	2/21 (9.5)
Innominate	1/1 (100.0)	2/2 (100.0)	0/1 (0.0)	1/2 (50.0)	2/7 (28.5)	0/0 (0)	1/1 (100)	1/6 (16.7)	3/21 (14.3)	0/6 (0.0)
Ribs	0/0 (0.0)	1/5 (20.0)	4/5 (80.0)	5/15 (66.6)	1/18 (5.5)	0/0 (0)	0/0 (0)	0/18 (0.0)	5/71 (7.0)	2/95 (2.1)
Scapula	1/5 (20.0)	0/1 (0.0)	2/4 (50.0)	9/19 (47.3)	0/3 (0.0)	0/0 (0)	1/1 (100)	0/3 (0.0)	0/20 (0.0)	1/10 (1.0)
Humerus	1/1 (100.0)	3/4 (75.0)	3/5 (60.0)	28/46 (58.3)	8/9 (88.8)	0/0 (0)	4/8 (50)	5/29 (17.2)	8/82 (9.8)	2/24 (8.3)
Radius	0/1 (0.0)	1/3 (33.3)	2/4 (50.0)	16/28 (57.1)	3/5 (60.0)	0/0 (0)	5/12 (41.6)	3/18 (16.7)	9/58 (15.5)	5/28 (17.9)
Ulna	0/0 (0)	0/0 (0)	0/0 (0)	0/2 (0)	0/2 (0)	0/0 (0)	1/2 (50)	0/5 (0.0)	3/12 (25.0)	2/4 (50.0)
Carpals	0/3 (0)	0/6 (0)	0/2 (0)	0/17 (0)	0/5 (0)	0/2 (0)	0/17 (0)	0/3 (0.0)	0/10 (0.0)	0/4 (0.0)
Metacarpal	1/3 (33.3)	4/6 (66.6)	0/3 (0.0)	8/30 (26.6)	1/2 (50.0)	0/0 (0)	5/20 (25)	2/18 (11.1)	2/35 (5.7)	0/8 (0.0)
Femur	0/1 (0.0)	2/6 (33.3)	4/7 (57.1)	11/27 (40.7)	9/17 (52.9)	0/0 (0)	0/0 (0)	4/38 (10.5)	6/61 (9.8)	1/27 (3.7)
Patella	0/2 (0)	0/2 (0)	0/2 (0)	0/6 (0)	0/2 (0)	0/2 (0)	0/0 (0)	0/3 (0.0)	0/2 (0.0)	0/2 (0.0)
Tibia	0/2 (0.0)	2/14 (14.2)	3/5 (60.0)	24/49 (48.9)	6/13 (46.1)	0/0 (0)	2/2 (100)	4/38 (10.5)	19/100 (19.0)	2/32 (6.3)
Tarsals	0/1 (0)	0/6 (0)	0/3 (0)	1/19 (5.2)	0/2 (0)	0/2 (0)	0/18 (0)	0/12 (0.0)	0/18 (0.0)	0/20 (0.0)
Metatarsal	0/1 (0.0)	2/5 (40.0)	0/5 (0.0)	6/27 (22.2)	1/3 (33.3)	0/0 (0)	0/0 (0)	3/23 (13.0)	6/53 (11.3)	1/11 (9.1)
Phalanges	0/5 (0)	0/3 (0)	0/11 (0)	0/11 (0)	0/4 (0)	0/1 (0)	0/31 (0)	0/8 (0.0)	0/12 (0.0)	0/7 (0.0)
Sesamoids	0/2 (0)	0/5 (0)	0/5 (0)	0/3 (0)	0/2 (0)	0/0 (0)	0/16 (0)	0/3 (0.0)	0/17 (0.0)	0/0 (0.0)
LBS	0/0 (0)	0/1 (0)	0/0 (0)	5/15 (30)	0/4 (0)	2/4 (50)	4/10 (40)	8/77 (10.4)	15/248 (6.0)	1/102 (0.9)
Total	6/37 (16.2)	22/77 (28.5)	20/70 (28.5)	116/375 (31)	34/110 (30.9)	2/17 (11.7)	23/140 (16.3)	31/333 (9.3)	85/907 (9.4)	20/421 (4.8)

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses, LBS = unidentified limb bone shaft fragment.

Bone surface modifications

Supplementary Table S1 (see online Supplementary material) provides the catalog information for each specimen identified as preserving a tooth mark and/or butchery mark. Cortical surface preservation is good to excellent at HWKE 3-5, MNK Main, SHK, and BK. Unfortunately, surface preservation at FC West and especially TK is very poor, which hindered the identification of surface modifications in these assemblages (see

also Monahan, 1996b: 139). The surface mark data from FC West and TK are not discussed further here, as it is likely that the grand total of three modified bone fragments (all from FC West and all of them tooth-marked) underestimates the actual incidence of surface marks in these assemblages. Table 8 summarizes tooth-mark data by skeletal element and carcass size for HWKE 3–5, MNK Main, SHK, and BK. Figure 8 shows examples of typical tooth marked fragments from the Bed II sites. Tooth marks appear on all elements, suggesting that, in most cases, carnivores had access to resources from all skeletal regions. Figure 9 displays midshaft tooth mark frequencies for HWKE 3–5, MNK Main, and BK relative to several actualistic control assemblages. The HWKE 3–5 and MNK Main data fit better with “carnivore-only” actualistic assemblages in which carnivores (mainly hyenas) enjoyed sole access to carcasses. The BK data fall within the range of “hammerstone-to-carnivore” assemblages. However, BK also matches a scenario where hominids demarrowed bones initially defleshed by felids. This potential equifinality is addressed below.

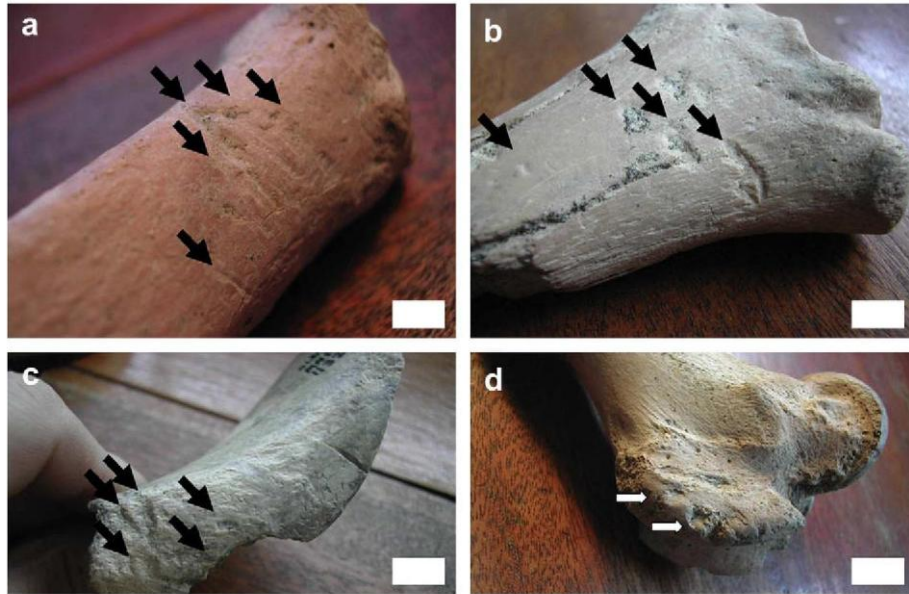


Fig. 8. Examples of tooth-marked fragments from MNK Main. Specimen numbers: (a) 1587; (b) 3050; (c) 729; (d) 1132.

Table 9 provides summary statistics for the dimensions of tooth pits preserved on medium-sized carcass limb bone diaphyses for MNK Main and BK (the only two sites with statistically meaningful sample sizes). Figure 10 plots these data with those gathered from studies of modern carnivores. The overall range of tooth pit sizes match better with those created by larger carnivores with more robust dentitions, such as lions and hyenas, although it is likely that smaller carnivores and even hominids inflicted some of the observed tooth marks in the Bed II bone assemblages.

No butchery marks were identified from HWKE 3–5, SHK, FC West, or TK, and a total of only four (one percussion-marked and three cutmarked) fragments preserve butchery damage from MNK Main. Site BK, on the other hand, preserves significant evidence for hominid butchery in the form of cutmarks (e.g., Fig. 11) and per-cussion marks (e.g., Fig. 12). Table 10 summarizes butchery mark frequencies by element and carcass size for BK. Butchery marks tend to cluster on the limb bones, although cutmarked pelvises, ribs, and vertebrae were identified. Medium carcasses preserve the highest frequency of butchery marks, and both cutmarks ($\chi^2 = 3.28$; $p > 0.05$) and percussion marks ($\chi^2 = 1.33$; $p > 0.05$) are distributed equally among the limb bones, as measured by NISP. However, BK butchery mark frequencies fall far below those attained in actualistic assemblages processed by humans, where limb bones are cutmarked and percussion-marked at rates of about 20% and 30%, respectively (Bunn, 1982; Blumenschine and Selvaggio, 1988, 1991; Domínguez-Rodrigo, 1997, 1999b; Lupo and O’Connell, 2002; Domínguez-Rodrigo and Barba, 2005; Pobiner and Braun, 2005; Pickering and Egeland, 2006). Figure 13 shows that most of the limb bone cutmarks at BK occur on shaft sections. Although this pattern has been linked to defleshing and early hominid access to carcasses (e.g., Bunn and Kroll, 1986; Domínguez-Rodrigo, 1997, 1999a,b, 2002; Bunn, 2001; Domínguez-Rodrigo and Pickering, 2003; Pickering et

al., 2004b), it is important to keep in mind that epiphyseal deletion via attrition probably erased the evidence for cutmarking on these less dense bone portions. Nevertheless, cutmarks on the meaty upper limb bones occur on what Dominguez-Rodrigo and Barba (2007: 90) have termed “Hot Zones.” These are anatomical zones that never preserved any flesh scraps after having been defleshed by lions in a sample of 28 carcasses analyzed from naturalistic settings in eastern Africa. Therefore, the occurrence of cutmarks on these zones makes it unlikely that hominids accessed carcasses after they had been fully defleshed by felids or other large carnivores.

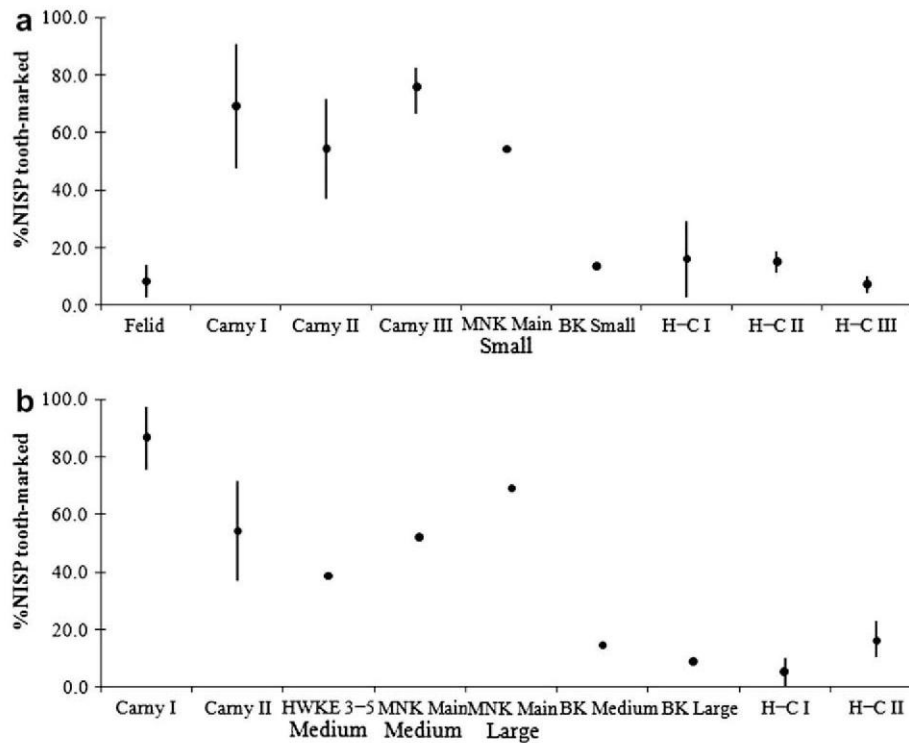


Fig. 9. Percentage of tooth-marked midshaft fragments for (a) small and (b) medium/large carcasses for the Bed II sites and several actualistic controls. Abbreviations: felid = felid-to-hominid; carny = carnivore (mainly hyena) only; H-C = hammerstone-to-carnivore. Felid data are from Dominguez-Rodrigo et al. (2007b); carny I and H-C I data are from Blumenschine (1995); carny II and H-C II data are from Capaldo (1997); carny III and H-C III data are from Marean et al. (2000).

Table 9
Summary statistics for tooth pit dimensions on medium carcasses from MNK Main and BK

	MNK Main	BK
Length		
<i>n</i>	63	17
Mean	3.94	3.12
SD	1.5	2.12
95% CI	3.52–4.36	2.03–4.21
Breadth		
<i>n</i>	63	17
Mean	3.08	2.22
SD	1.0	1.78
95% CI	2.80–3.36	1.30–3.14

Bone breakage

Green breakage predominates in all the Bed II assemblages ($\geq 70\%$ limb bone NISP), with the exception of HWKE 3–5, where dry breakage affects almost 50% of the limb bone NISP. Complete limb bones are rare at MNK Main, HWKE 3–5, and BK, whereas they are completely absent at FC West and TK (Table 11). Limb bone circumference representations at FC West, TK, and BK are similar to those of actualistic assemblages with intense hyena ravaging, while the data from HWKE 3–5 and MNK Main, which show relatively high frequencies of complete circumferences, are not indicative of intense ravaging (see Fig. 4). Table 12 provides limb bone fragmentation ratios for the Bed II sites and several actualistic assemblages (keeping in mind that the lack of small fragments artificially depresses fragmentation ratios in the fossil assemblages). With the exception of HWKE 3–5, levels of limb bone fragmentation are higher than those created by felids and small canids and similar to those created by hyena ravaging and human marrow processing. Sites MNK Main, FC West, TK, and BK all show epiphysis-to-shaft ratios slightly higher than heavily ravaged hyena assemblages, but well below

lower-competition dens and those created by other carnivores lacking the bone-destruction capabilities of hyenas. These data are all consistent with those presented previously by Monahan (1996a: Table 10, 1996b: Table 4.7).

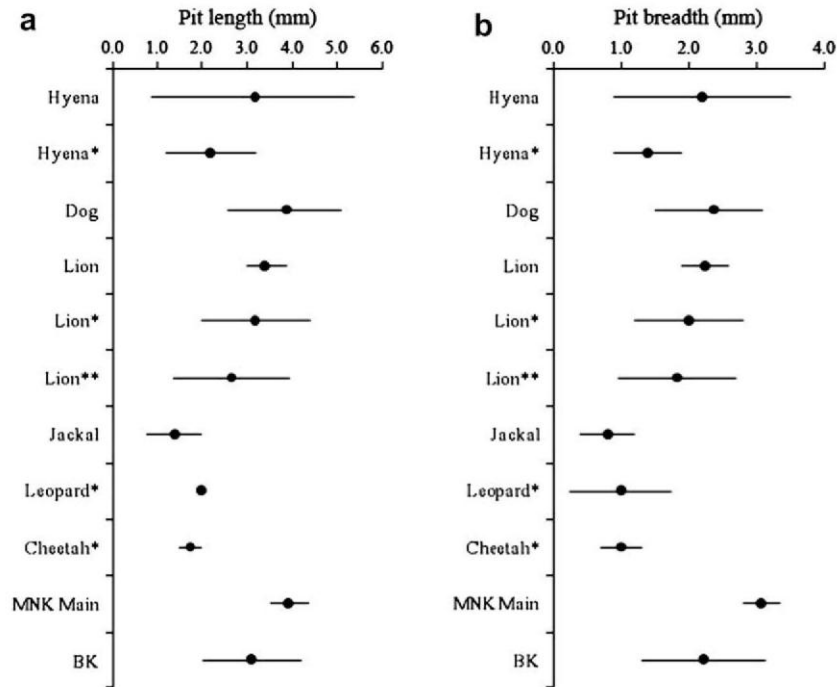


Fig. 10. Range (95% confidence intervals) of tooth pit (a) lengths and (b) breadths on medium-sized carcasses from BK and MNK Main compared to several actualistic controls. Data marked with an asterisk (*) are from Selvaggio (1994); data marked with two asterisks (**) are from Pobiner (2007). All other actualistic data are from Domínguez-Rodrigo and Piqueras (2003).

Table 13 provides summary data for longitudinal and oblique fracture planes in the MNK Main and BK assemblages. Figure 14 plots fracture plane data for BK and the medium carcasses from MNK Main relative to experimentally determined ranges of dynamic and static breakage. The MNK Main data show most angles within the static (i.e., carnivore) range while BK shows a substantial proportion of angles outside the static and within (and beyond) the dynamic (i.e., hammerstone) range. Only MNK Main and BK produced more than one measurable notch; these data are plotted in relation to experimental ranges of carnivore- and hammerstone-created notches in Fig. 15. All of the notches from MNK Main, regardless of carcass size, fall within the range produced by carnivores. The data from BK, on the other hand, show several notches that fall completely outside the carnivore range, although more experimental data are needed to fully define the range of notch dimensions created by hammerstone breakage on medium-sized carcasses. A variety of notch types characteristic of both hammerstone and carnivore breakage are present in the Bed II assemblages (Fig. 16). However, a higher frequency of notched fragments display tooth marks than display percussion marks for both MNK Main and BK (Table 14).

Discussion

We discuss the formation of the Bed II faunal assemblages at three inferential levels (Egeland et al., 2004: 345): (1) carcass modification, (2) carcass accumulation, and (3) carcass acquisition. Carcass modification involves the fragmentation and differential destruction of skeletal parts or portions and/or the creation of surface marks. Carcass accumulation is defined as the transport and/or deposition of carcasses or carcass parts at a particular locality. Finally, carcass acquisition entails gaining access to a carcass, regardless of the mode of access (e.g., hunting or scavenging) or the nutritional status of the carcass (e.g., fresh or desiccated). Because bone breakage and surface mark data can in many cases be clearly linked to particular taphonomic agents, the modification component of assemblage formation provides the most robust basis for interpretation. The accumulation and acquisition components are more remote and must rest on data gained from interpretations of carcass modification.

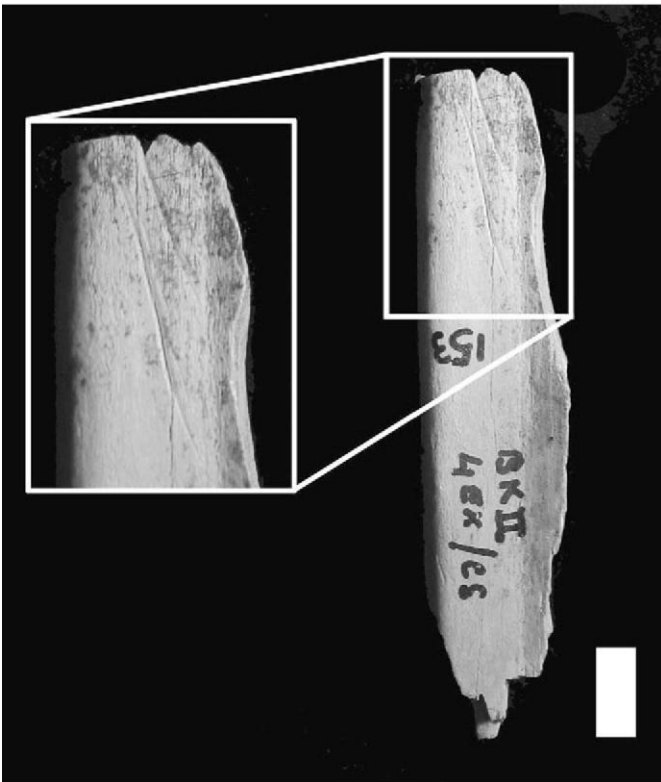


Fig. 11. Bovid metatarsal fragment from BK with cutmarks. Scale bar = 2 cm.



Fig. 12. Bovid femoral fragment from BK with percussion marks (arrows). Scale bar = 1 cm.

Carcass modification

Although only tooth marks are preserved at FC West, the poor condition of most cortices at both FC West and TK hindered the secure identification of surface marks in these assemblages. Un-fortunately, data from fracture planes are also ambiguous, as the overall sample size amounts to only a handful of measureable angles from each site. Levels of limb bone fragmentation at these sites are too high to attribute to felids or small canids, which implicates hyenas and/or hominids in bone breakage. The extent of epiphyseal loss and the general scarcity of axial bones are strongly suggestive of hyena ravaging. Similarly, the SHK assemblage preserves evidence for carcass modification by carnivores only, although butchery marks may have been present on the discarded portion of the fauna.

The total lack of butchery marks at HWKE 3–5 and their virtual absence at MNK Main point to little or no hominid participation in carcass modification at these sites. Midshaft tooth mark frequencies fall within the range of “carnivore-only” controls, and all measureable notches and most of the fracture angles (at least from MNK Main) fall within experimental carnivore ranges. None of the notched specimens from either site preserve percussion marks, while notched specimens with tooth marks are relatively common. Tooth pit dimensions point to a larger carnivore modifying at least the medium carcasses from MNK Main. Other lines of data, including limb bone fragmentation, epiphyseal loss, and a low number of axial bones, point to hyenas as a major modifying agent. However, the presence at MNK Main of a few complete bones with conspicuous tooth-marking on the epiphyses (e.g., Fig. 8d) may signal felid participation in carcass modification as well (Domínguez-Rodrigo et al., 2007a,b; Egeland, 2007; Pobiner, 2007).

Evidence for hominid modification is much more common in the BK assemblage. Butchery mark frequencies are (a distant) second to only FLK 22 among the Olduvai assemblages (Bunn, 1982; Bunn and Kroll, 1986; Domínguez-Rodrigo and Barba, 2007). Several notches, many of which do not preserve percussion marks (see also Monahan, 1996b: 184), and a high percentage of fracture planes fall within the experimental hammerstone range. Despite ample evidence for hominid behavior, it is also clear that carnivores played an important role in modifying carcasses at BK. Tooth marks appear in higher frequencies on notched specimens than do percussion marks. Although hammerstone notches are certainly present at BK, notches characteristic of carnivore bone

breakage are common as well. Fragmentation levels suggest hominid and/or hyena bone breakage, and low epiphysis-to-shaft ratios indicate rather intense hyena ravaging. Tooth mark frequencies on mid-shafts are consistent with both “hammerstone-to-carnivore” and felid-modified actualistic samples. However, the low frequencies of complete bones and high levels of fragmentation argue against cats as major carcass modifiers. Tooth pit dimensions on medium carcasses suggest large felids and/or hyenas, but, again, other data implicate hyenas rather than felids as the major, though not exclusive, carnivore agent of carcass modification.

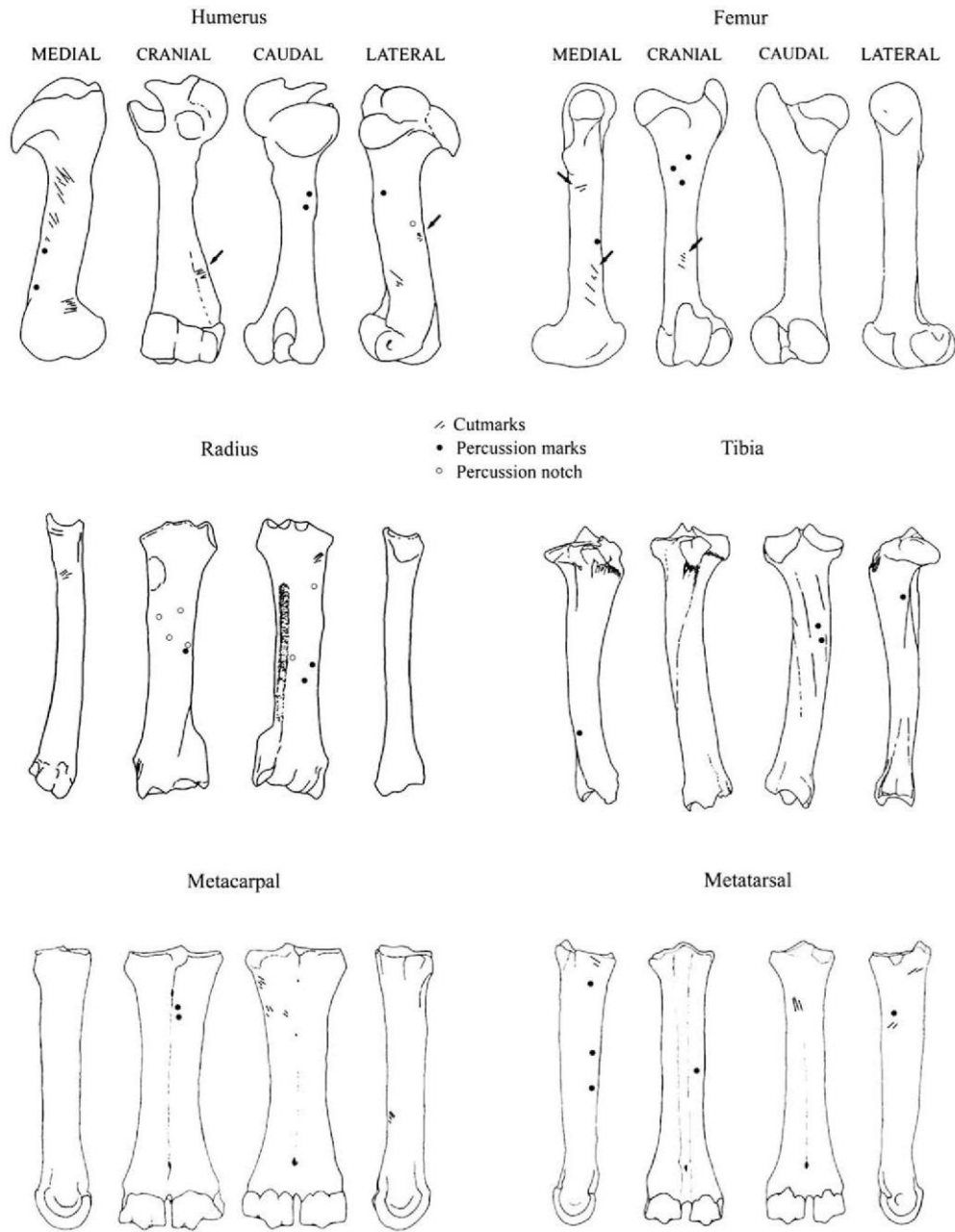


Fig. 13. Composite diagram showing location of cutmarks and percussion marks and notches on limb bones from BK (all Size Classes combined). Arrows indicate cutmarks on “Hot Zones.”

The pattern observed at BK (i.e., a good deal of evidence for hominid carcass modification but low frequencies of butchery marks relative to actualistic controls) is paralleled in several Plio-Pleistocene assemblages, including many Koobi Fora sites (Bunn, 1994; Domínguez-Rodrigo, 2002; Pobiner, 2007) and Swartkrans (Pickering et al., 2004b, 2007, 2008). Depending on the assemblage under consideration, a number of factors can lead to this result. First, that other processes can potentially mimic and/or obscure butchery marks in fossil assemblages forces analysts to be more conservative in their identifications. Poor surface preservation can exacerbate this process. Second, the artificial increase in fragments caused by dry breakage will also contribute to lower surface mark frequencies. Third, the preferential destruction of less dense axial elements and epiphyses, both of which may have preserved butchery marks, will also depress mark frequencies. Finally, it is

likely that hominids simply did not modify all the carcasses represented in many of the fossil assemblages (see also discussions by Cruz-Uribe, 1991: 477; Monahan, 1996b: 177, 184; Pickering, 2002: 134). There are assemblages such as Peninj (Domínguez-Rodrigo et al., 2002) and FLK 22 (Domínguez-Rodrigo and Barba, 2007; Bunn and Kroll, 1986) where butchery mark frequencies do approach actualistic controls.

In terms of bone surface modifications from MNK Main, there are some important differences between this study and that of Monahan (1996a,b). For example, Monahan (1996a: Table 5, 1996b: Table 4.2) documented a total of 45 tooth-marked specimens on Size Class 1–4 carcasses. By contrast, this study has identified a total of 170 tooth-marked fragments. Especially significant is the difference in midshaft tooth mark frequencies: whereas Monahan (1996a: Table 7, 1996b: Table 4.4) reported a 0.6% tooth mark rate, our identifications result in a rate of over 50%. Butchery mark frequencies for MNK Main also differ between studies. While we have identified only four butchered fragments, Monahan (1996a: Table 5, 1996b: Table 4.2) listed a total of 28 (13 cutmarked, 15 percussion-marked). The new estimates of butchery and tooth mark frequencies implicate carnivores rather than hominids as the primary carcass modifiers at MNK Main.

Table 10
Cutmark frequencies by skeletal element and carcass size for BK

Element	Small carcasses			Medium carcasses			Large carcasses		
	NISP	CM	PM	NISP	CM	PM	NISP	CM	PM
Mandible	16	0 (0.0)	0 (0.0)	41	0 (0.0)	0 (0.0)	20	0 (0.0)	0 (0.0)
Vertebrae	15	0 (0.0)	0 (0.0)	46	1 (2.2)	0 (0.0)	21	0 (0.0)	0 (0.0)
Innominate	6	0 (0.0)	0 (0.0)	21	1 (4.8)	0 (0.0)	6	1 (16.7)	0 (0.0)
Ribs	18	0 (0.0)	0 (0.0)	71	4 (5.6)	0 (0.0)	95	1 (1.1)	0 (0.0)
Scapula	3	0 (0.0)	0 (0.0)	20	0 (0.0)	0 (0.0)	10	1 (1.0)	0 (0.0)
Humerus	29	1 (3.4)	1 (3.4)	82	6 (7.3)	4 (4.9)	24	1 (4.2)	0 (0.0)
Radius	18	0 (0.0)	0 (0.0)	58	1 (1.7)	1 (1.7)	28	0 (0.0)	0 (0.0)
Ulna	5	0 (0.0)	0 (0.0)	12	0 (0.0)	0 (0.0)	4	0 (0.0)	0 (0.0)
Carpals	3	0 (0.0)	0 (0.0)	10	0 (0.0)	0 (0.0)	4	0 (0.0)	0 (0.0)
Metacarpal	18	0 (0.0)	2 (11.1)	35	1 (2.9)	1 (2.9)	8	1 (12.5)	0 (0.0)
Femur	38	1 (2.6)	1 (2.6)	61	2 (3.3)	2 (3.3)	27	0 (0.0)	0 (0.0)
Patella	3	0 (0.0)	0 (0.0)	2	0 (0.0)	0 (0.0)	2	0 (0.0)	0 (0.0)
Tibia	38	0 (0.0)	1 (2.6)	100	1 (1.0)	2 (2.0)	32	0 (0.0)	0 (0.0)
Tarsals	12	0 (0.0)	0 (0.0)	18	0 (0.0)	0 (0.0)	20	0 (0.0)	0 (0.0)
Metatarsal	23	1 (4.3)	0 (0.0)	53	3 (5.7)	2 (3.8)	11	0 (0.0)	0 (0.0)
Phalanges	8	0 (0.0)	0 (0.0)	12	0 (0.0)	0 (0.0)	7	0 (0.0)	0 (0.0)
Sesamoids	3	0 (0.0)	0 (0.0)	17	0 (0.0)	0 (0.0)	0	0 (0.0)	0 (0.0)
LBS	77	1 (1.3)	2 (2.6)	248	3 (1.2)	0 (0.0)	102	1 (0.9)	0 (0.0)
Total	333	4 (1.2)	7 (2.1)	907	23 (2.5)	12 (1.3)	421	6 (1.4)	0 (0.0)

Abbreviations NISP = number of identified specimens, CM = cutmark, PM = percussion mark, LBS = unidentified limb bone shaft fragment.

Carcass accumulation

Geological evidence, in addition to a general lack of very small bone fragments, indicates that fluvial activity played some role in accumulating and/or dispersing bones at the Bed II sites [see also discussions by Monahan (1996a: 110, 1996b: 218–221)]. In their study of the Olduvai lithic material, Petraglia and Potts (1994) concluded that neither FC West nor HWKE 4 represent a primary-context assemblage, although it seems that transport distance was minimal. Kimura (1999) also reported that very small pieces of debitage (<1 cm) are nearly absent at HWKE 3 and 4, again suggesting some level of hydraulic disturbance. Petraglia and Potts (1994) found that MNK Main shows a mixture of winnowed and lag lithic material; such a mixed signal is consistent with the depth of the deposit. Both TK UF and TK LF preserve many lithic pieces less than 20 mm in size (de la Torre, 2004), which suggests that both assemblages were in more or less primary context. However, given that the TK UF paleosol was slightly inclined, it is likely that over-land waterflow winnowed out some of the smallest pieces (Petraglia and Potts, 1994). Leakey (1971) reported that about 10% of the choppers from the Main Site at SHK were rolled, which suggests that hydraulic disturbance played some role in accumulating the remains there. As Monahan (1996b: 219) observed, the fresh condition of many of the BK bone fragments, in addition to high frequencies of small lithic debitage, supports Leakey's (1971: 199) contention that most of the assemblage was originally deposited on or near a stream bank and subsequently washed into the stream bed and buried as channel fill without long-distance transport. It is possible that the paucity of very small bone fragments from BK is the result of their being discarded or otherwise unavailable for study because, unlike HWKE 3–5 and MNK Main, no screened material (i.e., find bags with numerous bone fragments less than 2 cm in size and lacking catalog numbers) from this site was found on the museum shelves.

Table 11
Incidence of complete limb bones by carcass size for the Bed II sites

Element	HWKE 3-5		MNK Main			BK		
	S	M	S	M	L	S	M	L
Humerus	0/1 (0.0)	0/3 (0.0)	0/2 (0.0)	0/12 (0.0)	0/2 (0.0)	0/21 (0.0)	0/35 (0.0)	0/10 (0.0)
Radius	0/1 (0.0)	0/2 (0.0)	0/2 (0.0)	1/12 (8.3)	0/4 (0.0)	2/13 (15.4)	1/28 (3.6)	1/16 (6.3)
Metacarpal	0/2 (0.0)	0/4 (0.0)	1/2 (50.0)	1/8 (12.5)	0/2 (0.0)	2/8 (25.0)	1/13 (7.7)	1/6 (16.7)
Femur	0/2 (0.0)	0/1 (0.0)	1/4 (25.0)	0/9 (0.0)	0/6 (0.0)	0/22 (0.0)	1/23 (4.3)	1/11 (9.1)
Tibia	0/2 (0.0)	1/6 (16.7)	1/3 (33.0)	1/13 (7.7)	0/5 (0.0)	0/18 (0.0)	3/34 (8.8)	0/12 (0.0)
Metatarsal	0/2 (0.0)	0/4 (0.0)	0/0 (0.0)	3/10 (30.0)	0/3 (0.0)	0/12 (0.0)	0/13 (0.0)	0/3 (0.0)
Total	0/10 (0.0)	1/20 (5.0)	3/13 (23.1)	6/64 (9.4)	0/22 (0.0)	4/94 (4.3)	6/145 (4.1)	3/58 (5.2)

Abbreviations S = small carcasses, M = medium carcasses, L = large carcasses.

Table 12
Limb-bone fragmentation ratios by carcass size for the Bed II sites and several actualistic controls

	Small carcasses		Medium carcasses		Large carcasses	
	NISP:MNE	EP:SH	NISP:MNE	EP:SH	NISP:MNE	EP:SH
Olduvai Bed II						
HWKE 3-5	1.05	9.00	1.75	1.17	—	—
MNK Main	1.77	0.21	3.33	0.21	3.84	0.23
FC West	—	—	1.78	0.23	—	—
TK LF	—	—	3.29	0.14	—	—
TK UF	—	—	2.08	0.13	—	—
BK	2.38	0.16	4.28	0.14	3.78	0.12
Carnivore-experimental						
Hyena ¹	4.90	—	1.00	—	—	—
Spotted hyena ²	—	—	—	0.63	—	—
Lion-spotted hyena ²	—	—	—	0.43	—	—
Lion ²	—	0.05	—	0.71	—	—
Leopard ^{1,2}	1.00	0.70	—	—	—	—
Cheetah ²	—	0.67	—	—	—	—
Dog ¹	1.01	—	—	—	—	—
Jackal ^{1,2}	1.03	0.67	—	—	—	—
Carnivore-only I ³	—	0.03	—	0.02	—	—
Carnivore-only II ⁴	3.86	0.01	6.45	0.04	—	—
Carnivore-only III ⁵	—	0.08	—	—	—	—
Carnivore-dens						
Syokimau (spotted hyena) ⁶	—	—	—	0.63	—	—
KFHD 1 (spotted hyena) ⁷	1.60	—	—	—	—	—
Human-experimental						
Hammerstone-only I ³	—	0.36	—	0.50	—	—
Hammerstone-only II ⁸	—	—	3.08	0.42	—	—
Hammerstone-only III ⁹	12.03	0.20	—	—	—	—
HS - C I ³	—	0.01	—	0.03	—	—
HS - C II ⁴	7.12	0.06	9.39	0.06	—	—
HS - C III ⁵	—	0.11	—	—	—	—
Hunter-gatherer						
Kua ¹⁰	2.68	1.23	9.98	0.67	—	—

Superscripted numbers indicate the following data sources: 1 = Richardson (1980: Figure 4); 2 = Pobiner (2007: Tables 4.5, 4.6); 3 = Blumenschine (1995: Table 1); 4 = Capaldo (1997: Table 7); 5 = Marean [data cited by Monahan (1996a: Table 3)]; 6 = Bunn (1982: Table 3.4); 7 = Lam (1992: Table 3); 8 = Bunn (1989: Table 2a); 9 = Pickering and Egeland (2006); 10 = Bartram and Marean (1999: Table 3). The data presented here differ slightly from those presented by Pickering and Egeland (2006), as only fragments ≥ 2 cm [and not ≥ 1 cm as in Pickering and Egeland (2006)] are considered.

Limb-dominated faunal assemblages like those from the Bed II sites have been interpreted as reflecting the transport by behavioral agents of carcass parts away from death sites, especially for medium- and large-sized animals (e.g., Bunn, 1986; Bunn and Kroll, 1986; Potts, 1988). Although actualistic research substantiates the claim that axial elements tend to remain at death sites while appendicular elements are transported away (Behrensmeier and Dechant Boaz, 1980; Behrensmeier, 1983; Blumenschine, 1986), a limb-dominated pattern is at least as parsimoniously explained by selective deletion of axial bones via density-mediated processes like carnivore ravaging (Marean et al., 1992; Capaldo, 1998). More compelling evidence for a behavioral agent of accumulation comes from the density and ecological diversity of the Bed II faunas relative to modern landscape assemblages (cf. Bunn, 1982; Potts, 1982, 1988). The Bed II sites greatly surpass the density of faunal remains observed in modern background scatters (e.g., Behrensmeier, 1983; Blumenschine, 1989; Bunn et al., 1991; Sept, 1994; Tappen, 1995; Dominguez-Rodrigo, 1996). This, coupled with the observation that modern background scatters typically yield a maximum of only three to five individuals in areas much larger than those represented by the Bed II excavations (Behrensmeier, 1983; Domínguez-Rodrigo, 1993), strongly suggests a behavioral agent of accumulation for the fossil assemblages.

Despite the presence of stone tools, there are no taphonomic data that definitively assign hominid authorship to the accumulation of the FC West and TK faunas. Unfortunately, poor preservation also renders the carnivore contribution to carcass accumulation obscure. Although stone tools are also present at SHK, the available evidence indicates that carnivores played a major, if not exclusive, role in accumulating the fauna.

The taphonomic data clearly implicate large carnivores as the likely accumulators of the HWKE 3–5 and MNK Main bone assemblages. In fact, midshaft tooth mark frequencies at MNK Main are among the highest of any Olduvai assemblage (Domínguez-Rodrigo et al., 2007a,b; Egeland, 2007; Pobiner, 2007). One possible behavioral mechanism for the accumulation of these assemblages is carnivore (especially hyena) denning, which has been shown to produce dense bone collections in spatially restricted areas (Mills and Mills, 1977; Henschel et al., 1979; Bunn, 1982,1983; Hill, 1989; Lam, 1992; Pokines and Kerbis Peterhans, 2007). Based largely on skeletal part frequencies and levels of bone destruction, Binford (1981) classified MNK Main within his “Factor 1” cluster of sites, which were interpreted as dens. However, other lines of data argue against a den interpretation for both HWKE 3–5 and MNK Main. First, and most importantly, no stratigraphic evidence for an excavated den or any horizontal concentration of material was documented within either deposit. Second, no limb bone fragments from HWKE 3–5 and only six from MNK Main have been identified that show extensive pitting and scoring across the entire cortical surface. Such fragments are most likely the result of “worrying” or “boredom chewing” (cf. Binford and Bertram, 1977; Binford, 1981) and are encountered frequently in at least modern spotted hyena (*Crocuta crocuta*) dens (CPE and MDR, pers. obs.). Finally, the fossil assemblages lack the juvenile hyena remains that are common in modern dens (Cruz-Uribe, 1991; Pickering, 2002).

Table 13
Summary statistics for fracture angles by carcass size from nonmetapodial fragments for the Bed II assemblages

	MNK Main		BK		
	S	M	S	M	L
Longitudinal <90°					
<i>n</i>	—	15	22	52	11
Mean	—	81.2	80.5	76.1	71.5
SD	—	6.1	8.5	13.4	17.9
95% CI	—	77.7–84.7	76.7–84.3	72.3–79.8	59.4–83.5
Longitudinal >90°					
<i>n</i>	3	26	2	31	10
Mean	96.6	103.6	97.0	101.3	101.9
SD	12.5	6.8	5.7	9.4	8.2
95% CI	80.4–112.8	100.3–106.1	46.2–147.8	97.8–104.7	96.0–107.8
Oblique <90°					
<i>n</i>	—	14	27	115	45
Mean	—	80.7	71.7	65.5	65.6
SD	—	5.3	14.0	17.3	17.9
95% CI	—	77.5–83.9	66.2–77.3	62.3–68.7	60.2–71.0
Oblique >90°					
<i>n</i>	3	31	15	70	39
Mean	109.3	106.4	111.6	107.4	110.1
SD	6.0	6.4	15.4	13.8	13.9
95% CI	101.6–117.0	103.9–108.9	103.1–120.1	104.1–110.7	105.6–114.6

Abbreviations: S = small carcasses, M = medium carcasses, L = large carcasses.

The depths of the HWKE 3–5 and MNK Main deposits leave open the possibility that both sites simply represent natural deaths occurring over long periods of time. However, even when the thickness of the deposits is taken into account, the density of faunal material at these sites (HWKE 3–5: 0.31 bones/m²; MNK Main: 0.58 bones/m²) is much higher than that documented in scatters of natural deaths on modern landscapes (≤ 0.005 bones/m²; Behrensmeyer, 1987: 431) that have been accumulating presumably over very many years.¹ We therefore favor a mechanism variously referred to as “predation foci” (Behrensmeyer, 1982: 42), “predation patches” (Behrensmeyer, 1983: 97), “predation arenas” (Behrensmeyer, 1987: 430), or “serial predation” areas (Haynes, 1988: 219). These are locations on the landscape particularly conducive to successful hunting and, because they are essentially conglomerations of individual kills, can result in relatively dense bone concentrations (Behrensmeyer and Dechant Boaz, 1980; Behrensmeyer, 1982, 1983, 1987; Haynes, 1985, 1988). Predation arenas require a geomorphological feature that concentrates animal activity. In modern savanna ecosystems, predation areas typically occur near cover and/or water sources (Behrensmeyer and Dechant Boaz, 1980; Behrensmeyer, 1982,1983,1987; Haynes, 1985, 1988). Given the location of both HWKE 3–5 and MNK

Main within the eastern lake margin, it is not surprising that site-specific studies of plant macrofossils and phytoliths indicate that herbaceous vegetation, trees, and wetlands were common (particularly at HWKE) in this area during at least lower Bed II times (Albert et al., 2006; Bamford et al., 2006). Sites HWKE 3–5 and MNK Main are slightly more ecologically diverse than modern predation arenas, which tend to contain only species from a single ecological context (Dominguez-Rodrigo, 1993). However, a predation arena utilized frequently by both lions and hyenas to procure prey in Hwange National Park (Zimbabwe) contained both open savanna [e.g., wildebeest (*Connochaetes taurinus*)] and woodland [e.g., waterbuck (*Kobus ellipsi-prymnus*)] species (Haynes, 1988). The common occurrence at both sites of sediment abrasion characteristic of trampling [HWKE 3–5: 15 out of 39 (38.5%) limb bone fragments; MNK Main: 121 out of 349 (34.7%)] suggests that they may have been high traffic areas for passing ungulates. If HWKE 3–5 and MNK Main were particularly active predation arenas, then serial predation by carnivores over an extended period of time (perhaps hundreds of years or more given the depth of the deposits), supplemented by additional carcass input via natural deaths and natural background scatter, may have produced the dense collections of faunal material at the sites (see also Tappen et al., 2007).

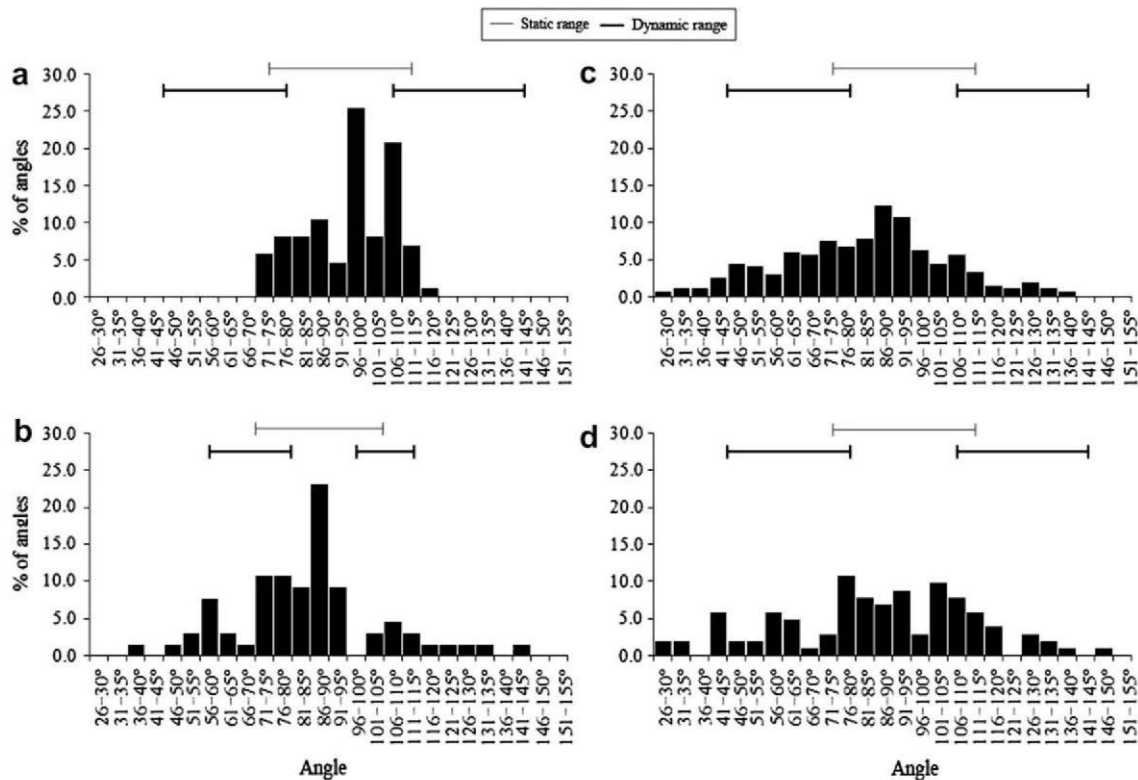


Fig. 14. Distribution of longitudinal and oblique fracture angles on (a) small carcasses from MNK Main; (b) medium carcasses from MNK Main; (c) small carcasses from BK; (d) medium carcasses from BK. Gray line denotes 95% confidence intervals of experimental static loading angles; black line denotes 95% confidence intervals of experimental dynamic loading angles. Experimental data are from Pickering et al. (2005).

There is little doubt that hominids played a major role in modifying carcasses from BK (see also Monahan, 1996a,b); therefore, their participation in at least some carcass accumulation is strongly implied. However, given that BK is a lumped sample of deeply stratified deposits representing many individual episodes of accumulation over (potentially) many years, only general trends in carcass transport by hominids can be identified at this time. Among small and medium carcasses, upper and intermediate limb bones are better represented even than crania, suggesting some selective transport of high-utility limb bones [and perhaps non-narrow-bearing axial bones, although the incentive to transport these elements would have been reduced given the current lack of evidence at Olduvai during upper Bed II times for the boiling technology required to extract grease (Bunn, 2007)]. The scarcity of lower-utility metapodials relative to other limb bones may indicate their abandonment at carcass acquisition points or, alternatively, their removal from the site by scavengers. The presence of at least lions and hyenas, inferred both from their fossil representation at the site and their known general occurrence in savanna ecosystems, means that they (or other large carnivores) cannot be ruled out as accumulators of at least a portion of the BK fauna. Given the secondary context of the site, it is not known

whether a den structure existed in the vicinity. Natural background bones (e.g., highly rolled pieces transported in streams) were also incorporated into the assemblage.

Carcass acquisition

No direct evidence can be brought to bear on the issue of hominid carcass acquisition at FC West and TK. None of the carcasses represented at either SHK or HWKE 3–5 appear to have been acquired by hominids. Surface modifications link hominids to the acquisition of two carcasses (both medium-sized) at MNK Main and eleven (three small, six medium, two large) at BK. It therefore appears that carcass acquisition rates were nearly zero at MNK Main during the time interval sampled by the deposits. At BK, the depth of the deposits makes it possible that carcass acquisition was spread over a potentially long period of time (i.e., decades or more), which would result in very low rates of carcass acquisition. Excavations at BK in 2006 did not identify stable land surfaces in the form of paleosols. However, three-dimensional spatial analysis reveals that faunal material is not spread uniformly throughout the deposits but is confined to several vertically discrete horizons averaging 15 to 20 cm in thickness (Dominguez-Rodrigo et al., unpublished data). Even so, and despite the fact that all but one of the butchered carcasses from this analysis are weathered to stage 0 or 1, it is difficult to make meaningful estimates of carcass acquisition rates until systematic geological and taphonomic analyses of the newly excavated material are completed.

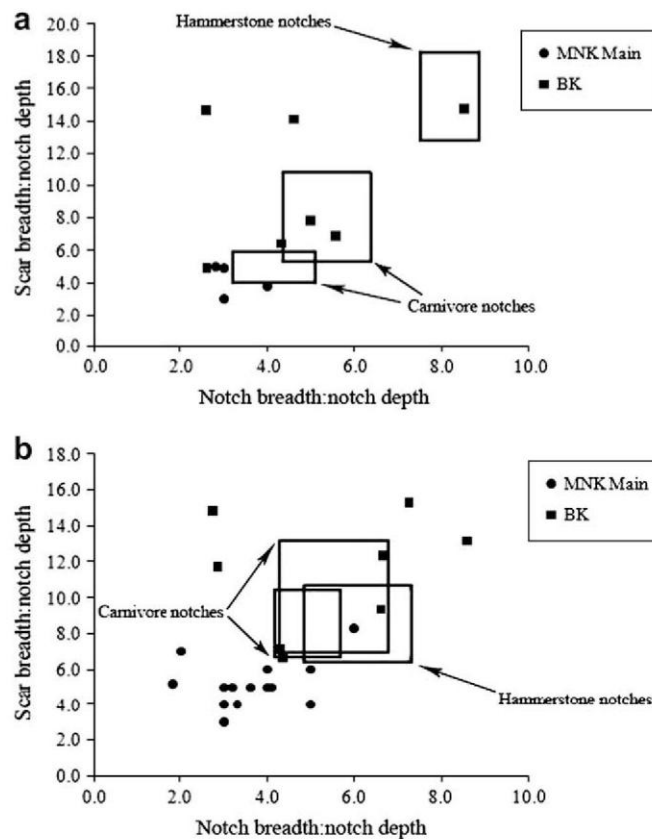


Fig. 15. Notch dimensions on specimens from (a) small and (b) medium carcasses from MNK Main and BK. Boxes represent 95% confidence intervals of notch breadth: notch depth and scar breadth: notch depth ratios for experimental assemblages (Capaldo and Blumenshine, 1994) and a sample of notches from a hyena den in the Masai Mara National Reserve (Egeland et al., unpublished data).

The timing of hominid access to carcasses at MNK Main, FC West, and TK is impossible to establish with any confidence due to extremely small samples of butchered fragments and/or poor preservation. On the other hand, the frequency and anatomical placement of cutmarks at BK strongly suggest that, when hominids did acquire large mammals, they enjoyed early access to fully fleshed carcasses (see also Monahan, 1996a,b). Data from both cutmarks and skeletal part frequencies indicate a pattern of access to high-utility upper and intermediate limb bones in addition to rib cages and meaty pelvises.

Palimpsests, site formation, and the use of space by hominids and carnivores

The taphonomic data presented above clearly demonstrate that the Bed II sites are palimpsests reflecting the interdependent and independent actions of several agents, including most prominently hominids and large carnivores. As such, each of the assemblages reflect varying degrees of integrity and resolution, where “integrity” refers to the “homogeneity of the agents responsible for materials in a deposit” and “resolution” to the “homogeneity of the events or situational conditions whose by-products are preserved in the deposit” (Binford, 1981: 19).

It is unfortunate that FC West and TK are so poorly preserved because small assemblages like these often sample a narrow range of behaviors (Lupo, 2001). In other words, it is small sample sizes that furnish such assemblages with potentially high integrity and resolution (cf. Foley, 1981; Isaac, 1981; Isaac et al., 1981). Overall, little can be determined concerning the formation of these faunal assemblages other than to say carcasses were accumulated by hominids and/or large carnivores and subsequently ravaged by hyenas.

If HWKE 3–5 and MNK Main represent predation arenas, both faunal assemblages are the result of serial predation by large carnivores with additional carcass input via natural deaths and back-ground scatter. A strong hyena signal, especially at MNK Main, indicates that carcasses were ravaged subsequent to their deposition on site. Although hominids may have sporadically visited MNK Main to process parts of two carcasses, it is also possible that a few butchered bones were scavenged and transported to the site by carnivores. It is likely that several large carnivore species utilized the HWKE and MNK Main localities, and, given the depth of the deposits, this utilization occurred over an extended period of time. Integrity and resolution are therefore probably low for these two assemblages (Binford, 1981).

It is clear that, at BK, dozens of individual episodes of carcass transport and processing by several agents, including hominids, are sampled. Although this accumulative effect masks variability in carcass transport and processing, the overall pattern, as Monahan (1996a,b) argued, is one of hominids accessing and transporting high-utility carcass portions for processing at or near the BK locality. Like HWKE 3–5 and especially MNK Main, a strong hyena taphonomic signature exists at BK, which in most cases is the result of scavenging hominid food refuse. Hyenas were therefore relegated to consuming (1) the few remaining bones left unbroken by hominids; (2) nutritionally depleted limb-bone shaft fragments; and (3) grease-laden axial elements and limb bone epiphyses. Bunn (2006) suggested that this may indicate intermittent rather than continuous site usage by hominids, given the limited amount of time that axial bones and limb epiphyses retain nutritionally attractive grease. In some ways, the taphonomic data from BK resemble those from other Plio-Pleistocene sites such as FLK 22 and FxJj 50 (Koobi Fora, Kenya), both of which have been interpreted as “central places” [i.e., locations to which large numbers of mammal carcasses were repeatedly transported and shared with other members of the group (Bunn, 1982, 2006; Bunn et al., 1980, 1997)]. However, our current understanding of BK urges a cautious approach to such an interpretation for two reasons. First, FLK 22 and FxJj 50 were excavated from within thin paleosols. This contextual evidence, when coupled with the taphonomic data on weathering and hominid butchery, provides good evidence for carcass acquisition rates that were high enough to encourage food-sharing. The BK sample analyzed here is from over a meter of deposit, which, as argued above, makes it difficult to argue for high rates of carcass acquisition. Second, although the BK materials appear not to have been transported long distances via fluvial action, the geological context of the site indicates that the remains are not in primary context. Thus, it is possible that the BK fauna is in fact a mixture of individual sites from within the general vicinity, all of which may have resulted from different hominid activities. A full analysis of the newly excavated materials should illuminate these issues.

The presence of stone tools at all of the Bed II sites considered here confirms that hominids utilized these areas. Three types of occurrences can be identified: (1) stone tools occurring with well-preserved faunal remains and substantial evidence for butchery; (2) stone tools occurring with well-preserved faunal remains and little or no evidence for butchery; and (3) stone tools occurring with poorly preserved faunal remains. If sharp-edged flakes are considered among the most effective butchery tools in early stone toolkits (Toth, 1985), it is not surprising that the BK lithic assemblage (which can be linked taphonomically to carcass butchery) is rich in flakes (Leakey, 1971; de la Torre, 2004). The HWKE and MNK Main lithic assemblages, on the other hand,

apparently cannot be linked to carcass processing. A possible explanation for this pattern, which has also been documented at a number of Bed I sites (Dominguez-Rodrigo et al., 2007a,b; Egeland, 2007), lies in Mora and de la Torre's (2005) recent reexamination of the idea that percussion activities unrelated to flake production were an important aspect of stone utilization at Olduvai during Bed I and II times [see also Willoughby (1987) and Schick and Toth (1994) for important discussions of battered materials]. Mora and de la Torre (2005) proposed that the non-knapping percussion components (which include anvils, angular fragments, and some hammerstones and spheroids) of the Olduvai lithic assemblages could have been used to process plant resources like nuts, fruits, or even wood (see also Toth, 1985; Schick and Toth, 1993).

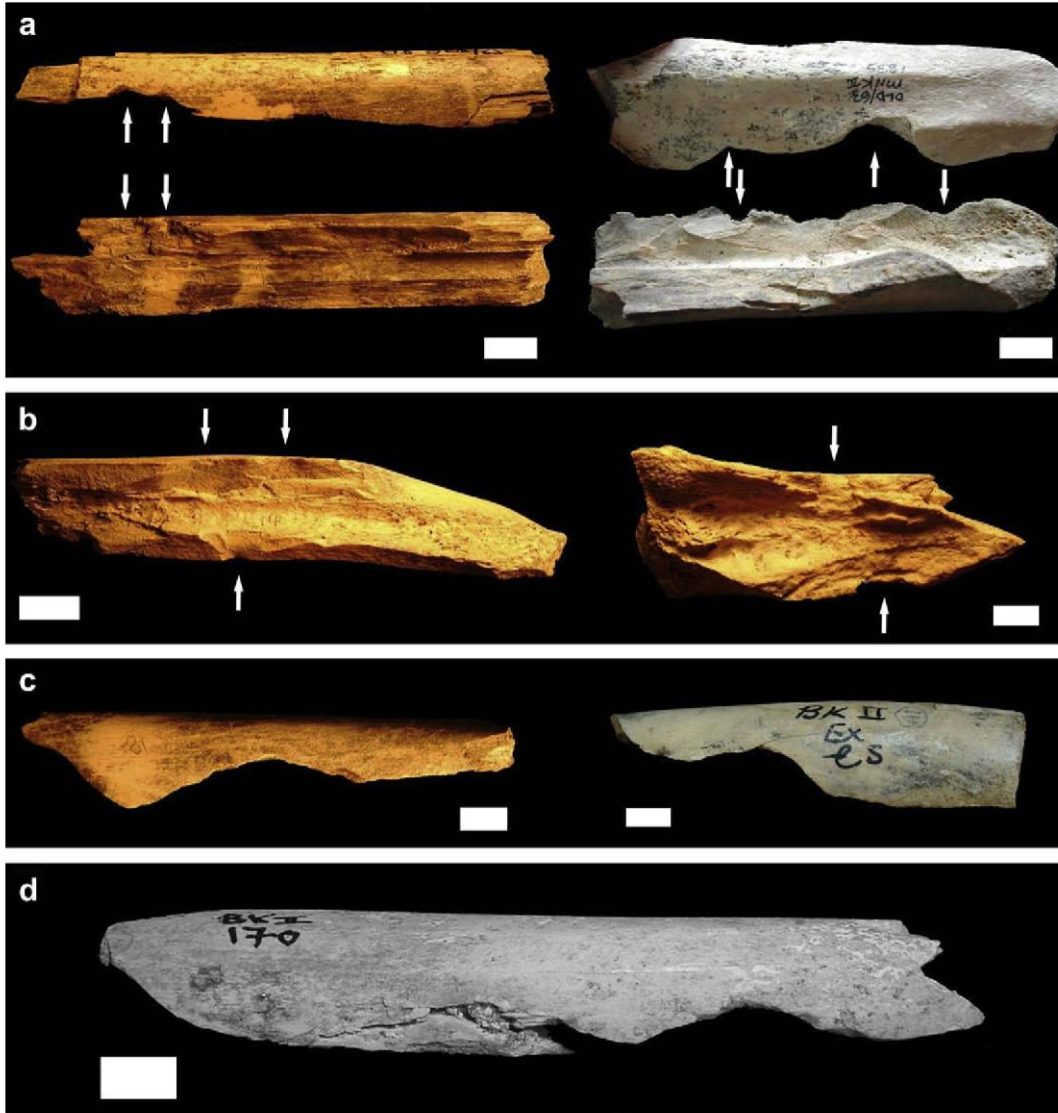


Fig. 16. Examples of notches from the Bed II sites. (a) Cortical and medullary views of "Incomplete Type C" notches, which often, though not exclusively, result when the adjacent tooth cusps of a carnivore create multiple, closely spaced loading points. (b) Medullary views of "Opposing Complete" notches; these notches are common in carnivore assemblages where opposite loading points are created by the opposing forces of the upper and lower dentition. (c) Probable hammerstone notches; note the broad, shallow outlines of the notches. (d) Incipient notch; note the incompletely detached impact flake that is common in hammerstone-generated assemblages. Scale bars = 1 cm.

At HWKE, a low frequency of lava (basalt and phonolite) flakes relative to the number of cores suggests that flake production in this raw material was not the major goal of hominid tool-makers (Kimura, 1999). Although quartz and chert flakes are relatively common at the site, many of the quartz cores show evidence of battering (Kimura, 1999), which may indicate that they were subsequently used for percussion activities unrelated to carcass butchery. The lack of butchery marks at MNK Main and SHK is somewhat surprising considering complete flakes are relatively common in both lithic assemblages; however, battered pieces make up significant portions of the assemblages as well, especially in terms of weight (Leakey, 1971). Kimura (2002) and Mora and de la Torre (2005) documented a high incidence of battered pieces at both FC West and TK, which again could indicate that activities other than or in addition to carcass butchery were carried out at these sites.

For those Bed II sites where lithic assemblages cannot be linked exclusively to carcass butchery, it appears that the transport, use, and discard of stone tools by hominids and the consumption of carcasses by large carnivores occurred serially and in unrelated depositional events. Such an overlap in the use of space is consistent with Isaac's (1983: 9) "common amenity" model of early site formation (see also Isaac and Crader, 1981; Binford, 1983), in which water, trees, and food attracted both hominids and carnivores to the same localities on the landscape independently. Some interdependence in site formation is documented at MNK Main and BK, as bone fragments preserving both butchery marks and carnivore tooth marks have been identified in these assemblages (Monahan, 1996a,b). Levels of bone destruction indicate that competition for carcasses was relatively high at BK (Monahan, 1996a,b; Egeland, 2007). Carcass processing by hominids in such habitats would certainly have enticed local groups of carnivores. The ability to butcher and control carcasses under these circumstances speaks to the superior competitive abilities of *H. erectus* during upper Bed II times. This may contrast with their Bed I counterparts, as taphonomic evidence suggests that FLK 22 (and many of the Bed I sites in general) was situated in an area of relatively low competition (Capaldo, 1997; Egeland, 2007; but see Faith and Behrensmeier, 2006; Faith et al., 2007).

Table 14
Tooth-mark frequencies on notched specimens from the Bed II sites

	NISP notched	Tooth mark		Percussion mark	
		NISP	%	NISP	%
HWKE 3–5					
Medium carcasses	4	2	50.0	—	—
MNK Main					
Small carcasses	7	3	42.8	—	—
Medium carcasses	41	19	46.3	—	—
BK					
Small carcasses	14	4	28.6	3	21.4
Medium carcasses	18	5	27.8	1	5.6
Large carcasses	6	0	0.0	0	0.0
Masai Mara hyena den ¹					
Small carcasses	56	21	37.5	—	—
Medium carcasses	67	29	43.3	—	—
Total	123	50	40.7	—	—
Experimental carnivore ²					
Medium carcasses	45	35	77.8	—	—
Experimental percussion I ²					
Small carcasses	90	—	—	58	64.4
Experimental percussion II ³					
Small carcasses	27	—	—	13	48.1

Superscripted numbers indicate the following data sources: 1 = Egeland et al. (unpublished data); 2 = Blumenschine and Selvaggio (1991; Tables 1a, b); 3 = Pickering and Egeland (2006; Table 1). Only specimens with complete notches were included.

Conclusions

There is no definitive taphonomic evidence to indicate that hominids played a substantial role in the formation of the HWKE 3–5, MNK Main, FC West, SHK, or TK faunas. The bone assemblages from HWKE 3–5 and MNK Main may be the result of predation by a number of large carnivore species over an extended period of time. Poor surface preservation at FC West and TK and selective retention at SHK hinders interpretations of assemblage formation at these localities. Nevertheless, it can be said that FC West and TK were ravaged by hyenas, while SHK probably represents a carnivore accumulation of some sort. On the other hand, the data presented here indicate that hominids participated significantly in the formation of the BK fauna, in agreement with Monahan's (1996a,b) analysis. It is further apparent that hominids accessed fully fleshed carcasses and that carnivores (mainly hyenas) were relegated in many cases to scavenging hominid food refuse (see also Monahan, 1996a,b). Although the secondary context of the site and the low integrity and resolution of the faunal assemblage recommends caution in assigning a socio-economic function to BK, Monahan (1996a: 118) convincingly argued that hominids "were able to minimize predation risk and to control carcasses until processing and consumption were accomplished."

It now appears that the lithic assemblages from several sites in both Bed I and II cannot be associated exclusively with the processing of large mammal carcasses. Regardless of the exact resource(s) hominids were processing with these lithic assemblages, it seems that plant foods [whose importance in early hominid diets is undeniable (Peters, 1987; Sept, 1992)] and their seasonal availability (Peters et al., 1984) dictated to some

extent when and where hominids used and discarded stone tools at Olduvai (Peters and Blumenschine, 1995) and elsewhere (Sept, 2001). In many cases, the palimpsest assemblages from Bed II reflect serial site usage by hominids and carnivores over decades or perhaps much longer. We suggested a similar pattern of site formation for many Bed I sites as well (Dominguez-Rodrigo et al., 2007a,b; Egeland, 2007).

Overall, hyena taphonomic signals are stronger and more frequent in Bed II relative to Bed I. Monahan's (1996a,b) analysis of the HWKE 1–2 fauna suggests that hyenas during at least basal Bed II times were particularly active in lacustrine woodland habitats, which is potentially significant because modern hyenas tend to concentrate their activities in the more open habitats of savanna mosaic environments (Blumenschine, 1986). The Bed I sites in general show higher survival of axial bones and limb bone epiphyses (even from small-sized carcasses) and greater frequencies of complete or nearly complete limb bones. In addition to lower levels of bone destruction, many of the Bed I sites show tooth mark frequencies and patterns of bone modification that are more consistent with large cats than with hyenas (see Dominguez-Rodrigo et al., 2007a,b; Egeland, 2007). This taphonomic shift appears to parallel the changing configuration of the large-carnivore guild, which occurred during middle Bed II times and involved the disappearance of the large felids *Megantereon* and *Homotherium* from eastern Africa at about 1.5 million years ago (Werdelin and Lewis, 2005). This event, as documented both in the paleontological and taphonomic records, is broadly coincident with a general shift towards more open, arid environments within the Olduvai Basin (Cerling and Hay, 1986; Kappelman, 1986; Sikes, 1994,1999). Although climatic change was not unidirectional towards environments that were permanently drier and more open, it is likely that vegetation changes triggered the events that led to the extinction of these cats (Turner and Antón, 1998). Regardless of the reasons for these extinctions, hominids would have encountered a less diverse large-carnivore guild after 1.5 million years ago.

Our recent analyses indicate that among the Bed I faunas excavated by Mary Leakey (1971), only FLK 22 can be considered as largely anthropogenic in origin (Dominguez-Rodrigo et al., 2007a,b; Egeland, 2007). Similarly, only BK shows a significant hominid signal among their Bed II counterparts. Although the socio-economic repercussions of early access and systematic transport proposed for FLK 22, including food-sharing (e.g., Bunn, 2006) and mate- or offspring-provisioning (e.g., Oliver, 1994), may apply to BK, the site's context precludes a definitive statement on this point. Nevertheless, the taphonomic, geological, and paleoecological data do document a diverse pattern of hominid site use during Bed II times. Coupled with nearly 30 years of taphonomic studies of various Bed I assemblages and more recent data from ongoing excavations in basal Bed II (e.g., Blumenschine and Masao, 1991; Cushing, 2002; Blumenschine et al., 2003; Tacktikos, 2005; Pobiner, 2007), there is compelling evidence for significant variability in hominid site use in the Olduvai Basin over a period of about 600,000 years.

Notes:

1 Density for the Bed II sites was calculated by first dividing the depth of each deposit by 9 cm [the average thickness of the Olduvai paleosols (Leakey, 1971)] to estimate the number of "surfaces" represented at each excavation. Second, the number of bones was divided by the number of "surfaces." This number was then divided by the estimated excavation area (see Potts, 1988: 41).

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