THE LARGER MAMMAL FOSSIL ASSEMBLAGES FROM BEDS III AND IV, OLDUVAI GORGE, TANZANIA: IMPLICATIONS FOR THE FEEDING BEHAVIOR OF *HOMO ERECTUS*

by

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ABSTRACT OF THE DISSERTATION

THE LARGER MAMMAL FOSSIL ASSEMBLAGES FROM BEDS III AND IV, OLDUVAI GORGE, TANZANIA: IMPLICATIONS FOR THE FEEDING BEHAVIOR OF *HOMO ERECTUS*

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This dissertation represents the first taphonomically-informed assessment of the feeding behavior of *Homo erectus.* Until now studies of the feeding behavior of Early Stone Age hominins based on the assemblage-wide proportions of tooth, cut, and percussion marks have focused on Oldowan sites attributed to *Homo habilis* leaving assessments of the subsistence capabilities of *Homo erectus* to inference. This trend is the direct result of the river/channel depositional settings for most sites that are attributed to *Homo erectus* and the lack of a theoretically-grounded basis for interpreting fossil assemblages from such sites.

Using a flume I have generated the first experimental sample designed to interpret bone assemblages that were modified by hominins and carnivores and subsequently disturbed by flowing water. Results show that the transportability of bone fragments is inversely related to the size of bone fragments as measured by length,

width, cortical thickness, and indirectly by the size group of the carcass from which the fragments were generated. More importantly, fluvial processes should not significantly alter the assemblage-wide proportions of tooth, cut, and percussion marks in low-energy fluvial environments.

The results of flume experiments are applied here in the first taphonomic analysis of the larger mammal fossil assemblages from JK2, Bed III and WK, Bed IV, Olduvai Gorge, Tanzania. The results for both sites indicate that *Homo erectus* likely acquired earlier access to carcasses than its Oldowan hominin ancestors. However, only the younger WK site exhibits evidence for cooking indicating that the feeding behavior of the species was continually evolving.

The significance of this research lies not only in the results reported for the Bed III and IV fossil assemblages, but also in the methodology that was developed to interpret the results, which is broadly applicable to archaeological sites regardless of age or geographic location. Further application of these methods will allow paleoanthropologists to track the increasingly pervasive role played by Homo erectus in the larger carnivore guild. For it is through this research that the social behavior of the species may ultimately be revealed and a greater understanding of our own behavior and societies can be obtained.

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Chapter 1

Introduction and Background

Research Problem

One of the most important events in human evolution was the dietary shift towards meat-eating that for the first time put our ancestors in competition with large carnivores that remained dangerous predators. While a large body of research concerning Oldowan hominin carnivory has been developed (Blumenschine, 1988; 1995; Bunn and Kroll, 1986; Binford, 1988; Capaldo, 1995; 1997; 1998; Dominguez-Rodrigo, 1997; Oliver, 1995; Selvaggio, 1994; 1998), little is known about the subsistence strategies of Acheulean hominins due to the typical occurrence of Acheulean bone assemblages in fluvial contexts and the paucity of taphonomically oriented studies of these assemblages. Current models of site formation that address the relative timing of hominin and carnivore access to carcasses were designed to interpret bone assemblages associated with Oldowan stone tools, which are typically deposited in lacustrine or low-energy fluvial contexts (Blumenschine, 1988; 1995; Capaldo, 1995; 1997; 1998; Dominguez-Rodrigo, 1997; Selvaggio, 1994; 1998). As a result, with few exceptions, Acheulean bone assemblages had not been studied from an ecological-taphonomic point of view and it was not possible to evaluate the subsistence capabilities of *Homo erectus*, a species with more sophisticated technology, a larger relative brain size and larger body size than its Oldowan hominin predecessors (Shipman and Walker, 1989).

Homo habilis was the first hominin species to regularly incorporate animal foods from larger mammals into its diet. Evidence from Bed I, Olduvai Gorge, suggests that the species acquired larger mammal carcasses through scavenging and typically had access to as much as 50% of the flesh and all bone marrow (see Chapter 2). However,

virtually nothing is known about the carnivorous component of the diet of *Homo erectus*, a species that is characterized by increased brain and body size (Kappelman, 1996; Walker and Leakey, 1993; Wood, 1992).

The metabolic costs associated with greater brain and body mass would likely have required a corresponding increase in nutritional intake through the consumption of higher quality foods (Aiello and Wheeler, 1995; Milton, 1987; Ruff and Walker, 1993; Shipman and Walker, 1989). It has been suggested that *Homo erectus* may have incorporated more animal products into its diet affording individuals the necessary intake of energy to manage increasing metabolic costs (Shipman and Walker, 1989). However, the common assumption that the species was more predatory than its Oldowan hominin predecessors has not been tested and is only supported by the more sophisticated stone tool technology associated with the species, a skeletal morphology that may have been adapted to long distance running (Shipman and Walker, 1989, Bramble and Lieberman, 2004), and the alpha predatory role of its modern descendants. The best test of this hypothesis is to apply feeding trace models that are based on the proportions of tooth, cut, and percussion marks on bone surfaces to fossil assemblages associated with *Homo erectus*.

This dissertation introduces a methodology for interpreting hominin and carnivore behavior from fossil assemblages deposited in fluvial contexts. This methodology is applied to larger mammal fossil assemblages from Beds III and IV (1.15-.6 ma), Olduvai Gorge, Tanzania (Hay, 1976). There are two main research questions addressed in this dissertation. 1) Is the effect of fluvial processes on the proportion of

bone fragments with tooth, percussion, and cut marks great enough to significantly alter the hominin and/or carnivore signal in fossil assemblages disturbed by flowing water. It is predicted that fluvial processes would have had a significant effect on the assemblage-wide proportions of tooth, percussion, and cut marks as bone surface modifications are more likely to occur on longer fragments that are less likely to be transported. 2) How do the carcass processing capabilities of *Homo erectus* (*ergaster*) at Olduvai Gorge during Bed III and IV times differ from those of (presumably *Homo habilis*) during Bed I times? It is predicted that Homo erectus would have obtained earlier access to carcasses than its Oldowan hominin ancestors who were most likely scavengers. Ultimately, these research questions afford the first test of the hypothesis that the encephalization and presumed corresponding reduction of gut size in *Homo erectus* was made possible through an increased intake of animal foods (Aiello and Wheeler, 1995; Milton, 1987; Ruff and Walker, 1993; Shipman and Walker, 1989).

Background

Acheulean Fossil Assemblages

Very few taphonomically informed archaeological investigations of hominin and carnivore interactions have been conducted on bone assemblages created after the emergence of Acheulean technology. Sites that have received this attention include Ambrona, Atapuerca, and Torralba, Spain; Swartkrans, Elandsfontein and Duinefontein, South Africa; Boxgrove, England; and Peninj, Tanzania (Carlos Díez et al., 1999; Cruz-Uribe et al., 2003; Domínguez-Rodrigo et al., 2002; Freeman, 1975; Howell et al., 1991; Klein, 1987; Milo, 1994; Parfitt and Robert, 1999; Pickering *et al.,* 2004a; 2004b; Villa et

al., 2005). While the presence of hominin-modified bone is minimal or absent at most Acheulean sites including Ambrona, Torralba, Elandsfontein, and Duinefontein, bones from Atapuerca, Boxgrove, Swartkrans and Peninj do preserve butchery marks (Carlos Díez et al., 1999; Cruz-Uribe et al., 2003, Domínguez-Rodrigo et al., 2002; Freeman, 1975; Howell et al., 1991; Klein, 1987; Milo, 1994; Parfitt and Robert, 1999; Pickering et al., 2004a; 2004b; Villa et al., 2005).

At Atapuerca the incidences of bone surface modifications are consistent with hominins having had primary access to flesh (Carlos Díez et al., 1999). Further, several of the hominin remains are cut-marked indicating cannibalism at the site (Fernández-Jalvo et al., 1999). At Boxgrove a higher incidence of butchery marks than is typical for later Acheulean archaeological sites, has been used to suggest frequent hunting or scavenging by hominins at the site (Parfitt and Robert, 1999). At Swartkrans and Peninj, hominins are inferred to have obtained early access to carcasses based on a low incidence of tooth marking on long bone midshaft fragments, a high incidence of cut marking on upper limb fragments (humerus and femur), and an incidence of percussion marking that is consistent with hominins breaking the majority of long bones for marrow removal (Domínguez-Rodrigo et al., 2002; Pickering et al., 2004a; 2004b). While the association of stone tools and faunal remains at Swartkrans is uncertain due to the complex and time-averaged nature of the deposits, sites at Peninj demonstrate clear differences in the ecological contexts of accumulations associated with Developed Oldowan tools and Acheulean bifaces (Domínguez-Rodrigo et al., 2001; 2002). Developed Oldowan tools are found close to the lake margin with animal bones that

exhibit evidence of butchery, while Acheulean tools are found in fluvial contexts devoid of associated faunal remains (Domínguez-Rodrigo et al., 2001; 2002), suggesting Acheulean bifaces were used for tasks other than butchery at Peninj.

Excavations at other Acheulean sites, including Olorgesailie, Olduvai Gorge and the Middle Awash have recovered Acheulean bifaces in association with extensive faunal remains (de Heinzelin et al., 2000; Leakey, 1994; Potts et al*.,* 1999). Olorgesailie preserves an association between the bones of 57 giant gelada baboons and over 4000 stone artifacts, which along with breakage patterns lead some researchers to infer hominins were hunting the baboons (Shipman et al*.,* 1981). While additional fossil assemblages have since been excavated at Olorgesailie, they have yet to be subjected to taphonomic analyses (Potts et al*.,* 1999). The Middle Awash Valley of Ethiopia has preserved an extensive record of the Acheulean dating between 1.0 ma and .1 MYR (de Heinzelin et al., 2000). The artifact-bone concentrations preserve bifaces in association with hominin-modified bone, suggesting the possibility for more detailed comparisons with feeding trace models.

<u>Beds III and IV, Olduvai Gorge</u>

Beds III and IV are dated by palaeomagnetism and sedimentation rates, with Bed III dating between 1.15 and 0.8 Ma and Bed IV between 0.8 and 0.6 Ma (Hay, 1976; 1994). Forty-three archaeological occurrences were excavated from Beds III and IV (summarized in Table 1.1), but only seventeen of these have been described in detail (Hay, 1994, Leakey, 1971; Leakey, 1994). The seventeen occurrences described by Leakey (1994) are from seven sites stratigraphically located in Bed IV including, WK, WK

East, WK Hippo Cliff, HEB, HEB EAST, HEB West, and PDK, and two sites located within Bed III; JK and JK2. JK2, excavated by Maxine Kleindienst from 1961-1962, is the only site that was not excavated by Mary Leakey during her 1968-1971 field seasons. Although they have received different site designations, JK and JK2 represent the same archaeological locality. Kleindienst designated the site JK2 during her earlier excavations because Louis Leakey was unsure if it was the same site that he had discovered during his 1931-1932 Olduvai expedition (Pers. com. Kleindienst). Mary Leakey later referred to the site as JK (Leakey, 1994). To avoid further confusion, I will maintain the published terminology using JK when discussing Mary Leakey's excavations and JK2 for Kleindienst's.

Mary Leakey stated that "A detailed study [of modifications on bone surfaces excavated from Bed III and Bed IV], such as that carried out by Dr. P. Shipman on bones from earlier levels at Olduvai (Shipman, 1981) would undoubtedly be rewarding." (Leakey, 1994:311). Leakey is referring to Pat Shipman's scanning electron microscopic analysis of bone from Bed I, Olduvai Gorge. Despite her suggestion, this detailed taphonomic work had never been extended to the fossil assemblages from Beds III and IV. The stratigraphic contexts, detailed descriptions of associated stone tools and brief descriptions of faunal remains for several of the bone assemblages from Beds III and IV were published in Volume 5 of the Olduvai Gorge Monographs (Leakey, 1994). Below is a brief overview of what is known about the sites, focusing on depositional context, bone assemblages, and associated stone artifacts.

Stratigraphic Context and Paleoclimate

Three sedimentary facies are present in the deposits of Beds III and IV, including the eastern fluvial facies, the western fluvial facies and the fluvial-lacustrine facies (Hay, 1976). The eastern fluvial facies accumulated on an alluvial plain sloping gently to the north and west, with sediment transported mostly by braided streams that flowed intermittently throughout the year (Hay, 1976). The western fluvial facies accumulated on a well-watered alluvial plain that sloped southeastward and was deposited by meandering streams ranging from 1-2.5 meters deep (Hay, 1976). Most of the archaeological sites are found in the western fluvial facies where water may have been present throughout the year, as indicated by hippopotamus and crocodile remains (Hay, 1976). The fluvial-lacustrine facies was deposited in streams and intermittent standing water on the margin of a lake (Hay, 1976).

Beds III and IV are only stratigraphically distinct in the eastern Main and Side Gorges (Hay, 1976; 1994). West of FLK the two Beds are combined into one unit termed Beds III-IV undivided. Both Beds III and IV are dominantly claystone with Bed III ranging in thickness from 4.5-11 m and Bed IV ranging from 2.4-7.3 m (Hay, 1976; 1994). Bed III is divided by four different tuffs labeled from 1-4 with 1 being the oldest and the only that is useful in correlating sites. Bed IV contains two marker tuffs, IVA (the lower tuff) and IVB. These tuffs are used to divide Bed IV into three stratigraphic units identified as the Base of Bed IV, Lower Bed IV, and Upper Bed IV (Table 1.2).

Climate during Bed III and IV times appears to have been drier than that recorded during Bed I and II times. A climatic shift occurred at Olduvai Gorge, indicating

a shift to semi-arid conditions after the deposition of Bed II dating between 1.3-1.17 Ma that persisted until .62 Ma (Cerling and Hay, 1986). Oxygen isotopes indicate a mean annual rainfall of less than 800 mm compared with 800-1000 mm during Bed I and II times, while carbon isotopes indicate a dominance of C4 grasses, which made up between 60 and 80% of the vegetation biomass (Cerling and Hay, 1986). This is substantiated by the bovid fauna which suggest that grasslands with scrub and brush were present throughout the area (Gentry and Gentry, 1978; Hay, 1976).

Stone Tool Industries and Faunal

The stone artifact assemblages from Beds III and IV are lumped into either the Acheulean Industry or Developed Oldowan C Industry. While both industries have bifaces in various forms, Leakey (1975) distinguishes them based upon the manufacturing method employed with bifaces representing the Developed Oldowan being made from cores, and those representing the Acheulean made from large flake blanks. More detailed studies of the artifacts from Beds III and IV have revealed significant overlap in the size and shape of bifaces among those assemblages defined as Acheulean and Develop Oldowan C (Callow, 1994; Jones, 1994; Roe, 1994). Both Industries exhibit a range of raw material types including basalt, quartzite, phonolite, trachyte, and nephelinite and both persist until the end of Bed IV times when the Developed Oldowan C dies out, while the Acheulean industry continues through the Masek Beds (Jones, 1994). The relative abundances of different raw materials vary for both Acheulean and Developed Oldowan assemblages, suggesting raw material selection was likely based on the proximity to stone sources. Despite the similarities

between the two industries a general distinction is apparent. Specifically, Acheulean bifaces are made on large flake blanks and are consistent in basic morphology, while those considered to be Developed Oldowan C are more variable in their morphology and often produced from cores (Jones, 1994). Further discussion of the Bed III and IV stone artifacts can be found in Volume 5 of the Olduvai Monographs. Ultimately, the application of new methods including raw material sourcing and morphometric analyses is necessary to understand the transition from Oldowan to Acheulean stone tool types.

The faunal remains from Beds III and IV are abundant (Leakey, 1994). Mammals represented in the described assemblages include Primates, Rodentia, Carnivora, Elephantidae, Equidae, Rhinocerotidae, Suidae, Hippopotamidae, Giraffidae, and Bovidae, the last of which is by far the most numerous taxon (Leakey, 1994). Most of the bones in the assemblages are considered by Leakey to be indeterminate fragments (see table 1.3 for skeletal part profiles of select Bed III and IV sites). Many of these indeterminate fragments have either been lost since their excavation or were dumped on site. Therefore, the numbers of fossils that are available for study from Beds III and IV is far fewer than Leakey's counts would suggest. More detailed information on the Bed III and IV fauna will be discussed in Chapters 4 and 5.

Methods and Theory in Zooarchaeology

Binford's concept of middle-range research argues for the adoption of a scientific approach in archaeological theory that addresses the events and conditions of the past, makes inferences into the dynamics of cultural systems, and gives meaning to the archaeological record (Binford, 1981). This cannot be accomplished without a reasoning

process that converts “observational statements about the present into meaningful statements about the past” (Binford, 1981:22). A basic concept must be accepted for this conversion to be substantiated; the past can be known through inferences drawn from studies of processes in the contemporary world (Binford, 1981). The intellectual tools required for middle-range research are a paradigm, or a conceptual frame of reference consisting of ideas and concepts, and theory, which seeks to explain the world through the use of paradigm.

Binford defines his concept of middle-range research through the goals it should be attempting to achieve. These goals are:

> 1) Accurate means of identification and good instruments for measuring specified properties of past cultural systems.
>
> 2) Reliable cognitive devices that permit the conversion from observation on statics to statements about dynamics.
>
> 3) To build a reliable paradigmatic frame of reference for giving a meaning to selected characteristics of the archaeological record through a theoretically grounded body of research (Binford, 1981:25).

The archaeological record is composed of statics that can be used to infer the dynamics processes that occurred in the past, through the theoretically grounded body of research Binford advocates. In order to create a body of research to be used as a reference tool, archaeologists must study living systems where both dynamics and the static traces they leave can be observed. It is in the study of living systems that Binford provides the guidelines for archaeologists to conduct middle-range research.

In the study of living systems in the contemporary world archaeologists must isolate the different agents in the present that might contribute to a given pattern and develop criteria for the recognition of these agents in the archaeological record (Binford, 1981). This statement is addressing the anthropocentric views of archaeologists in the mid-twentieth century, who chose to ignore the fact that agents of bone modification include carnivores, natural processes, and hominins and not only the latter. The patterns or traces left by different agents must be distinguishable from one another in the present to be useful in diagnosing the agent of bone modification in the archaeological record. This was perhaps one of the most important realizations in the field of archaeology and led to the development of diagnostic criteria used in the identification of different agents of bone modification. Gifford-Gonzalez (1991) outlined a method for identifying taphonomic processes that she presented in a hierarchical model of causal relations. The hierarchy is the basis for the actualistic research presented in this dissertation. The steps in the hierarchy follow:

1) Identify the trace, or mark left on an archaeological specimen that has undergone a taphonomic process.
2) Identify the causal agency or the immediate physical cause of a trace.
3) Identify the effector or the material that modifies the specimen.
4) Identify the actor or the source that creates the trace.
5) Determine the behavioral context
6) Determine the social and ecological context

The conceptual frameworks articulated by Binford and Gifford-Gonzalez have led to the a theoretically grounded body of research that describes bone surface modifications in such a way that the patterns left by different agents can be distinguished from one another (Blumenschine et al., 1996).

Over the past 35 years zooarchaeologists have produced a theoretically grounded body of research by implementing the experimental or actualistic studies advocated by Binford (1981). Much of this research began as a method of identifying and removing the taphonomic overprint from fossil assemblage in order to improve the integrity of paleoecological and paleoenvironmental data (Binford, 1981). This approach to the analysis of faunal remains often considered taphonomy to be a necessary evil in zooarchaeology because it further complicated the analysis of fossil assemblages (Marean, 1995). More recent research has embraced taphonomy by exploiting the marks left on bone surfaces in interpreting the behavior of hominins and carnivores (Blumenschine, 1988; 1995; Bunn and Kroll, 1986; Capaldo, 1995; Gifford-Gonzalez, 1991; Selvaggio, 1994). The actualistically based theoretical framework developed by these and other scientists is the basis for all of the research conducted in this dissertation.

Conclusions

This dissertation seeks to shed light on the feeding behavior of African *Homo erectus*, through studying the refuse produced by the species as it was competing with carnivores for larger mammal carcass foods. This methodology has been successfully applied in interpreting the feeding behavior of *Homo habilis* and has been refined here

to address the challenges associated with generating inferences from Acheulean fossil assemblages that were subject to the effects of fluvial processes. The results of this research are presented in four chapters, two of which (Chapters 2 and 3) have already been submitted for publication.

Chapters 2 and 3 build on the actualistically based theoretical framework developed by previous researchers investigating the feeding behavior of our Early Stone Age hominin ancestors. Chapter 2 validates and refines previously developed feeding trace models using statistical methods that address the relatively small sample sizes on which the models are based. This step was necessary to curb recent criticisms of the methodology and re-establish the primacy of the feeding trace models to interpretations of hominin and carnivore feeding behavior. Chapter 3 describes the effect of fluvial transport on the assemblage-wide proportions of tooth, cut, and percussion marks, on which the models are based. It is also the first systematic study of the transport of long bone fragments by fluvial processes and serves to provide a basis for interpreting the Beds III and IV fossil assemblages.

Chapters 4 and 5 present the results from analyses of the Bed III, JK2 fossil assemblage, and the Bed IV, WK assemblage. These chapters represent the first application of the feeding trace models to fossil assemblages associated with *Homo erectus* and Acheulean bifaces. As such, they are also the basis for interpretations of the feeding behavior of *Homo erectus*.

The interpretive challenges imposed by the overprint of taphonomic processes, particularly those associated with fluvial contexts, are great and can only be met with

the continued advancement of middle-range research and theory building, as prescribed by Binford. This dissertation contributes to the development of a paradigm for the study of Acheulean fossil assemblages.

Site #	Geologic Locality	Name	Stratigraphic Position	Nature of Finds	Industry	Lithology
2	74	Hoopoe Gully	Beds III-IVa: 22-24' above base	Fragmentary faunal remains	None	NR
3	77	Kar. K	Beds III-IVa: Near Base	Artefacts, faunal remains and buffalo skull	Acheulean	NR
4	79	Not Named	Beds III-IVa	Artefacts, bifaces, etc.	Acheulean	Surface
5a	80	RHC	Beds III-IVa: 40' below base of IVb	Artefacts, bifaces, etc.	Acheulean	Quartz Sand
6	80	not named	Beds III-IVa: base	Bifaces and faunal remains	Acheulean	Surface
7	80	Not Named	Horizon Uncertain	Artefact and faunal remains	Acheulean	Surface
8	83	Vth Fault K	Beds III- IVa: 18' below base of IVb.	Remains of 13 antelope skulls and skeletons	Indeterminate	NR
9	84	Kestrel K	Beds III- IVa	A few artefacts	Acheulean	NR
10	84	Handaxe C	Beds III- IVa	Bifaces, etc.	Acheulean	NR
11	84	Rhino K	Beds III- IVa	Partial skull of rhinocero, bifaces	Acheulean	NR
12a	25	FK East	Beds III- IVa: Near base	Bifaces and faunal remains	Acheulean	NR
12b	25	FK West	Beds III- IVa: Near base	Buffolo Skull	None	Surface
14	24	Dal. K	Beds III- IVa	Scattered faunal remains	None	NR
16	23	Not Named	Beds III- IVa	Bifaces, etc.	Acheulean	NR
18a	18	TK, Fish Gully	Beds III-IVa: Conglomerate 8' above base	Scattered bifaces and faunal remains	Acheulean	Claystone
18b	18	TK, Fish Gully	Beds III-IVa: approx. 26' higher than a	Biface, etc. and faunal remains	Acheulean	Claystone
18c	18	TK, Fish Gully	Beds III-IVa: approx. 20' higher than b	Occupation site with many fish remains	Acheulean	NR
18d	18	TK, Fish Gully	Beds III-IVa: approx. 4' higher than c	Occupation site with many fish remains	Acheulean	Claystone
18e	18	TK, Fish Gully	Beds III-IVa: approx. 4' below IVb	Type specimen of *Xenocephalus robustus*, a few artifacts	Indeterminate	Conglomerate
20a	14	JK 1 and 2	Bed III	Occupation site	Indeterminate	Claystone
20b	14	JK 1 and 2	Bed III-IVa: 9' above base	Occupation site with type specimen of *Damaliscus niro*	Acheulean	Sandstone/ conglomerate
20c	14	JK 1 and 2	Bed III, IV	Occupation site remains of Hominid 34	Acheulean	NR
23b	12	EF-HR	Bed IVa:	Bifaces, etc. and faunal remains	Acheulean	NR
24c	11	MK	Bed IVa: Middle of bed	Bifaces, etc.	Acheulean	Siltstone
25b	10	LK	Bed IVa: Reddened horizon above basal sand	Bifaces, etc. and type specimaen *Taurotragus arkelli*	Acheulean	Siltstone with filled fissue

Table 1.1) Summary of sites from Beds III and IV, modified from Leakey (1971) and Hay (1976). Beds III-IV a refers to areas where the beds are not divisible, NR; not reported.

Site #	Geologic Locality	Name	Stratigraphic Position	Nature of Finds	Industry	Lithology
27b	7	CK	Bed IVa: base	Occupation site with bifaces, etc.	Acheulean	Siltstone
27c	7	CK	Bed IVa: 15' above base	Occupation site with bifaces, etc.	Acheulean	Siltstone
29	4	Not Named	Bed IVa: lower part	Type specimen of *Simopithecus leakeyi* and other faunal remains	None	NR
33	53	MLK West	Beds III-IVa: approx. 20' above base	Primate skull of *Colobus sp.*	None	Sandstone
34	52	MLK East	Beds III-IVa: base	Occupation site with bifaces, etc.	Acheulean	Tuff IVb with Conglomerate
35	49	Not named	Beds III-IVa: basal part of beds	Bifaces, etc.	Acheulean	Surface
36	49	Bos K	Beds III-IVa	Artefacts and buffalo skull	Acheulean	NR
37	48	Croc. K	Beds III-IVa	Artefacts, faunal remains inc. croc skull	Acheulean	NR
45b	86	VEK, North side of gulley	Bed IVa: above marker tuff IVA	Parts of skull of Hominid 12	Acheulean	NR
45c	87	VEK, North side of gulley	Bed IVa: base	Bifaces and other artefacts	Acheulean	Claystone
46d	44	HWK, Castle	Bed IVa: base	Bifaces, etc and faunal remains	Acheulean	NR
47	44	HEB/G	Bed IVa	Occupation Floor	Acheulean	Sandstone/ conglomerate Tuff IVA
51b	38,39	Long K	Bed IVa: Various Levels	Scattered artefacts and faunal remains	Acheulean	Surface
52	36	WK	Bed IVa	bifaces, faunal remains and hominid 28	Acheulean	Conglomerate/ Tuff IVB
53b	36	PDK	Bed IVa: in channles cutting through tuff IVA	Biface, etc. and faunal remains on living sites	Acheulean	NR
53c	36	PDK	Bed IVa: Below Tuff IVA	Biface, clever, etc.	Acheulean	Sandstone
56	97	NGC	Bed IVa	Bifaces, etc.	Acheulean	Surface
57a	96	CMK	Bed IVa: basal part	Faunal remains, bifaces and other artefacts	Acheulean	Surface
57b	96	CMK	Bed IVa: sandy level a below IVb	Bifaces, faunal remains	Acheulean	Sandstone, surface
58	95	GTC	Bed IVa: basal part	Bifaces, etc. and faunal remains	Acheulean	Sandstone/ conglomerate
61	95	GRC	Bed IVa	Bifaces, etc. and faunal remains	Acheulean	NR
63b	89	FC	Bed IVa: basal part	Artefacts and faunal remains including skeleton of python	Indeterminate	NR
65	46	GC	Bed IVa: basal part	Bifaces, etc. and faunal remains	Acheulean	Surface
70b	92	SWK	Bed IVa	Bifaces, faunal remains	Acheulean	NR
71d	88	MNK	Bed IVa: basal part	Bifaces, etc. and faunal remains and fragments of Hominid 2	Acheulean	NR

Table 1.1) Continued

Table 1.2) Stratigraphic location of Archaeological sites in Beds III and IV (Leakey, 1994).

Stratigraphic Location	**Archaeological Occurrences**
Upper Bed IV	HEB West Level 1
	PDK Trenches I-III
	WK East C
	WK East A
	WK Upper Channel
Tuff IVB	
Lower Bed IV	WK Intermediate Channel
	HEB West Levels 2a and 2b
	HEB
	HEB East
Tuff IV A	
Base of Bed IV	WK Lower Channel
	PDK Trench IV
	WK Hippo Cliff
Bed III/IV contact	
Bed III	JK and JK2

	Bed III			Bed IV								
Skeletal Parts	JK Pink Siltstone	JK Ferriginous Sand	JK Grey Sand	WK Lower Channel	HEB East	HEB/ HEB West	WK Inter-mediate Channel	WK Upper Channel	WK East A	WK East C	PDK I-III	Total
Skull parts, horn cores	7	31	12	10	4	5	1	38	5	4	6	
Maxillae, manibles	5	18	5	6	6	9	1	25	3	2	2	
Teeth, isolated	60	142	131	31	21	83	11	307	115	61	54	
Axial: vertbre and ribs	11	108	28	17	9	37	6	80	7	7	5	
Scapulae	12	22	2	4	0	5	2	17	6	1	1	
Pelves	2	9	2	4	1	12	3	7	1	3	0	
Fore Limb, Long bones	1	33	4	5	5	16	0	29	2	3	4	
Hind Limb, Long bones	1	19	5	7	2	17	2	17	6	4	10	
Podials, Patellae, etc	2	81	20	16	6	34	5	64	31	5	21	
Indeterminate bone frags	580	10455	3475	6978	805	3454	1343	7349	9461	8010	1200	
Total	681	10918	3684	7078	859	3672	1374	7933	9637	8100	1303	55239
Minimum Number of Individuals	4	36	24	21	13	29	9	48	32	18	16	250

Table 1.3) Skeletal part profiles for fossil assemblages from Bed III and IV (Leakey, 1994).

Chapter 2

Validation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania

Introduction

Evidence of the timing of hominin and carnivore access to carcasses at Stone Age archaeological sites has important implications for understanding the adaptive capabilities of our ancestors during their initial and increasingly pervasive encroachment on the larger carnivore guild (e.g., Shipman and Walker, 1989; Blumenschine and Pobiner, 2007). Tooth, cut, and percussion marks on bone surfaces are the most direct and definitive traces for inferring the carnivorous component of fossil hominin diets, and are also the clearest means for assessing hominins' ecological interactions with carnivores. As such, bone surface modifications are often the basis for interpretations of Stone Age archaeological bone assemblages, with the well preserved and large Oldowan assemblage from the FLK 22 (*Zinjanthropus* site; Leakey, 1971) receiving the majority of the attention (Binford, 1981, 1986, 1988; Bunn and Kroll, 1986, 1988; Oliver, 1994; Selvaggio, 1994, 1998; Blumenschine, 1995; Capaldo, 1995, 1997; Domínguez-Rodrigo, 1997; Marean and Kim, 1998; Marean et al., 2000; Egeland, et al., 2004; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al., 2007a).

Bunn (1981; Bunn and Kroll, 1986, 1988) was the first to use stone tool cut mark evidence for defleshing to suggest hominins had early access to carcasses at FLK 22. Binford (1986, 1988) countered Bunn by concluding that the FLK 22 hominins were only marginal scavengers of carcasses defleshed and ravaged by carnivores, basing his argument largely on the apparent dominance of lower over upper limb elements indicated by Leakey's (1971) skeletal part profiles from the assemblage. However, Bunn's interpretation lacked a statistical and actualistic foundation, and the skeletal part

profiles used by Binford excluded midshaft fragments in long bone element counts (Bunn and Kroll, 1986). Subsequently, Blumenschine (1988, 1995) used the proportion of carnivore tooth-marked and hammerstone-on-anvil percussion-marked bovid long bone fragments derived from experimental butchery and marrow extraction, and observations of free-ranging carnivore carcass consumption in the Serengeti and Ngorongoro ecosystems to suggest that hominins at FLK 22 were scavenging from largely defleshed, abandoned carnivore kills.

The results of Blumenschine's statistical modeling of experimental bone assemblages defleshed and broken by stone tools and/or carnivores were later replicated and expanded upon by Marean (1991) with captive spotted hyenas; in the Serengeti ecosystem by both Selvaggio (1994) with a carnivore-followed-by-hominin scenario and Capaldo (1995) using the full range of skeletal parts; and by Lupo and O'Connell (2002) in an ethnographic context. Despite the large size (hundreds to thousands of specimens) of most of these samples, many of the models derived from them incorrectly use parametric statistics to describe nonparametric data. The models are nonparametric because each comprises a relatively small number of assemblages (groups of bones from a single individual and feeding episode/experimental trial), among which proportions of various feeding traces are not normally distributed. Marean et al. (2000) were the first to acknowledge the nonparametric distributions of the samples and to address the statistical shortcomings of the models using a bootstrap protocol. Their analysis was limited to Marean's sample and did not include Blumenschine's and Capaldo's data.

Efron (1979) introduced the bootstrap method and demonstrated the effectiveness of the technique on a variety of estimation problems. Tibshirani (1988:433) later noted that the bootstrap "provides a useful method for constructing confidence intervals for functional parameters in settings where likelihood methods are not applicable, particularly in nonparametric problems." The bootstrap is applied here to address the nonparametric distributions of assemblage means within the feeding trace models.

Some analyses of FLK 22 long bones have generated discrepant surface mark frequencies, and interpretation of the timing of hominin and carnivore access to carcasses is apparently counter-indicated by cut marks on the one hand, and tooth and percussion marks on the other. Specifically, cut mark data have been used to suggest hominin hunting or "power scavenging" from carnivore kills (e.g., Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Dominguez-Rodrigo, 1997), while percussion and tooth mark data have been used to suggest secondary hominin access to partially defleshed carcasses (e.g., Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998; Blumenschine, et al. 2007). Clearly, there is a need to consider all three mark types simultaneously.

The original feeding trace models refined in this study have been used by a number of researchers to interpret feeding sequences at FLK 22 and other Paleolithic assemblages. The results obtained by these various studies and the sensitivity of the models to consumer sequence are now in question given the statistical limitations noted above. The value of the original feeding trace models and the bootstrap models presented here lies in their ability to distinguish between various sequences of hominin

and carnivore carcass consumption. The models are controls grounded by actualistic observations and are intended to be used as comparative samples of known origin from which unknown feeding sequences associated with archaeological site formation can be inferred. The application here is to the FLK 22 assemblage, but the models are not specific to the site, nor should they be viewed as a simulation of it. As such, the greater significance of the models is that they are broadly applicable, allowing temporal and spatial comparisons between fossil assemblages.

The above mentioned issues are addressed by: 1) validating and refining the statistical models produced by Blumenschine (1995) and Capaldo (1995) using a bootstrap protocol; 2) incorporating a previously unexplored consumer sequence; 3) considering the carcass consumption sequence (Blumenschine, 1986a, b) when interpreting cut mark frequencies; and 4) applying the refined models to all surface traces of hominin and carnivore feeding found on long bones from FLK 22.

Methods

The statistics used here describe five distinct feeding trace models (Tables 2.1 and 2.2), four of which are published and named: Blumenschine's (1988, 1995) hammerstone-only (HO), carnivore-only (CO), and hammerstone-to-carnivore (H-C) models, and Capaldo's (1995) additional H-C sample, and whole-bone-to-carnivore (WB-C) model. The hammerstone-only and hammerstone-to-carnivore models are more appropriately labeled hominin-only and hominin-to-carnivore, respectively, because they also involve complete metal-knife defleshing (see below). A fifth scenario, vulture-to-hominin-to-carnivore (V-H-C), models a three and in some cases four-stage sequence

of carcass consumption. This sample was previously included in Blumenschine's H-C sample, but comprises a separate sample here due to the inclusion of cut mark frequencies not considered in his previous work. All models are based on only the major long bones, including the femur, humerus, tibia, radius-ulna, and metapodials. Long bones are divided into three portions: epiphyseal, near-epiphyseal, and midshaft portions, following Blumenschine (1988). None of the models describe hominin consumption of grease in cancellous long bone ends using boiling technology. As such, any model describing hammerstone breakage of long bones to extract marrow leaves both greasy bone ends still attractive to carnivores, and midshaft fragments that are devoid of edible tissues and ignored by scavengers (Blumenschine, 1988; Blumenschine and Marean, 1993; Capaldo, 1995, 1998).

One Consumer Type

The HO model describes hominins as the only consumer of a carcass, where all bone specimens were defleshed with a metal knife and broken using a hammerstone-on-anvil technique to remove marrow, producing assemblages of specimens with cut and percussion marks, but no tooth marks (details in Blumenschine, 1988). In the CO model, all bones were defleshed by various mammalian carnivores and then fragmented by spotted hyenas, and in one case lions, as they consumed marrow and grease from long bones, producing assemblages of specimens with tooth marking as the only feeding trace (details in Blumenschine, 1988).

Two Consumer Types

The H-C model simulates carnivore scavenging of carcasses from which hominins had consumed all flesh and marrow, producing assemblages with all three types of feeding traces. Unlike Blumenschine's long bone sample (N = 7 assemblages), Capaldo's also included crania, ribs, vertebrae, pelves and scapulae (N = 39 assemblages). Only long bone fragments are included in this analysis, and Blumenschine's and Capaldo's samples are combined here because their published mean tooth and percussion mark frequencies differ by less than three percentage points.

In Capaldo's WB-C model, bones were defleshed with a metal knife before carnivores fragmented them to access marrow and grease, producing assemblages with cut and tooth marks. Capaldo conducted 30 WB-C experiments, but only 19 were included in his analysis due to the complete consumption or removal of bone by carnivores in the others. The sample discussed here is further reduced to 11 experiments by excluding those with sample sizes of less than five bone fragments in order to limit the effect of small sample sizes on mean assemblage values.

Three Consumer Types

The V-H-C sample is composed of five assemblages using long bones from four carcasses, all of which were fed upon by vultures. Some may have been defleshed minimally by carnivores, and one had been defleshed substantially by carnivores prior to their discovery. Most exhibited moderately to highly fat-depleted marrow (Sinclair and Duncan, 1972; Blumenschine and Madrigal, 1993), resulting in reduced or no spotted hyena consumption of hammerstone-generated epiphyseal fragments. Minimal

carnivore defleshing is evidenced by at most marginal gnawing on processes of only proximal long bones. Subsequently, bones were disarticulated with a metal knife and hammerstone-broken to extract all marrow before being left on the landscape for carnivores. As such, specimens in this model collectively bear carnivore tooth marks, in some cases from defleshing and in others from breakage of hammerstone-generated epiphyseal fragments. The specimens in this model can also bear cut marks on epiphyseal fragments and percussion marks on all long bone portions. Despite the involvement of vultures in the defleshing of carcasses, beak and/or claw marks were not observed on any of the V-H-C specimens. Further, raptor damage is usually characterized by "can opener" perforations (Sander et al., 2003:99) or digestive rounding and thinning of bone (Robert and Vigne, 2002), with neither being commonly found on larger mammal long bones or easily mistaken for the diagnostic pits and scores, v-shaped straie and microstriations that precisely characterize tooth, cut, and percussion marks, respectively (Blumenschine et al., 1996). While these assemblages are grouped into one sample due to small numbers of constituent assemblages, they are variable in carcass size, type of initial consumers, and the number and type of elements included, as follows:

Assemblage 1: a sub-adult, animal size group 3 wildebeest (*Connochaetes taurinus*) with moderately fat-depleted marrow that was discovered with virtually no flesh on the bones and with the metapodials covered with skin. Scavenging opportunities included the brain and all other within-bone nutrients. It was likely killed and fed upon by lions (inferred on the basis of marginal gnawing on some long bone

epiphyses) prior to removal of remaining flesh by vultures. Blumenschine disarticulated all long bones and extracted all marrow before placing the hammerstone-broken fragments on the landscape for scavengers.

Assemblage 2: a sub-adult, animal size group 4, buffalo (*Syncerus caffer*) that was discovered by Blumenschine after all flesh had been consumed. Only the tibia is included in the sample. The buffalo had been highly nutritionally stressed as seen in its low-fat marrow. The absence of gnawing on even the femoral greater trochanter and the tuberosities of the ischia and humeri indicates that vultures had likely consumed all flesh. The tibia was hammerstone-broken to remove all marrow, and resulting bone fragments were placed on the landscape for carnivores to exploit.

Assemblages 3 and 4: an adult, animal size group 3 wildebeest with highly fat-depleted marrow. Upon discovery, ten vultures were feeding and a single spotted hyena was in the vicinity. All flesh had been consumed and only the lesser tuberosity of one humerus exhibited marginal carnivore gnawing typically coincident with flesh removal by felids, in this case most likely lions. All limbs were collected and hammerstone-broken. Two bone fragment clusters were placed in different landscape settings for carnivores to scavenge. Assemblage 3 comprised the right forelimb fragments, while assemblage 4 comprised those of the left forelimb and left hindlimb. In both cases, tooth marking was minimal and epiphyses were left unconsumed by scavengers, an apparent result of the poor condition of the animal at death.

Assemblage 5: a juvenile Thompson's gazelle (*Gazella thomsonii*) that is the only carcass representing animal size group 1 in the V-H-C sample. Three jackals, the likely

predators, and 20 vultures were observed to feed on the carcass. Unlike other V-H-C assemblages, this is the only one to have been defleshed largely by mammalian carnivores. Subsequent defleshing by vultures justifies the inclusion of the assemblage in the V-H-C sample. Vultures are capable of completely consuming small flesh scraps left by carnivores that would otherwise have been available for hominins to scavenge, thereby depressing cut mark frequencies. Remaining food comprised all podium skin, flesh scraps on the humerus and radius, and within-bone nutrients. After hammerstone breakage, all bones were left for carnivore scavengers to consume.

The FLK 22 Assemblage

Data presented in this paper for the incidences of tooth-, percussion-, and cut-marked bones from FLK 22 are based on Blumenschine's (1995) analysis of the assemblage. Details on the coding of marks and the sample (NISP = 731) used can be found in Blumenschine (1995) for tooth and percussion marks, and in Capaldo (1997) for cut marks. The tooth and percussion mark frequencies for FLK 22 presented here were taken from Blumenschine's (1995) Table 3, while the cut mark data were generated anew from his database. Data for the incidence of specimens both tooth-marked and cut- and/or percussion-marked (tooth- and butchery-marked throughout) were also generated from Blumenschine's database. This class of marked bone was used by Selvaggio (1994, 1998) to describe specimens bearing feeding traces produced by both hominins and carnivores.

Bootstrap Methods

A bootstrap sample must reflect the structure of the original sample in order to estimate the sample distribution (Tibshirani, 1988; Efron and Tibshirani, 1993). In the case of this study, there are five models, each comprised of *N* assemblages (groups of bones from a single individual and feeding episode/trial) that are each comprised of *n* specimens. Thus, the bootstrap algorithm used here accounts for the number of assemblages within each model and the number of specimens within each assemblage.

The Bootstrap Algorithm

A bootstrap algorithm developed using R version 2.8.1 (The R Foundation for Statistical Computing, 2008) was applied to the data on the presence and absence of bone surface modifications (tooth, percussion, and cut marks) within the modern control assemblages. This algorithm consisted of three functions that generated bootstrap distributions of assemblage bone modification proportions for each model. The first function is designed to provide equal potential weight to each bone within a given assemblage. The second function provides equal potential weight to each assemblage within a given model and weights the bootstrap samples according to the number of assemblages within each feeding trace model. The third function replicates the first two 10,000 times. The three functions used are explained in detail below using the WB-C model as an example.

The first function selects an assemblage at random from a given feeding trace model. For example, one assemblage would be selected at random from the eleven comprising the WB-C model. The data for the assemblage are selected and are equal to

bone modification type, in this case the presence or absence of tooth marks on each specimen. The function then determines the number of specimens (*n*) that are within the selected assemblage and resamples the data (tooth marks) with replacement *n* times to create a bootstrap replicate of the assemblage. A specimen can be selected more than once or not at all providing equal potential weight to each specimen. The final step of this function is to obtain the mean proportion of specimens that were modified, in this case tooth-marked. At this stage, obtaining the mean in the algorithm serves to model the proportion of specimens from a single assemblage that are tooth-marked.

The second function applies the first function *N* times, with *N* being equal to the number of assemblages in the model that is being resampled. For the WB-C model, the first function is applied eleven times, and any of the eleven assemblages that comprise the WB-C model may be selected more than once or not at all, providing equal potential weight to each assemblage. This generates eleven different means for the proportion of tooth-marked bone that are then averaged into a single mean. At this stage there is a single bootstrap replicate of the WB-C model. The reduction of variability that results from taking the mean of means is necessary to allow the bootstrap algorithm to accommodate the disparity in the number of assemblages among models. If the second function had not accounted for the number of assemblages in a given model, variability would have increased with sample size, rather than decrease as expected.

The third function applies the second function 10,000 times, producing 10,000 randomly generated means, which are then used to calculate the summary statistics on

central tendency and dispersion. At this stage, the WB-C model has been replicated 10,000 times. This process is repeated for each model and type of bone modification (tooth marks, cut marks, percussion marks, and tooth and butchery marks). In the case of the WB-C model, this included tooth, cut, and tooth and butchery marks, but not percussion marks as the model describes bone breakage by carnivores rather than hominins.

Samples sub-divided by animal size groups and long bone portion represent separate samples of 10,000 means, rather than a portion of the original bootstrap sample. The bootstrap samples for each bone modification type were generated independently, such that the tooth- and butchery-marked class was created as a separate category within the original non-randomized database prior to applying the bootstrap.

Interpreting Bootstrap Distributions

The bootstrap distributions presented model 10,000 possible outcomes that represent the behavioral processes that created the original non-randomized feeding trace models. As such, had a second bootstrap been conducted, the 10,000 values generated and the summary statistics describing their distribution would differ slightly from the first. It is also important to note that the bootstrap distributions only reflect the conditions (e.g. habitat, number/type/hunger of carnivore consumers, and butchery tools used) under which the original experiments were generated.

Standard box and whiskers plots and 95% interquantile ranges are used to depict the bootstrap distributions. The 95% interquantile ranges are based on the 2.5% and

97.5% percentiles for the distributions of means in the bootstrap samples and can more generally be referred to as bootstrap confidence intervals (Efron and Tibshirani, 1993). The 95% interquantile ranges are used to assess differences among models at the 0.05 level of probability and can be interpreted much like a traditional 95% confidence interval. Here, when the 95% interquantile ranges overlap among models, the models are considered to be indistinguishable. When they do not overlap they are considered as likely distinct.

Results

Percussion Marks

The incidences of percussion marking from the HO, H-C, and V-H-C models are statistically indistinguishable from one another with one exception: the 95% interquantile ranges for all size group 3-4 long bone fragments in the HO and H-C models do not overlap (Table 2.3, Figures 2.1a-c). Despite overlap among the size group sub-samples and among the bone portion sub-samples of the bootstrapped models, the mean incidence of percussion marking in the HO model is generally slightly higher than in the H-C and V-H-C models. The only exception is for size group 1-2 midshaft fragments, where the H-C model has the highest mean incidence of percussion-marked specimens.

The incidence of percussion marking in the FLK 22 assemblage falls within the 95% interquantile ranges of all size group and bone portion sub-samples of the bootstrapped V-H-C model. FLK 22 is slightly below the 95% interquantile ranges of all long bone fragments from both the combined size groups and size group 3-4 of the HO

model, and is slightly above them for size group 3-4 midshaft fragments of the H-C model.

Tooth Marks

The incidence of tooth marking differentiates the CO and WB-C models from the H-C and V-H-C models for all long bone fragments and midshaft fragments of the combined size groups (Table 2.4, Figure 2.2a). However, when broken into size group sub-samples, the discriminatory power of the models is weakened by overlap in the relatively large 95% interquantile ranges for all long bone fragments and midshaft fragments of size group 1-2 (Figure 2.2b) of the V-H-C model, and for midshaft fragments of size group 3-4 (Figure 2.2c) of the WB-C model.

For all size groups combined and for size group 3-4, the incidence of tooth marking in the FLK 22 assemblage is outside the 95% interquantile ranges for nearly all sub-samples of all models. The exception is for midshaft fragments of all size groups combined and of size group 3-4, where FLK 22 is within the 95% interquantile ranges of the WB-C model. For all long bone fragments and midshaft fragments of size group 1-2, the value for the FLK 22 assemblage falls within the 95% interquantile ranges of the CO and WB-C models, and is marginally above the 95% interquantile range of the V-H-C model.

Cut Marks

The incidence of cut marking does not differentiate most sub-samples of the bootstrapped models (Table 2.5, Figures 2.3a-c). For all size group 3-4 long bone fragments, the 95% interquantile ranges of the H-C and V-H-C models overlap, but are

statistically distinct from the intervals of the overlapping HO and WB-C models. For the V-H-C model, cut marking is absent in the size group 1-2 sub-sample of all long bone fragments, and in all size group sub-samples of midshaft fragments.

The incidence of cut marking in the FLK 22 assemblage falls within the 95% interquantile ranges of all sub-samples of only the H-C model. For all long bone fragments, the value for FLK 22 also falls within the 95% interquantile ranges of the WB-C model for all size groups combined and for the size group 1-2 sub-sample. For all size group sub-samples of midshaft fragments, the value for FLK 22 is within the 95% interquantile ranges of both the HO and WB-C models, but not the V-H-C model.

Tooth and Butchery Marks

The incidence of specimens bearing both tooth and butchery marks does not differentiate the bootstrapped models for most sub-samples (Table 2.6, Figures 2.4a-c). The exception is for all long bone fragments of the size group 3-4 sub-sample, where the 95% interquantile range of the WB-C model is above that of the H-C model. Generally, the WB-C model has the highest mean incidence of specimens bearing both tooth and butchery marks. The only exception is for midshaft fragments of the size group 1-2 sub-sample, where the V-H-C model has the highest value.

The incidence of specimens bearing both tooth and butchery marks in the FLK 22 assemblage is higher than the 95% interquantile ranges of most sub-samples of the WB-C and V-H-C models, and all sub-samples of the H-C model. For all long bone fragments, the value for FLK 22 falls within the 95% interquantile ranges of the combined size groups and the size group 3-4 sub-sample of the WB-C model. For midshaft fragments,

the value for FLK 22 falls within the 95% interquantile ranges of the size group 1-2 sub-sample of the V-H-C model and the size group 3-4 sub-sample of the WB-C model.

Discussion

The Bootstrap Method Refines and Validates the Feeding Trace Models

The results of random resampling with replacement of data from feeding trace models validate Blumenschine's (1988, 1995) and Capaldo's (1995) published claims of the models' ability to discriminate the general identity, sequence, and tissues extracted by consumers of larger mammal long bone flesh, marrow, and grease. The CO model is distinguished from all others in having very high tooth mark frequencies along with an absence of percussion and cut marks. The HO model is distinguished from all others in having high percussion and cut mark frequencies, but an absence of carnivore tooth marks. The 95% interquantile ranges for both of these models closely approximate the 95% confidence intervals reported by Blumenschine (1995). The H-C model differs from the previous two in bearing all three types of marks, and is distinct from the WB-C model in the latter's absence of percussion marks. Further, the H-C model is distinct from the V-H-C model because it has cut marks on midshaft fragments not present in the latter. Blumenschine's and Capaldo's published 95% confidence intervals for H-C are similar to the 95% interquantile range that describes their combined H-C samples. Capaldo's published 95% confidence intervals for the WB-C model are slightly smaller than the 95% interquantile ranges, which describe a sample reduced by exclusion of assemblages with fewer than 5 specimens.

The bootstrap also improves the discriminatory power of sub-samples of the models, the usefulness of which were limited previously by large 95% confidence intervals resulting from small sample sizes. For example, the bootstrap reduced the interval indicative of significance at the 0.05 level within the size group 1-2 sub-sample of the CO model from 33.1-100% tooth-marked to 56.7-82.5% tooth-marked. Additionally, the bootstrap approach allows the use of 95% interquantile ranges to describe models comprised of a single assemblage (i.e. size group 3-4 of the HO model and size group 1-2 of the V-H-C model). This last point applies with the caveat that bootstrap distributions built from a single assemblage may reflect fewer conditions affecting rates of bone modification than those built from multiple assemblages.

Finally, the bootstrap has refined the models by allowing us to detect a sub-division of the H-C model on the basis of whether vultures or hominins removed the flesh. The V-H-C model was originally lumped together with the H-C model by Blumenschine (1995) because he was not considering cut marks, having used a metal knife instead of stone flakes to deflesh the bones. Modeled cut mark frequencies may differ in unknown ways if a stone flake had been used instead of a metal knife for butchery. Yet, the low or complete absence of cut marking for all size group and bone portion sub-samples of the V-H-C model differentiates it from the H-C model and also from the HO and WB-C models. In particular, cut marks within the V-H-C model result from disarticulation only, as reflected by their absence on midshaft fragments. Additionally, some assemblages in the V-H-C model were observed or inferred from marginal bone gnawing to have experienced some defleshing by carnivores prior to or

coincident with vulture access. In one case, assemblage 5, the only size group 1-2 assemblage, jackals were observed to have consumed all but flesh scraps from the long bones. This produced the relatively high mean incidence of tooth marking on long bone midshafts in assemblage 5 when compared with size group 1-2 of the H-C model and size group 3-4 of the V-H-C model (Figure 2). In fact, the incidence of tooth marking in Selvaggio's (1998) carnivore-to-hominin-to-carnivore model, of which assemblage 5 is an example, lies within the upper end of the 95% interquantile range for this assemblage, but is beyond the range of all other models' size group 1-2 sub-samples.

Unwarranted Doubts Surrounding the Use of Feeding Trace Models

The validity and discriminatory power of feeding trace models have been questioned by Lupo and O'Connell (2002) and Faith (2007). For example, Faith (2007:1602) states,

> "Doubts surrounding the usefulness of bone surface modifications stem from a large and currently inexplicable range of variation across experimental and archaeological assemblages. It is clear that unless the sources of variability can be identified and corrected for in our analytical frameworks, bone surface damage patterns will continue to be problematic as indicators of the timing and impact of human and carnivore agents on archaeological bone assemblages."

Yet the source of variability is known, reported unambiguously in the description of the flesh consumers and bone breakers in the original published definition of each model (Table 2.1). These descriptions show that Lupo and O'Connell's and Faith's characterizations of the models as "human-first," "carnivore-first," or "carnivore only" are oversimplified, thereby masking the full range of behavioral processes (defleshing, bone breakage, and/or grease removal) simulated by the various models. The

descriptions also reveal that Lupo and O'Connell (2002: Figure 3), Faith (2007: Figure 1), and others (Marean et al., 2000: Table 3; Domínguez-Rodrigo and Barba, 2006: 171) have misclassified the WB-C model variously as "carnivore first" or "carnivore only". As well, they inappropriately lump into "carnivore first" both Selvaggio's (1994, 1998) carnivore (defleshing only) to hominin (defleshing and marrow removal) model and Blumenschine's CO model.

The WB-C is a "human first", not "carnivore first" or "carnivore only" model, because it describes total flesh removal with a metal knife prior to carnivore access (see Capaldo, 1995: 55-58; 1997: 565-566; 1998: 314-315). The absence of defleshing by carnivores depresses tooth mark frequencies below those in the CO model, but they remain significantly higher than the H-C model because the WB-C model describes carnivore breakage of epiphyseal ends and midshaft cylinders. Likewise, the lower rate of tooth marking on Selvaggio's (1998) carnivore-to-hominin model (65.7%) relative to that on CO, results from an absence of bone-breaking tooth marks. Hence, cut mark values co-vary with the tooth mark values: the lower rate of tooth marking on both the WB-C model and Selvaggio's carnivore-to-hominin model relative to CO is matched by the presence of cut marks in the former pair, but not CO, and additionally for Selvaggio's model by the presence of percussion marks. Similarly, the higher tooth mark values on WB-C relative to H-C results from carnivore breakage of intact long bones in the former *versus* only hammerstone generated epiphyseal fragments in the latter. Conversely, the WB-C model lacks percussion marks present in the H-C model.

When comparisons of mark frequencies are limited to independently produced models that describe the same actions of hominins and carnivores, a remarkably high degree of correspondence is evident. Hence, Marean's and Blumenschine's CO models produced overall mean tooth marking frequencies within six percentage points of one another, while their and Capaldo's H-C model have a three-way correspondence of mean tooth mark frequencies that differ by less than seven percentage points. Therefore, the claim of a large range of variation across comparable models is false.

Claims of low inter-analyst correspondence in surface mark estimates of the FLK 22 assemblage (Lupo and O'Connell, 2002; Domínguez-Rodrigo and Barba, 2006) are also unwarranted (Blumenschine, 1995; Blumenschine et al., 2007a). Lupo and O'Connell (2002) cite statistical differences between tooth and cut mark frequencies on long bone specimens recorded independently by Blumenschine (1995) and Oliver (1994). Oliver reported a lower frequency of tooth-marked bone than Blumenschine. He also reported a higher frequency of cut-marked bone than Blumenschine, whose data were first reported by Selvaggio (1994) and Capaldo (1997). Lupo and O'Connell (2002:97, 99) correctly hypothesized that either the researchers did not use the same samples in their analyses, or the criteria used for the identification of tooth and cut marks were defined differently. In fact, both the samples analyzed and the criteria used for the identification of bone surface modifications, described fully by Blumenschine (1995) and Oliver (1994) within the methods sections of their respective papers, differ considerably. Oliver's (1994) analysis was based on a larger sample than Blumenschine's, probably because Blumenschine explicitly excluded specimens smaller

than 2 cm in maximum length, as well as those with poor surface visibility and/or recent breaks. Oliver's inclusion of specimens smaller than 2 cm and with poor surface visibility would likely depress frequencies of all marks, while his inclusion of specimens with major recent breaks would have an unpredictable effect on tooth and cut mark frequencies. More importantly, Oliver (1994:272) was overly conservative in his identification of tooth marks stating,

> "pits and scores define carnivore activity only if (1) the two co-occur on the same area of bone, (2) one or the other occur in large numbers so that there is little doubt that potential mimics could not have produced the marks, and/or (3) they are associated with other more diagnostic carnivore-induced damages such as furrows, punctures and lever-up breaks."

These criteria will always produce underestimates of tooth mark frequencies compared to those such as Blumenschine's and Capaldo's that include less conspicuous and solitary tooth marks. Specimens with such marking are common in control collections. Blumenschine et al. (1996) have shown that they are morphologically diagnostic and reliably identified in blind testing by both experienced analysts, and by novices with as little as two hours experience with control collections.

More recently, Domínguez-Rodrigo and Barba (2006) argued that the incidence of tooth marking on long bone midshaft fragments from FLK 22 is significantly lower (11%) than the numbers reported by Blumenschine (1995; 57.9%). They claim that Blumenschine (1995) confused the assemblage's previously undescribed "biochemical marks" produced by microorganisms with carnivore tooth marks, resulting in a revised estimate of tooth mark proportions consistent with the H-C model. However,

Blumenschine et al. (2007) show that Domínguez-Rodrigo's and Barba's (2006) assertion that microbes will bioerode bone surfaces in ways that mimic carnivore tooth marks is unsubstantiated due to general methodological flaws that have yet to be remedied.

When Oliver's (1994) and Domínguez-Rodrigo's and Barba's (2006) analyses are excluded, strong inter-analyst correspondence of tooth mark estimates at FLK 22 is evident. In fact, Blumenschine's (1995) estimate for the frequency of tooth marking in the FLK 22 assemblage is the only one that has been independently replicated. Capaldo also recorded relatively high tooth mark frequencies on long bone midshaft fragments (49.0%, see Blumenschine et al., 2007b). The slightly lower incidence of tooth marking observed by Capaldo is most likely related to the larger sample that he used (n=1153). Many (28.0%) of the additional specimens Capaldo included are small bone fragments (2 to 3 cm in maximum length), which have been shown to be tooth-marked at lower frequencies than their larger counterparts (Blumenschine, 1988, 1995; Faith, 2007). Blumenschine's and Capaldo's similar estimates arise because both analysts have extensive experience with bone tooth-marked by carnivores under controlled conditions. Both also employ the same published criteria for identifying conspicuous and inconspicuous tooth marks, use the same standards to create the analytical sample of specimens from FLK 22 upon which mark frequencies are based, and have been successfully blind-tested on bone surface mark identification (Blumenschine et al., 1996). Most importantly, both independent tooth mark frequency estimates are intermediate to the 95% interquantile ranges of the H-C and CO models, indicating that neither model describes the dominant feeding interactions at FLK 22.

Implications for Hominin and Carnivore Behavior at FLK 22

Results indicate the pattern of feeding traces found at FLK 22 cannot be accounted for by some of the models. Most clearly, the co-occurrence in the assemblage of tooth-marked specimens and butchery-marked specimens eliminates individually the CO and/or HO models as exclusive descriptors of the behavioral sequences that produced the FLK 22 assemblage. Likewise, individual specimens bearing both tooth and butchery marks eliminate a combination of CO and HO as exclusive descriptors.

Results also indicate the pattern of feeding traces found at FLK 22 can be accounted for by some of the behavioral sequences modeled by the experimental assemblages. Other sequences thus far unexplored by feeding trace modelers might also account for the FLK 22 pattern. For example, hominins cannot be discounted as tooth mark producers on at least some bones (White & Toth, 2007). Hominin tooth marking might be expected principally on long bone fragments of size group 1-2 animals, but is less likely to contribute to the frequency of tooth-marked bones from larger animals. In fact, size group 1-2 long bones from FLK 22 are tooth-marked more frequently than their size group 3-4 counterparts, suggesting the possibility that some of the tooth marks were inflicted by hominins. Still, the models available are ecologically realistic (Blumenschine, 1986b), and are consistent with what is known of Plio-Pleistocene East African carnivore guild structure (Werdelin and Lewis, 2005).

The bootstrap results support Blumenschine's (1995) contention that the incidence of percussion marking in the FLK 22 assemblage indicates hominins to have

been the primary consumers of marrow at the site. FLK 22 is within or close to the 95% interquantile ranges for all of the site formation models that describe primary access to marrow by hominins. When compared with the HO model, the slightly lower incidence of percussion marking in the FLK 22 assemblage for all long bone fragments, and the nearly identical incidence of percussion marking for midshaft fragments, is indicative of bone-crunching carnivores having deleted from the site or partly consumed percussion-marked epiphyseal and near-epiphyseal specimens from bones that were hammerstone-broken by hominins. The incidence of percussion marking at FLK 22 is most similar to the H-C model for size group 1-2 and the V-H-C model for size group 3-4.

The incidence of tooth marking in the FLK 22 assemblage is consistent with carnivores, not hominins, having primary access to flesh. FLK 22 has a far greater incidence of tooth marking than is predicted by the H-C model. The similar incidences of tooth marking at FLK 22 and in the WB-C model, which simulates hominin defleshing of carcasses prior to carnivore scavenging, is not surprising, nor does it counter the hypothesis that carnivores were the primary consumers of flesh at the site. Defleshed but unbroken long bone shafts are highly attractive to bone-crunching carnivores, which in exposing marrow cavities produce tooth-marked fragments at frequencies only slightly lower than those described by the CO model. However, fragmentation and extraction of marrow by hominins (i.e., the H-C and V-H-C models) leaves nutritionally unattractive midshaft fragments; the relatively few tooth-marked midshaft fragments are produced through carnivore fragmentation of hammerstone-generated epiphyseal fragments when they subsequently access grease. Of course, the WB-C model as the

dominant process is rejected because it lacks percussion marks, which are present in high frequencies in the FLK 22 assemblage.

The incidence of tooth marking on size group 1-2 midshaft fragments at FLK 22 is only slightly above the 95% interquantile range for the one assemblage (5) of like-sized specimens from the V-H-C model. Because this assemblage represents carnivore defleshing, this result is fully consistent with indications from tooth marks described above. The incidence of tooth marking on long bone midshaft fragments for all size groups from FLK 22 (57.9%) is also similar to the mean incidence of tooth marking for midshaft fragments from Selvaggio's (1998) carnivore-hominin model (47.0%) and especially her carnivore-to-hominin-to-carnivore model (54.2%), both of which also describe carnivores having primary access to flesh and hominins having primary access to marrow.

The relatively high incidence of cut marking in the FLK 22 assemblage is consistent with hominins having had access to flesh on many skeletal parts, but this does not contradict the tooth marking results. The frequency of cut-marked bone in the FLK 22 assemblage is nearly identical to that for all sub-samples of the H-C model, which simulates hominins having had sole access to flesh, and is higher than predicted by all sub-samples of the V-H-C model. Particularly interesting is the high incidence of cut marking on long bone midshafts from FLK 22, and the absence of cut-marked midshafts in the V-H-C model, indicating many of the cut marks in the FLK 22 assemblage may be related to defleshing. However, whether this reflects defleshing of whole muscle masses or only the still attractive scraps that typically remain after mammalian

carnivore defleshing is uncertain: Cut mark frequencies have not been shown to be sensitive to the amount of flesh remaining on bones (Capaldo, 1998; Pobiner and Braun, 2005; Blumenschine and Pobiner, 2007).

The apparent contradiction between tooth and cut marking is resolved by examining the distribution of cut marks among flesh bearing long bone elements at FLK 22 (Table 2.7). A chi-square test of association demonstrates that the incidence of cut marking on humeral midshaft fragments (39.5%) is significantly greater than on femoral midshaft fragments (12.5%; $p = .02$, $X^2 = 5.19$, d.f. = 1). The same pattern was noted by Oliver (1994:280) for all long bone fragments, but his interpretation of the data was focused on the "preferential placement of cut marks on meaty limbs," speculating that the paucity of cut marks on the femur resulted from a deficiency of femoral ends in the assemblage. The above data show this difference is apparent despite the exclusion of long bone epiphyses. It is also predicted by Blumenschine's (1986a, b) carcass consumption sequence, which demonstrates that carnivores typically consume the higher yielding upper hindquarter flesh prior to forequarter flesh. As well, tibia midshaft fragments are cut-marked more frequently (33.3%) than midshafts from the radius/ulna (19.6%), but, as expected from their near equivalent ranking in the carcass consumption sequence, this difference is not significant at the .05 level. Overall, the pattern of cut marking in the FLK 22 assemblage is consistent with hominins typically having access to humerus flesh more often than femur flesh. This indicates that hominins may have been acquiring carcasses after carnivores had defleshed at least the upper hindquarters, and possibly the lumbar vertebrae and the rib cage. This would yield approximately

50% of total flesh weight of bovids if the remaining parts were fully fleshed (Blumenschine and Caro, 1986), or much lower amounts if they had been partially consumed. These interpretations apply with the caveat that differences in soft tissue anatomy between the forelimb and hindlimb may influence cut mark frequencies in currently unknown ways.

The high incidence of specimens bearing both tooth and butchery marks for FLK 22 supports hominins having typically acquired carcasses partially defleshed by felids. Such high incidences are only described by models that have high frequencies of tooth marks on long bone midshaft fragments, including the WB-C model, assemblage 5 of the V-H-C model, and Selvaggio's (1998) carnivore-to-hominin and carnivore-to-hominin-to-carnivore models (which have 95% confidence intervals of 15.0-36.0% and 18.0-43.2%, respectively, for the incidence of specimens bearing tooth and butchery marks). However, all of the butchery marks for the WB-C model are cut marks, while those from FLK 22 also include percussion marks, such that only the remaining models that describe carnivore defleshing prior to hominin access fit the co-occurring tooth and butchery mark data.

The high incidence of specimens bearing both tooth and butchery marks at FLK 22 does not allow rejection of a common amenity scenario for the assemblage, as has been argued by Egeland et al. (2004). The high incidence of tooth marks suggests a possible CO assemblage component, while the high incidences of cut and percussion marks suggest a possible HO component. However, these components would involve the minority of carcasses, with most being best described by the carnivore-to-hominin-

to-carnivore model. On the other hand, a high incidence of tooth- and butchery-marked specimens could result from hominins having had variable points of initial access in the carcass consumption sequence. Hominin access early in the consumption sequence of some carcasses could produce a dominance of butchery over tooth marks on these bones, while late access could produce dominantly carnivore tooth-marked bone. All of these scenarios are consistent with new information that specifies the paleolandscape setting of FLK 22, including a lightly wooded peninsula at which hominins might have acquired tree-stored leopard kills, and an adjacent wetland at which carnivores seem to have ambushed prey and left scavengeable carcasses that could be exploited by hominins (cf. Blumenschine et al., in review).

Finally, a low incidence or absence of midshaft specimens bearing both tooth and butchery marks does not provide evidence that hominins and carnivores fed on different carcasses. For example, Egeland et al. (2004) claim that the low incidence of such specimens in the Early Pleistocene large mammal assemblage from Swartkrans (2.3%) implies such independent feeding by hominins and carnivores. Instead, the ranges of the WB-C (0-27.8%), H-C (1.5-10%), and V-H-C (0-22.9%) models accommodate the Swartkrans value despite the dual consumption of all carcasses by hominins and carnivores they describe.

Conclusions

Refinement and expansion of feeding trace models produced by Blumenschine (1995) and Capaldo (1995) through resampling validates the primacy of bone surface modification studies for inferring the behavioral ecology of hominin carnivory. It has

been shown that published criticisms of these models are unfounded and that the models can be used to test hypotheses about hominin subsistence ecology. Other interpretive criteria such as skeletal part and age profiles (Klein, 1980; Shipman et al., 1981; Cruze-Uribe, 1991) have not been shown to be sensitive to the order in which hominins and carnivores accessed carcasses largely because they are influenced heavily by density-dependent destruction of bone (Marean et al., 1992; Lam et al., 1998). As such, the frequency of bone surface modifications should be emphasized in behavioral analyses of archaeological assemblages bearing traces of both hominin and carnivore carcass consumption. This prescription comes with the caveat that analysts reporting surface mark frequencies use the same criteria for excluding specimens from which surface mark frequencies are to be calculated, have experience with collections of bones marked by known consumers under controlled conditions, use published criteria for differentiating marks, and have demonstrated the reliability of their identifications through blind testing using control collections.

Doubts surrounding the usefulness of bone surface modification models have stalled their further development by other researchers for nearly a decade. The results presented here justify their refinement with the goal of expanding the range of modeled behaviors, environments, and consumers sequences.

The integration of tooth, cut, and percussion mark data, and consideration of the carcass consumption sequence to explain cut mark distributions, provides evidence for a more specific scenario of hominin and carnivore carcass consumption for the FLK 22 assemblage than was possible previously. Percussion mark frequencies for FLK 22

suggest that hominins broke the majority of long bones. Tooth and cut mark data indicate both hominins and carnivores had access to flesh, although whether hominin access was to entire muscle masses or only scraps, as suggested by Selvaggio's (1994, 1998) models, is uncertain. Finally, the high incidence of specimens that are both tooth- and butchery-marked demonstrate frequent hominin and carnivore feeding from the same carcasses.

Together these data are consistent with a dominant three-stage carnivore-to-hominin-to-carnivore model of site formation. In the first feeding stage, carnivores (most likely felids) typically consumed at least upper hindquarter flesh and possibly all axial flesh posterior to the cervical vertebrae before abandoning the carcass or being displaced from it by hominins. In the second feeding stage, hominins typically acquired carcasses affording all within-bone tissues and at least widespread flesh scraps if not whole muscle masses usually from the forequarters, neck, and head. Whether this was through passive scavenging of abandoned kills (cf. Blumenschine, 1986b, Cavallo and Blumenschine, 1989), or through active appropriation of attended, but partially consumed carcasses (cf. Bunn and Ezzo, 1993; O'Connell et al., 2003) cannot be ascertained from the feeding trace models currently available. In the third and final feeding stage, bone-crunching carnivores (most likely hyaenids) consumed grease within hammerstone-broken long bone epiphyseal fragments and marrow from any long bones shafts left unbroken by hominins. This three-stage feeding trace model explains the at-first contradictory tooth (Selvaggio, 1994, 1998; Blumenschine, 1995; Capaldo, 1995,

1997) and cut (Domínguez-Rodrigo, 1997) mark data, and is consistent with the lack of evidence for hunting technology in the Oldowan.

The evolutionary significance of conclusions based on the bootstrapping results for FLK 22 lies in the indication that the initial encroachment by hominins on the larger carnivore guild during the Oldowan may have been in the role of a scavenger. However, application of the feeding trace models to additional sites of similar age is necessary to determine whether the results for the FLK 22 assemblage are specific to the site or are indicative of the subsistence capabilities of our Plio-Pleistocene ancestors. Conversely, the one published application of these models to later time periods, Marean and Kim's (1998) results for the assemblage from the Middle Paleolithic site of Kobeh, Iran, are best described by the H-C model, suggesting a more dominant hominin role in the carnivore guild characterized by either early confrontational scavenging or hunting. Thus, the models if more broadly applied will allow paleoanthropologists to track the increasingly pervasive role hominins played in the larger carnivore guild throughout the Plio-Pleistocene, an evolutionary transition that has culminated in modern humans' super-predator status in most terrestrial and some aquatic ecosystems.

Table 2.1) Nomenclature for feeding trace models used in this study

Feeding Trace Models with Abbreviations	Foods Extracted from Long Bones		
	Flesh	**Marrow**	**Grease**
One Consumer Type			
Carnivore-Only (CO)	Carnivore	Carnivore	Carnivore
Hammerstone-Only (HO)	Hominin	Hominin	Not Applicable
Two Consumer Types (hominin first)			
Hammerstone-to-Carnivore (H-C)	Hominin	Hominin	Carnivore
Whole-Bone-to-Carnivore (WB-C)	Hominin	Carnivore	Carnivore
Three Consumer Types			
Vulture-to-Hominin-to-Carnivore (V-H-C)	Vulture	Hominin	Carnivore

Carnivores refer to larger mammalian carnivores only and in the Serengeti samples included lion and spotted hyena most commonly, and also cheetah and black-backed and golden jackals. Vultures (Ruppell's griffon, white-backed, hooded, lappet-faced) and raptors (tawny, Egyptian, and bateleur eagles) were frequently involved in the defleshing stage of the carnivore only model. An alternative, two-consumer-type (carnivore first) model can be found in Selvaggio (1998), but the data as presented cannot be applied systematically here.

Table 2.2) Number of assemblages and specimens in feeding trace models used in this study

Type of Feeding Trace Model	Number of Assemblages	Number of Specimens	
		Midshaft Fragments	All Long Bone Fragments
Carnivore-Only			
Size group 1-2	2	56	64
Size group 3-4	7	118	167
Size group 1-4 (Total)	9	174	231
Hammerstone-Only			
Size group 1-2	6	212	303
Size group 3-4	1	15	24
Size group 1-4 (Total)	7	227	327
Whole-Bone-to-Carnivore			
Size group 1-2	7	60	72
Size group 3-4	4	95	121
Size group 1-4 (Total)	11	155	193
Hammerstone-to-Carnivore			
Size group 1-2	32	1079	1350
Size group 3-4	14	597	799
Size group 1-4 (Total)	46	1676	2149
Vulture-to-Hominin-to-Carnivore			
Size group 1-2	1	17	23
Size group 3-4	4	93	124
Size group 1-4 (Total)	5	110	147
Grand Total	**78**	**2342**	**3047**

Table 2.3) Incidence of percussion-marked bone generated by bootstrap analysis

	All Long Bone Fragments				Midshaft Fragments			
	HO	**H-C**	**V-H-C**	**FLK 22**	**HO**	**H-C**	**V-H-C**	**FLK 22**
Size group 1-4								
Mean %	38.5	26.5	24.9	27.4	27.7	24.9	19.8	27.1
Median ± I.Q.R.	38.5 ± 6.6	26.5 ± 3.5	24.3 ± 12.1	-	27.9 ± 7.5	24.9 ± 3.6	19.5 ± 10.3	-
Min.-Max.	20.4-55.9	16.8-36.3	1.5-62.3	-	3.3-46.6	14.3-36.1	0-51.9	-
95% Interquantile Range	29.1-47.7	21.6-31.6	9.1-43.6	-	16.4-37.9	19.8-30.2	6.4-35.8	-
Size group 1-2								
Mean %	36.6	30.3	17.5	32.4	26.7	29.4	23.6	32.4
Median ± I.Q.R.	36.6 ± 7.0	30.2 ± 4.3	17.4 ± 8.7	-	26.9 ± 8.4	29.4 ± 4.3	23.5 ± 11.8	-
Min.-Max.	18.3-54.6	17.9-43.3	0-56.5	-	0-45.6	19.2-42.1	0-70.6	-
95% Interquantile Range	26.3-46.2	24.3-36.6	4.4-34.8	-	14.0-37.8	23.6-35.8	5.9-47.1	-
Size group 3-4								
Mean %	49.9	18.0	26.9	25.3	33.5	14.6	19.2	24.8
Median ± I.Q.R.	50.0 ± 16.7	17.8 ± 4.7	26.4 ± 15.2	-	33.3 ± 13.3	14.3 ± 5.0	18.7 ± 12.4	-
Min.-Max.	8.3-83.3	7.4-33.8	1.9-69.2	-	0-80.0	3.8-29.9	0-58.0	-
95% Interquantile Range	29.2-70.8	11.5-25.5	7.7-49.1	-	13.3-60.0	8.1-22.4	3.7-38.3	-

Incidence is measured as the proportion of specimens bearing at least one percussion mark. HO, Hammerstone-Only; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. I.Q.R., Interquartile range; 95% Interquantile range, values between the 2.5% and 97.5% quantiles. Data for the FLK 22 assemblage is taken from Table 3 of Blumenschine (1995). Highlighted boxes indicate where FLK 22 is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 2.4) Incidence of tooth-marked bone generated by bootstrap analysis

	All Long Bone Fragments					Midshaft Fragments				
	CO	**WB-C**	**H-C**	**V-H-C**	**FLK 22**	**CO**	**WB-C**	**H-C**	**V-H-C**	**FLK 22**
Size group 1-4										
Mean %	83.9	73.7	20.1	23.6	60.7	82.6	65.7	14.5	11.7	57.9
Median ± I.Q.R.	84.1 ± 6.0	73.9 ± 7.7	20.9 ± 2.4	23.3 ± 8.6	-	82.8 ± 6.8	66.2 ± 11.2	14.5 ± 2.3	11.0 ± 9.1	-
Min.-Max.	60.9-98.0	50.6-92.2	14.8-28.6	4.0-47.3	-	64.3-98.3	32.9-91.8	8.7-21.3	0-40.0	-
95% Interquantile Range	74.6-92.1	62.3-84.5	17.4-24.6	12.2-37.0	-	72.5-91.9	47.8-80.8	11.4-18.1	1.3-26.2	-
Size group 1-2										
Mean %	70.9	70.6	19.1	43.4	65.3	69.1	70.5	14.5	35.5	59.7
Median ± I.Q.R.	71.3 ± 8.8	70.8 ± 9.7	19.1 ± 3.0	43.5 ± 17.4	-	69.1 ± 9.5	70.7 ± 10.0	14.4 ± 2.8	35.3 ± 11.8	-
Min.-Max.	41.7-91.7	44.0-95.6	11.4-28.6	8.7-82.6	-	38.1-88.6	38.1-96.8	6.4-24.4	0-76.5	-
95% Interquantile Range	56.7-82.5	55.7-84.3	14.9-23.7	21.7-65.2	-	54.8-81.0	56.1-84.7	10.5-18.9	11.8-58.8	-
Size group 3-4										
Mean %	87.6	78.9	24.9	18.5	58.9	86.5	57.3	14.8	5.6	57.1
Median ± I.Q.R.	88.0 ± 6.2	79.1 ± 12.2	24.9 ± 3.6	18.3 ± 6.7	-	86.8 ± 7.0	57.9 ± 25.7	14.5 ± 5.8	5.0 ± 5.3	-
Min.-Max.	69.4-100	44.5-100	15.7-35.7	1.9-40.6	-	63.1-100	0-100	3.2-33.9	0-26.3	-
95% Interquantile Range	77.9-95.5	61.9-95.0	19.6-30.3	9.1-28.7	-	75.7-95.8	18.1-89.8	7.3-23.5	0-14.4	-

Incidence is measured as the proportion of specimens bearing at least one tooth mark. CO, Carnivore-Only; WB-C; Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. I.Q.R., Interquartile range; 95% Interquantile range, values between the 2.5% and 97.5% quantiles. Data for the FLK 22 assemblage is taken from Table 3 of Blumenschine (1995). Highlighted boxes indicate where FLK 22 is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 2.5) Incidence of cut-marked bone generated by bootstrap analysis

	All Long Bone Fragments					Midshaft Fragments				
	HO	**WB-C**	**H-C**	**V-H-C**	**FLK 22**	**HO**	**WB-C**	**H-C**	**V-H-C**	**FLK 22**
Size group 1-4										
Mean %	29.9	27.0	18.3	6.7	18.7	11.7	25.0	14.4	0	15.9
Median ± I.Q.R.	29.8 ± 5.4	26.6 ± 10.2	18.3 ± 2.6	6.4 ± 5.3	-	11.6 ± 5.0	24.4 ± 12.6	14.3 ± 2.5	0 ± 0	-
Min.-Max.	15.6-46.3	6.6-57.8	12.0-27.5	0-23.4	-	0-24.8	1.6-68.8	8.6-23.0	0	-
95% Interquantile Range	22.2-38.3	13.7-42.8	14.8-22.3	0-15.3	-	4.5-19.3	9.1-44.6	11.0-18.3	0	-
Size group 1-2										
Mean %	27.2	18.4	18.9	0	17.8	10.3	16.4	15.4	0	14.4
Median ± I.Q.R.	27.3 ± 4.7	17.7 ± 10.3	18.8 ± 3.4	0 ± 0	-	10.3 ± 4.9	15.5 ± 11.9	15.2 ± 3.3	0 ± 0	-
Min.-Max.	13.6-39.0	0-53.4	11.4-31.8	0	-	0-23.9	0-58.1	6.9-28.6	0	-
95% Interquantile Range	20.3-33.7	5.5-34.8	14.4-24.4	0	-	3.1-17.6	2.5-36.0	10.9-20.6	0	-
Size group 3-4										
Mean %	45.9	41.9	16.8	8.5	19.1	20.1	40.0	12.2	0	16.5
Median ± I.Q.R.	45.8 ± 16.7	40.9 ± 18.4	16.7 ± 3.4	8.1 ± 6.3	-	20.0 ± 13.3	39.4 ± 29.5	12.2 ± 3.1	0 ± 0	-
Min.-Max.	12.5-83.3	11.4-95.0	7.9-29.5	0-29.7	-	0-66.7	0-100	4.1-21.2	0	-
95% Interquantile Range	25.0-66.7	22.1-69.5	12.1-21.9	0-18.4	-	0-40.0	13.0-80.1	7.9-16.9	0	-

Incidence is measured as the proportion of specimens bearing at least one cut mark. HO, Hammerstone-Only; WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. I.Q.R., Interquartile range; 95% Interquantile range, values between the 2.5% and 97.5% quantiles. Data for the FLK 22 assemblage is reworked from Blumenschine's (1995) analysis. Highlighted boxes indicate where FLK 22 is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 2.6) Incidence of tooth- and butchery-marked bone generated by bootstrap analysis

	All Long Bone Fragments				Midshaft Fragments			
	WB-C	**H-C**	**V-H-C**	**FLK 22**	**WB-C**	**H-C**	**V-H-C**	**FLK 22**
Size group 1-4								
Mean %	19.7	8.4	9.6	25.2	9.7	4.9	4.4	24.5
Median ± I.Q.R.	19.2 ± 8.0	8.3 ± 1.8	9.2 ± 6.3	-	9.4 ± 5.1	4.9 ± 1.5	4.0 ± 4.4	-
Min.-Max.	4.3-52.1	4.5-14.7	0-35.0	-	0-27.8	1.5-10.0	0-22.9	-
95% Interquantile Range	9.5-32.2	6.0-11.4	2.0-19.7	-	3.0-18.0	2.9-7.4	0-12.2	-
Size group 1-2								
Mean %	11.6	8.6	8.7	30.1	8.2	5.9	11.6	21.9
Median ± I.Q.R.	11.1 ± 6.5	8.5 ± 2.5	8.7 ± 8.7	-	7.4 ± 6.9	5.8 ± 2.2	11.8 ± 11.8	-
Min.-Max.	0-36.7	3.7-18.8	0-43.5	-	0-34.3	1.5-14.5	0-47.1	-
95% Interquantile Range	3.3-22.4	5.4-12.5	0-21.7	-	0-19.7	3.2-9.4	0-29.4	-
Sizes group 3-4								
Mean %	33.7	8.0	9.9	23.2	12.3	3.2	2.5	22.7
Median ± I.Q.R.	32.6 ± 14.9	7.9 ± 1.8	9.3 ± 7.4	-	12.0 ± 7.5	3.1 ± 1.5	2.5 ± 5.0	-
Min.-Max.	7.3-85.0	3.6-14.1	0-36.5	-	0-41.0	0.2-9.2	0-22.5	-
95% Interquantile Range	16.7-57.5	5.5-10.9	1.6-22.3	-	2.6-24.4	1.3-5.8	0-10.0	-

Incidence is measured as the proportion of specimens bearing at least one tooth and one percussion and/or cut mark. WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. I.Q.R., Interquartile range; 95% Interquantile range, values between the 2.5% and 97.5% quantiles. Data for the FLK 22 assemblage is reworked from Blumenschine's (1995) analysis. Highlighted boxes indicate where Zinj is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 2.7) Incidence of cut-marked flesh-bearing midshaft fragments within the FLK 22 assemblage by long bone element

Element	Cut-Marked	Total	% Cut-Marked
Femur	3	24	12.5
Humerus	15	38	39.5
Tibia	20	60	33.3
Radius-Ulna	11	56	19.6

Incidence is measured as the proportion of specimens bearing at least one cut mark. Data generated from Blumenschine's (1995) analysis. Elements are listed in order of their ranking in the carcass consumption sequence from earliest consumed to latest (Blumenschine, 1986a, b).

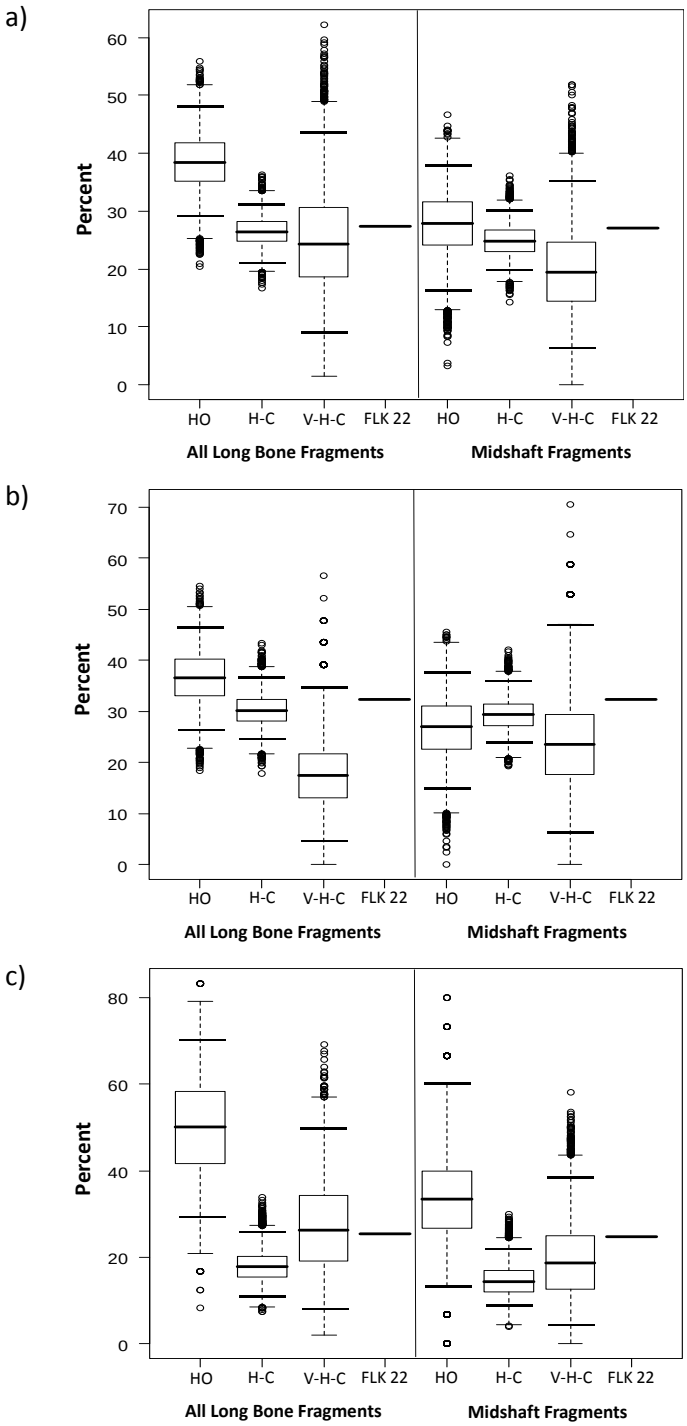


Figure 2.1) Incidence of percussion-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. HO, Hammerstone-Only; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** For the experimental feeding trace models the bold center lines represent the median; the lower boxes are the second quartiles; the upper boxes are the third quartiles; the bold longer lines beyond the boxes represent the 95% interquantile ranges; and the whiskers represent either the maximum value or 1.5 times the interquartile range. Any data outside 1.5 times the interquartile ranges are outliers and are depicted as circles. For FLK 22 the bold center line represents the proportion of percussion-marked bone.

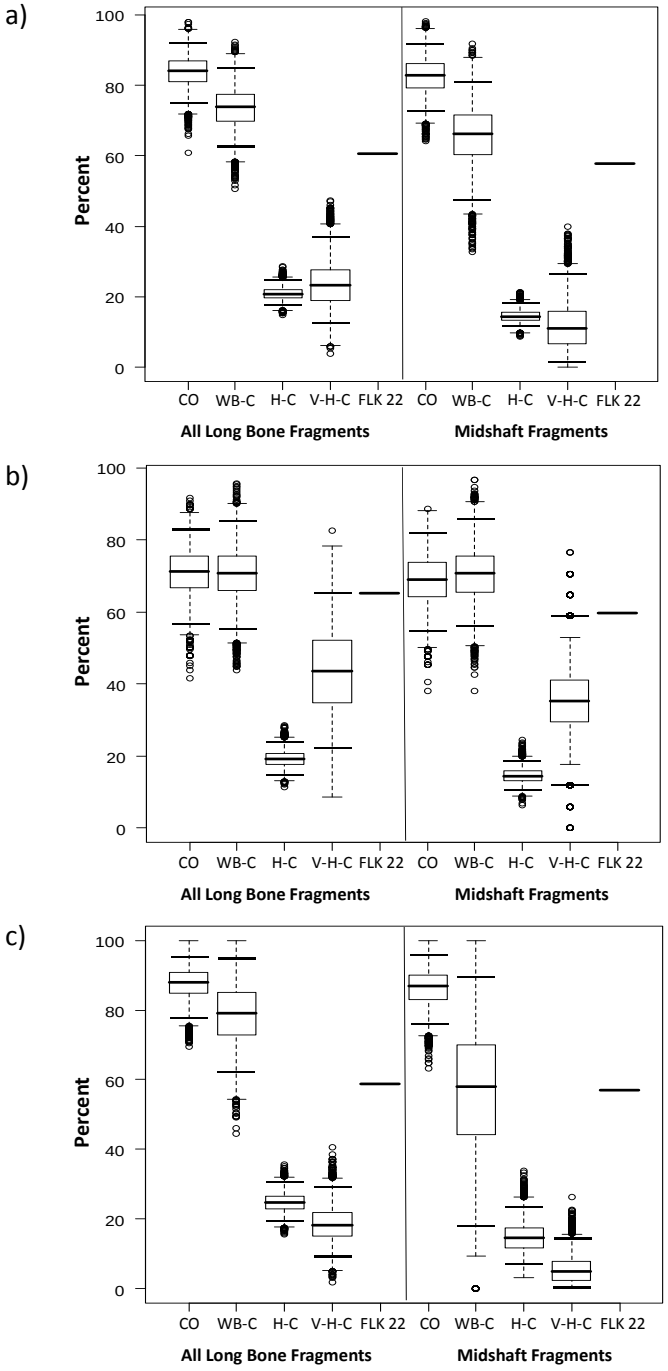


Figure 2.2) Incidence of tooth-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. CO, Carnivore-Only; WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** For the experimental feeding trace models the bold center lines represent the median; the lower boxes are the second quartiles; the upper boxes are the third quartiles; the bold longer lines beyond the boxes represent the 95% interquantile ranges; and the whiskers represent either the maximum value or 1.5 times the interquartile range. Any data outside 1.5 times the interquartile ranges are outliers and are depicted as circles. For FLK 22 the bold center line represents the proportion of tooth-marked bone.

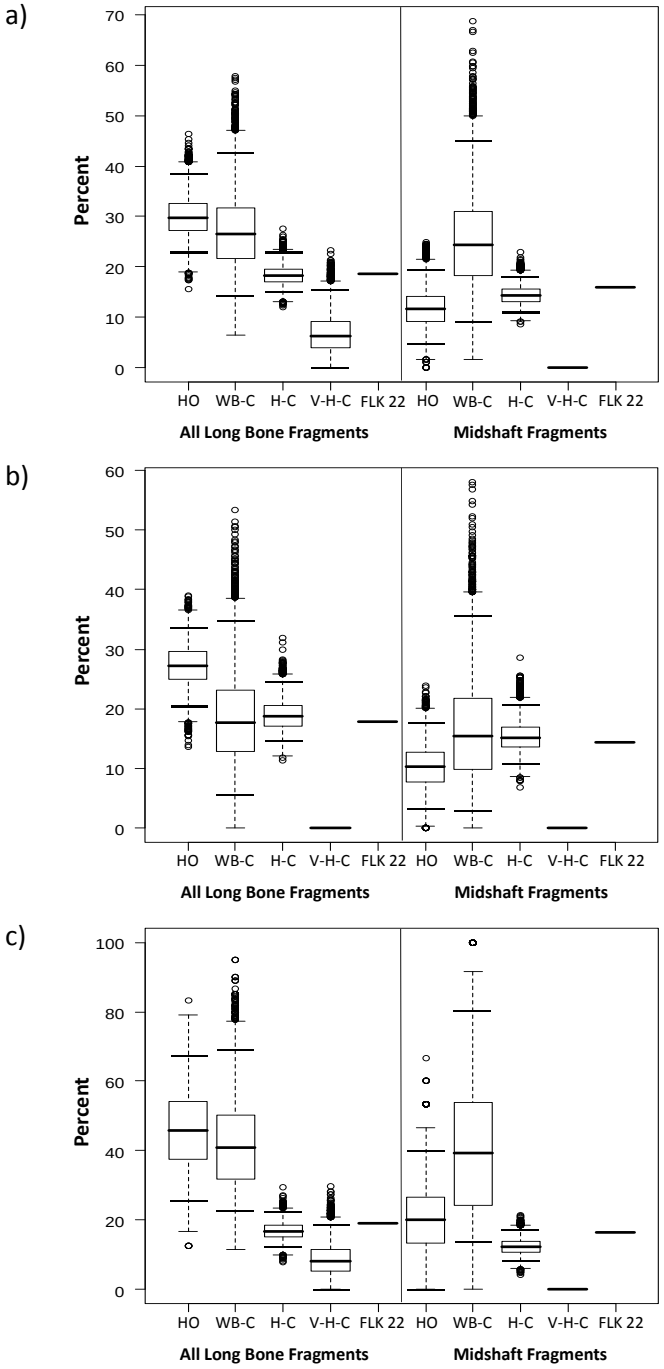


Figure 2.3) Incidence of cut-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. HO, Hammerstone-Only; WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** For the experimental feeding trace models the bold center lines represent the median; the lower boxes are the second quartiles; the upper boxes are the third quartiles; the bold longer lines beyond the boxes represent the 95% interquantile ranges; and the whiskers represent either the maximum value or 1.5 times the interquartile range. Any data outside 1.5 times the interquartile ranges are outliers and are depicted as circles. For FLK 22 the bold center line represents the proportion of cut-marked bone.

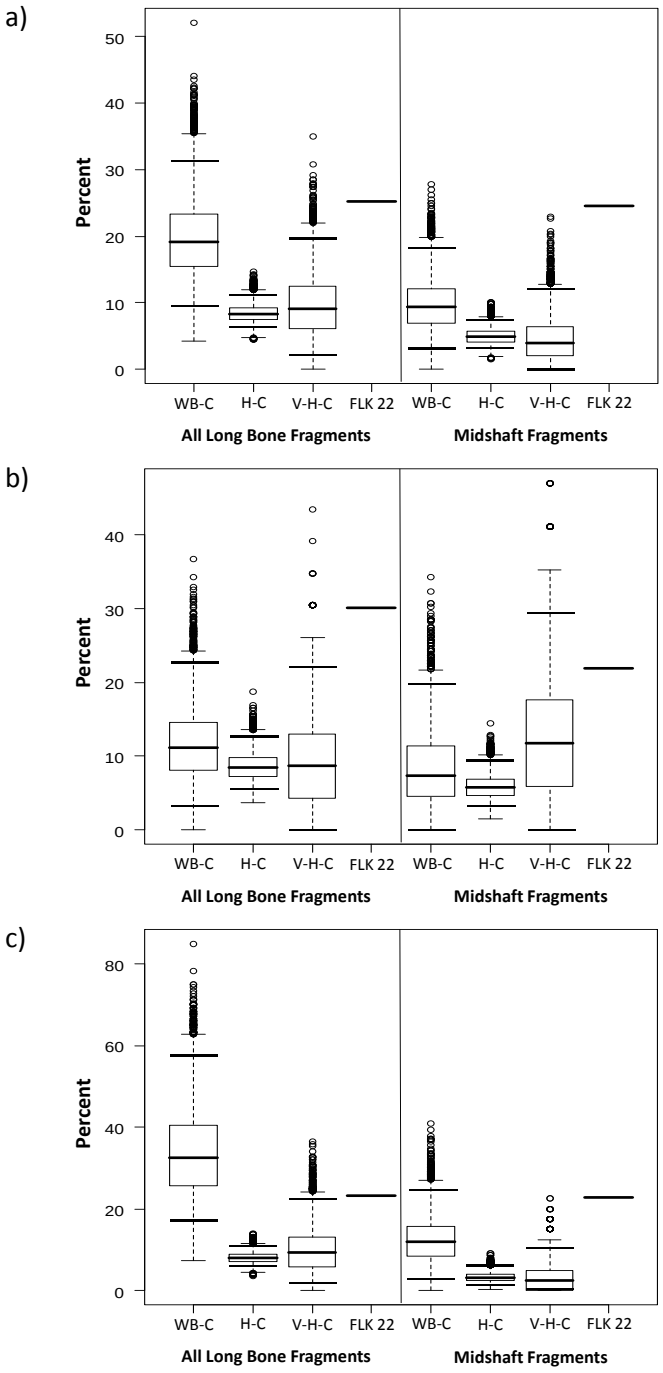


Figure 2.4) Incidence of tooth- and butchery-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** For the experimental feeding trace models the bold center lines represent the median; the lower boxes are the second quartiles; the upper boxes are the third quartiles; the bold longer lines beyond the boxes represent the 95% interquantile ranges; and the whiskers represent either the maximum value or 1.5 times the interquartile range. Any data outside 1.5 times the interquartile ranges are outliers and are depicted as circles. For FLK 22 the bold center line represents the proportion of tooth- and butchery-marked bone

Chapter 3

Fluvial Transport of Bovid Long Bones Fragmented by the Feeding Activities of Hominins and Carnivores

Introduction

This study tests the effect of fluvial processes on the transport of larger mammal long bone portions created through hominin and carnivore carcass consumption. Prior studies investigating the hydraulic transport of bone have focused on complete disarticulated and articulated skeletal elements and have not systematically addressed the differential transport potential of long bone fragments (Behrensmeyer, 1975, 1982, 1988; Coard, 1999; Coard and Dennell, 1995; Dodson, 1973; Korth, 1979; Schick, 1984, 1986; Voorhies, 1969; Wolff, 1973). Voorhies (1969) pioneered these studies by observing the transport of whole, disarticulated sheep and coyote bones in a flume. His results categorize the transport potential of individual skeletal parts into three groups, termed Voorhies Groups (Behrensmeyer, 1975). Voorhies Group One includes bones that are affected immediately by "slight" currents and may float or bounce along the bottom (ribs, vertebra, sacrum, and sternum); Group Two bones are moved from their positions later than group one and stay in contact with the bottom (femur, tibia, humerus, metapodials, pelvis, and radius); Group Three bones are lag elements (skull and mandible) that resisted transport up to current velocities of 150 cm/s (Voorhies, 1969). The scapula, phalanx, and ulna have transport potentials intermediate to Groups One and Two, while the ramus of the mandible is intermediate to Groups Two and Three (Voorhies, 1969).

Behrensmeyer (1975) found that Voorhies Groups are related to the density, size, and shape of bones, while Behrensmeyer (1975) and Korth (1979) independently found the settling rates of bones to correlate with their transport potential. Boaz and

Behrensmeyer (1976) used a flume and human bone fragments to show density is correlated negatively with the average rate of movement of skeletal parts in current velocities of 31 cm/s, but their study did not include long bone midshaft fragments. Schick (1984, 1986) considered the effect of fluvial processes on complete and fragmented bone relative to stone tools, but her focus was on lithic artifacts and the hydraulic disturbance of Stone Age assemblages in natural settings, rather than differential transport among bone fragments. More recently, Coard and Dennell (1995) demonstrated that articulated bones are more easily transported than disarticulated bones in a flume, while Coard (1999) found that dry bones have greater transport potential than bones saturated with water before entering the flume.

Thus far, the fluvial transport potential of bone fragmented by the feeding activities of hominins and carnivores has not been addressed systematically. As a result, the extent and timing of carnivore and hominin influence on bone assemblages disturbed by flowing water cannot be interpreted with confidence. The incidence of long bone fragments bearing bone surface modifications is an effective means of evaluating the sequence of hominin and carnivore consumption of carcass foods in non-fluvial lake margin or cave environments (Blumenschine, 1995; Capaldo, 1995, 1997; Domínguez-Rodrigo, 1997; Marean and Kim, 1998; Selvaggio 1994, 1998). For example, high frequencies of percussion-marked and tooth-marked fragments have been used to indicate that hominins processed carcasses scavenged from felid kills at the Bed I lake margin site of FLK 22 (*Zinjanthropus* level) from Olduvai Gorge, Tanzania (Blumenschine, 1995; Pante et al., in review; chapter 2). Such interpretive models can only be applied

to sites deposited in fluvial environments if the effect of hydraulic processes on bones fragmented by carnivores and hominins is understood.

This paper employs a flume and degreased, unweathered long bones modified by Blumenschine (1988) and/or modern Serengeti carnivores under controlled conditions to address the following questions:

1) What variables measurable on fragmented fossil specimens correlate with the fluvial transportability of bone?

2) Is the effect of fluvial processes on the proportion of bone fragments bearing tooth, percussion, and cut marks great enough to significantly alter the hominin and/or carnivore feeding signal in fossil assemblages disturbed by flowing water?

Methods

Flume

Flume trials were conducted with an oval racetrack flume located at the Institute of Marine and Coastal Sciences, Rutgers University. The flume is 70 cm wide, 30.5 cm deep (maximum working depth of 25 cm), and has a working channel length of 6.2 m. The flume's maximum flow velocity is 50 cm/s, equivalent to that of a low energy stream (Behrensmeyer, 1975). The flume was filled with fresh water to a depth of 14 cm. Water temperature was held at 19-20^{o}C.

Sample

All bovid long bone portions and elements were tested, including epiphyseal, near-epiphyseal, and midshaft fragments of the humerus, femur, radius/ulna, tibia, and metapodials for animal size groups one, two, and three. Long bone portions are divided

into epiphyses (fragments with an articular surface, including the proximal ends of metapodials), near-epiphyses (fragments with cancellous bone on the medullary surface and no articular surface), and midshafts (fragments that do not have an articular surface or cancellous bone). Specimens that have multiple portions are identified by the most diagnostic portion, with epiphyses being the most diagnostic and midshafts the least. For example, specimens identified as an epiphysis or near-epiphysis may contain a midshaft portion. The general term shaft refers collectively to near-epiphyseal and midshaft fragments.

311 modern bovid long bone fragments from Blumenschine's (1988, 1995) published control samples of hominin- and carnivore-modified bone make up the sample. Descriptive measurements of each specimen were taken including element, portion, segment, maximum length, maximum width, maximum cortical thickness, and maximum height above the flume floor. Length, width, cortical thickness, and height above the flume floor were measured to the nearest mm with digital calipers. Length is measured from the most proximal point to the most distal point parallel to the long-axis of the specimen for both epiphyseal (Figure 3.1a) and shaft (Figure 3.1c) fragments, while width is measured perpendicular to length (see Figure 3.1 for details). Cortical thickness for both epiphyseal and shaft fragments is the maximum thickness of bone along the circumference of the shaft measured from the outer surface to the medullary surface (Figure 3.1b). Cortical thickness could not be recorded for specimens where the medullary or cortical surface was missing along the entire fracture edge, e.g. bone flakes (n=73). Maximum height was measured on a flat table by placing the fragment in the

same position used in the flume trials (discussed below) and taking the maximum dimension of the fragment and table together with calipers. The thickness of the table was then subtracted from the total measurement.

The bone samples used here are a sub-sample of those used by Blumenschine (1988, 1995) to establish three models of site formation: hammerstone only, carnivore only, and hammerstone-to-carnivore. The hammerstone only model is a scenario in which hominins are the only consumer of a carcass and all bone fragments are generated with a hammerstone-on-anvil breakage technique after defleshing with a metal knife. In the published hammerstone only model 39% (n=327) of fragments are percussion-marked. In the carnivore only model, all bones are defleshed and fragmented by spotted hyenas and in one case lions in the process of extracting flesh, marrow, and grease from long bones. The mean incidence of tooth marking for the published carnivore only model is 84% (n=231). The hammerstone-to-carnivore scenario models carnivore scavenging of long bones from which hominins removed all flesh and marrow. The mean incidences of percussion and tooth marking on bone fragments in the published hammerstone-to-carnivore model are 29% and 19% (n=598), respectively. The incidences of the different mark types in the sub-samples used here differ somewhat from those in the published models, but this has no bearing on the results obtained.

Each model of site formation was represented by animal size groups one, two, and three. Animal size groups refer to live animal weights and are consistent with those used by Bunn and Kroll (1986) (see Table 3.1). All size one carcasses were Thompson's

gazelle (*Gazella thomsonii*); size two were either Grant's gazelle (*Gazella granti*) or impala (*Aepyceros melampus*); size three were either topi (*Damaliscus korrigum*) or wildebeest (*Connochaetes taurinus*).

Preparation of Experiments

All flume trials were carried out without bed load and bone fragments were placed directly on the plastic floor of the flume to minimize the number of variables affecting the transport potential of bone fragments. Bones were soaked in water until completely saturated (at least 24 hours), which was determined by an unchanged weight between two successive measurements on a balance accurate to 0.01 g.

Each specimen was subjected to six trials that varied both the position of the fragments throughout the width of the flume and the orientation of the long-axis of fragments relative to current direction. Specimens were placed in two rows, one 2 m down-flume from the other, with three specimens in each row, and were rotated through three positions relative to the inside wall of the flume; the first position was at 20 cm, the second at 35 cm, and the third at 50 cm. This placed the bones about 15 cm apart from one another, which minimized turbulence caused by adjacent specimens, and at least 20 cm away from both walls of the flume, which reduced the effect of friction on flow velocity. To determine the minimum and maximum flow velocity necessary to transport each fragment, the orientation of the bone fragments was varied between the smallest surface area exposed to flow (long-axis parallel to current) and the largest surface area exposed to flow (long-axis perpendicular to current). Each fragment was subjected to three trials with the long-axis perpendicular to the current

and three trials with the long-axis parallel to the current. In the parallel position the end of the fragment that was shorter in height was pointed toward the flow. Specimens were placed with medullary surfaces facing the floor of the flume unless they were unstable or rocking in this position, in which case the position that afforded the greatest stability of the fragment was used.

Experimental Procedure

Current velocity relative to flume paddle speed was calibrated using a two-axis laser doppler velocimeter operating in backscatter mode. Current velocity, as measured by the speed of the flume paddles, was held at 10 cm/s while bones were placed in the flume. This velocity was chosen because transport of long bone fragments did not occur at speeds below 25 cm/s, allowing specimens to be positioned without the risk of movement prior to the start of the trial.

Once positioned, flow velocity was increased in 5 cm/s increments ranging from 10 cm/s through 50 cm/s. Sufficient time (3-5 minutes) was allotted to each increment to allow the current to stabilize throughout the flume, as determined by the cessation of erratic movement of particles floating in the water. Once current flow had stabilized, further transport was not likely to occur unless a bone was rocking in place. In these cases the interval time was increased up to a maximum of 10 minutes, after which the flow was increased by the standard 5 cm/s. This method is similar to that used by Coard (1999), who placed bones in a flume at low velocities (0.05 cm/s), but increased current velocity at a steady rate, rather than in increments.

Two measurements were taken while the bones were in the flume: 1) the entrainment velocity, or the flow velocity necessary to cause rocking or movement of a bone, and 2) the transport velocity, the current velocity necessary to move each specimen 70 cm, the maximum distance a bone could travel before being obstructed by silicon used to seal the floor of the flume. If a specimen moved, but did not travel the entire 70 cm, it was considered not transported at that flow velocity. If the specimen traveled the remainder of the 70 cm upon increased flow velocity, it was recorded as transported at the higher flow velocity.

Treatment of Results

For analytical purposes, specimens were deemed transported if moved 70 cm in the flume at a maximum flow velocity of 40 cm/s; conversely, those that did not meet these criteria were deemed not-transported. Bones that were not transported at the maximum 50 cm/s were grouped with those transported at velocities above 40 cm/s. The 40 cm/s analytical threshold was chosen because it represents the center of the distribution for the minimum velocity at which individual fragments were transported (Figure 3.2).

Several inferential statistical tests are used to evaluate transportability. The chi-square goodness-of-fit test and Fisher's exact probability test, when 25% or more of expected cells had a value of less than 5, were used to evaluate the effect of long bone portion and animal size group on transport. Spearman's rank order correlation was used to test for the strength of relationships between maximum cortical thickness, maximum length, and maximum width as independent variables, and the proportions of

long bone fragments transported as the dependent variable. A single specimen with a maximum cortical thickness of 9 mm, the thickest in the sample, was not included in the correlation analyses between the proportion of specimens transported and cortical thickness so as not to skew results. However, this specimen is reported in the tables and figures and included in all other analyses. All results are considered significant when two-tailed probability values $\leq$ .05 are obtained.

A bootstrapping algorithm unweighted with respect to animal size or any other variable was developed using R version 2.8.1 (The R Foundation for Statistical Computing, 2008). The algorithm was applied to the data on the presence and absence of bone surface modifications (tooth, percussion, and cut marks) within the not-transported and transported sub-samples. This algorithm generates bootstrap distributions of 10,000 means for each sub-sample. 95% interquantile ranges (data between the 2.5% quantile and the 97.5% quantile) are used to assess differences among the not-transported and transported bootstrapped sub-samples at the 0.05 level of probability. The 95% interquantile range for a bootstrapped distribution can be interpreted much like a 95% confidence interval, but makes no assumptions with respect to normality. Here, when the 95% interquantile ranges overlap among sub-samples, the sub-samples are considered as not distinguishable. When they do not overlap they are considered as likely distinct. This inference is much like an inference based on a parametric or non-parametric statistic where alpha is set at the 0.05 level.

Results

Animal Size Group

Long bone fragments from smaller animal size groups are more likely to be transported than those from larger animal size groups (Table 3.1, Figure 3.3). A significant difference exists in the transportability of the three size classes for all long bone fragments and for midshaft fragments alone, with proportionately fewer specimens being transported as animal size increases. The proportion of specimens transported decreases about 16 percentage points at each size group transition.

Long Bone Portion

Portion does not affect the transport of long bone fragments (Table 3.2, Figure 3.4). There is not a significant difference in the proportion of midshaft, near-epiphyseal, or epiphyseal specimens transported for any of the three size groups. For size group one fragments, the proportions of epiphyses, near-epiphyses, and midshafts transported are nearly identical. The variation is greater for size group two fragments with a maximum difference between the proportions of epiphyses, near-epiphyses, and midshafts transported of < 30%. These differences for size group three fragments are < 15%.

Variables that Influence Transport

Maximum cortical thickness, maximum length, and maximum width are significantly and inversely correlated to the proportion of specimens transported at a maximum velocity of 40 cm/s. Maximum cortical thickness accounts for 100% of the variation in the percentage of specimens transported for all long bone fragments and

93% of the variation for midshaft fragments (Table 3.3, Figure 3.5). The proportion of all long bone specimens transported at 40 cm/s decreases from about 88% for fragments with a maximum cortical thickness of 2 mm to 0% for fragments with a maximum cortical thickness of 8 mm. The proportion of midshaft specimens transported decreases from 83% for fragments with a maximum cortical thickness of 2 mm to 0% for fragments with a maximum cortical thickness of 8 mm.

Maximum length accounts for 81% of the variation in the proportion of specimens transported for all long bone fragments and 69% of the variation for midshaft fragments (Table 3.4, Figure 3.6). The proportion of all long bone specimens transported decreases from about 73% for fragments with a maximum length less than 20 mm to 29% for fragments with a maximum length between 81 and 90 mm. The proportion of midshaft specimens transported decreases from about 73% for fragments with a maximum length less than 20 mm to about 24% for fragments with a maximum length greater than 90 mm.

Maximum width accounts for only 27% of the variation in the proportion of specimens transported for all long bone fragments, but 89% of the variation in the transport of midshaft fragments (Table 3.5, Figure 3.7). The proportion of all long bone specimens transported decreases from about 81% for fragments with a maximum width between 6 and 10 mm to 0% for fragments with a maximum width between 26 and 30 mm. The proportion of midshaft specimens transported decreases from 80% for fragments with a maximum width between 6 and 10 mm to 0% for fragments with a maximum width between 26 and 30 mm.

More variability characterizes the transport of individual bone fragments than the above correlation statistics suggest. This is demonstrated by plotting the maximum cortical thickness against the maximum length (Figure 3.8a) and the maximum cortical thickness against the maximum width (figure 3.8b) for bone fragments that were transported at different flow velocities. Spearman's rank order statistics show maximum cortical thickness (r_s=.36), maximum length (r_s=.28), and maximum width (r_s=.46) are all significantly correlated ($p<.0001$) with the minimum velocity at which individual fragments are transported. However, these measurements respectively account for only 13%, 8%, and 21% of the variability in the minimum velocity at which individual fragments are transported.

Fluvial Transport and Bone Surface Modifications

Fluvial transport does not differentially affect bone fragments with and without tooth or butchery marks (Table 3.6, Figure 3.9). In all cases, the 95% interquantile ranges for the incidences of tooth (Figure 3.9a), percussion (Figure 3.9b), and cut (Figure 3.9c) marks in the not-transported and transported bootstrapped sub-samples overlap, indicating they are statistically indistinguishable. However, the not-transported sub-samples almost always have a higher mean incidence of tooth, percussion, and cut marking than their transported counterparts. The exceptions are the incidences of tooth marking on all long bone fragments and midshaft fragments from the hammerstone-to-carnivore model, and the incidence of percussion marking on midshaft fragments from the hammerstone only model.

Discussion

Allochthonous and Autochthonous Assemblages

Flume experiments demonstrate a significant inverse relationship between animal size and the transportability of long bone fragments. This suggests animal size groups can be used to recognize fluvially winnowed bone assemblages. While the specific composition of allochthonous and autochthonous assemblages would depend on many factors including current velocity and the size of animals entering the system, it can be generalized that bone fragments from smaller animals in a fossil community should be disproportionately represented in allochthonous assemblages, while fragments in upstream lag assemblages should be biased toward the larger animal components.

Surprisingly, long bone portion was not found to significantly affect transport for any size group examined. Given the negative relationship between density and transport potential revealed by Behrensmeyer's (1975) study using whole bones, it was originally predicted that midshafts would be less likely to be transported than epiphyses, because they tend to be denser (Lam et al., 1998). While the proportions of size group one epiphyseal and midshaft fragments transported are virtually identical, long bone epiphyses from size groups two and three are less frequently transported, though to an insignificant degree, than long bone midshafts from the same size groups. Given the results that length and width of fragments are both negatively correlated to transport potential, the overall larger size of epiphyseal relative to midshaft fragments for size two and three animals may explain this result. While these data indicate that

epiphyseal:shaft fragment ratios should not be significantly affected by hydraulic processes in low energy fluvial environments, the relationship between bone portion and transport may be more complex.

Variation exists in the transportability of epiphyses that may be based in part on relative density. The small sample sizes of epiphyseal fragments in this study prohibit a full investigation of this relationship, but generally, when epiphyses are divided into two groups based on density measurements from Lam et al. (1998), 62% of epiphyses are transported in the low-density group (the proximal ends of the humerus and tibia, the distal end of the radius, and the proximal and distal ends of the ulna and femur), while only 26% of epiphyses are transported in the high-density group (the proximal and distal ends of the metapodials, the proximal end of the radius, and the distal ends of the humerus and tibia). These groupings do not consider the presence or lengths of midshafts attached to the epiphyses and are therefore characterized imprecisely by published data on bone density. Larger samples and more accurate assessments of density may show statistical differences in the transport of low- and high-density epiphyseal fragments. This consideration is important because epiphysis:shaft fragment ratios are used as a measure of carnivore competition for carcass foods. Specifically, heavily ravaged assemblages will be depleted of epiphyses and are indicative of higher levels of competition among carnivores (Blumenschine and Marean, 1993; Marean and Spencer, 1991). Fluvial processes will differentially affect the epiphysis:shaft fragment ratio based on the original composition of low- and high-density epiphyses in the fluvially-undisturbed assemblages. For example, there is a significant difference in the

transport of shafts (65%) and epiphyses (29%) for size two fragments from the hammerstone only model ($p=.01$, $x^2=6.12$, d.f.=1), despite the lack of significant differences when all three models are grouped together.

Significant correlations between cortical thickness, length, and width (for midshaft fragments only) and the proportion of specimens transported suggest that all are useful predictors of transport. However, when the data are broken down further to show the relationship of these variables to the minimum velocities at which individual specimens are transported, the correlations between fragment size and transport become much weaker. Despite these weaker correlations, it is apparent that smaller and thinner fragments are typically more prone to fluvial transport than larger and thicker fragments.

Differential Transport of Hominin- and Carnivore-Modified Bone Fragments

Models designed to infer the timing of hominin and carnivore access to carcasses are based largely on the incidences of tooth and percussion marking on long bone fragments (Blumenschine, 1988, 1995; Capaldo, 1995, 1997; Selvaggio, 1994, 1998). More recently, these inferences have incorporated the incidence of cut marking on long bone midshaft fragments (Pante et al., in review). Specifically, the incidence of percussion marking is a useful indicator of the proportion of long bones that were broken open by hominins in fossil assemblages. The incidence of tooth marking can be employed in establishing the relative timing of hominin and carnivore carcass consumption because the carnivore only model has a significantly higher incidence of tooth marking than the hammerstone-to-carnivore model (Blumenschine, 1995). The

incidence of cut marking on long bone midshaft fragments, which had been previously been considered incapable of discerning the relative timing of hominin and carnivore carcass consumption (Blumenschine and Pobiner, 2007; Pobiner and Braun, 2005), has now been shown useful in distinguishing between hominin access to carcasses with varying amounts of flesh (Pante et al., in review).

Results of flume experiments show a lack of significant differences in the incidences of tooth-, percussion-, or cut-marked fragments between the transported and not-transported sub-samples. Further, fluvial transport does not obscure the statistical distinction between the carnivore only and hammerstone-to-carnivore models for the incidence of tooth marking.

Results also show that the not-transported sub-samples usually have a higher mean incidence of tooth, percussion, and cut marks than the transported sub-samples. This pattern is not unexpected given that shorter long bone fragments are not only more likely to be transported than longer fragments, but have also been demonstrated to be less frequently tooth- and percussion-marked than longer fragments (Blumenschine, 1988, 1995; Blumenschine and Selvaggio, 1991). Two-tailed Mann-Whitney U tests show that this is in fact the case for all long bone fragments from the hammerstone-to-carnivore sample used here, where the mean lengths of tooth-, percussion-, and cut-marked long bone fragments are significantly greater than their unmodified counterparts ($U=1623.5$, $p=.004$; $U=1910$, $p<.0001$; $U=1093.5$, $p=.0006$, respectively). These results suggest that differences in the proportion of tooth-, percussion-, and cut-marked long bone fragments in transported and not-transported

sub-samples will increase to the point of being statistically distinct at a flow velocity greater than the 50 cm/s maximum tested here.

Together, these results show that the incidence of tooth, percussion, and cut marking on long bone fragments should remain a valid measure of the timing of hominin and carnivore carcass consumption, but only for autochthonous assemblages in low-energy fluvial environments. The statistical distinction between the carnivore only and hammerstone-to-carnivore models may be diminished in autochthonous assemblages subjected to higher flow velocities than those tested here. The application of these results to allochthonous assemblages may not be appropriate because transported fragments are not likely to accumulate in a single downstream location, a factor that could significantly affect not only the incidences of bone surface modifications, but also other assemblage parameters in ways not explored by this study. It is also likely that fluvial processes will abrade and round bone fragments in both autochthonous and allochthonous assemblages (Fernández-Jalvo, 2003; Shipman and Rose, 1983), potentially obscuring bone surface modifications and reducing traces of hominin and carnivore feeding activities. This can be corrected by excluding heavily rounded or abraded bone fragments from analyses concerning bone modification frequencies, but requires the assumption that hominin- and/or carnivore-modified bone fragments will not be disproportionately affected by fluvial abrasion in relation to their unmodified counterparts.

Flume and Natural Fluvial Environments

The results generated by these experiments are subject to some uncertainty due to the use of a flume to simulate natural fluvial environments. These experiments are general in that they are applicable to a wide range of fluvial environments and they are precise in that the results are replicable. However, they sacrifice model realism because flume experiments do not account for many of the variables that influence bone transport in natural settings. In the case of this study, sediment bed load and bed forms are not considered. These features are common in natural fluvial environments and may affect the transport potential of bone fragments. Smooth channel bottoms like those found on the flume used in these experiments have a low velocity sublayer that is separated from more turbulent higher velocity flow in the main part of the channel (Pettijohn et al., 1972). Behrensmeyer (1975) hypothesized that the sublayer effect could cause very small or flat bones to be sorted from larger bones in ways that do not fit the predictions for the fluvial transport of bone. She also suggested that this may have affected the lag behavior of mandibles in Voorhies' experiments that used a smooth-surfaced bed.

To investigate the effect of the low velocity sublayer in these experiments, the maximum height (mm) of long bone fragments from the floor of the flume was tested for correlations with the minimum velocity at which individual fragments were transported. Using Spearman's rank order correlation in order to include fragments that were not transported, the results show significant positive correlations for all long bone fragments (r_s=.36, r_s^2=.11, p<.0001) and for midshaft fragments (r_s=.33, r_s^2=.13,

$p<.0001$). If the low velocity sublayer had a significant affect on transport potential in this study we would expect negative correlations because shorter fragments would have required higher flow velocities to be transported. The fact that they did not is likely a reflection of the positive correlations of width with minimum transport velocity, rather than the effects of the low velocity sublayer.

Conclusions

Flume experiments using published collections of hominin- and carnivore-modified bone demonstrate that variables easily measured on fossil specimens, including animal size group, maximum cortical thickness, maximum length, and maximum width correlate with the hydraulic transport potential of long bone fragments and may be useful indicators of winnowing in fossil assemblages deposited in fluvial environments. Specifically, allochthonous assemblages should have higher proportions of smaller fragments from smaller animals when compared with upstream lag assemblages. Although these experiments are based on long bone portions that were created through hominin and carnivore carcass consumption, animal size groups and the linear dimensions explored here should also be applicable as indicators of transport in assemblages that are unmodified by hominins and carnivores, assuming bones are fragmented.

The surprising lack of variation in the transport of different long bone portions indicates that long bone portion is not useful in distinguishing allochthonous from autochthonous assemblages for the animal size groups examined here. However, the greater disparity between the transport of midshaft and epiphyseal fragments from size

groups 2 and 3 in comparison with size group 1 suggests that epiphyseal fragments from size group 4 and larger animals may be significantly less likely to be transported than their midshaft counterparts. Despite the absence of significant differences in the transport of long bone portions, epiphyseal:shaft fragment ratios may not be an accurate measure of carnivore competition in fluvial environments. Differences in the transportability of epiphyses based on relative density suggests that epiphysis:shaft fragment ratios will vary depending on the ratio of low- and high-density epiphyses in the original fluvially-undisturbed assemblage.

The absence of significant differences in the incidences of tooth, percussion, and cut marking between the not-transported and transported sub-samples indicates that low-energy hydraulic processes should not significantly affect interpretations of hominin and carnivore carcass consumption that are based on the proportions of marked and unmarked long bone fragments in an assemblage. The incidence of bone surface modifications on long bone fragments are often the focus of interpretations concerning hominin and carnivore feeding activities in non-fluvial environments. The results of this study suggest that it is possible to employ the same experimental models of site formation to interpret fossil assemblages found in low-energy fluvial environments.

Table 3.1) Proportion of specimens transported by animal size group.

Portion	Animal Size Group	Total NISP	NISP Transported	Percent Transported	Statistics
All Long Bone Fragments	Size 1	63	43	68.3	p=.0003 x^2=16.6 d.f.=2
	Size 2	141	74	52.5	
	Size 3	107	39	36.4	
	Total	311	156	50.2	
Midshaft Fragments	Size 1	38	26	68.4	p=.02 x^2=8.35 d.f.=2
	Size 2	119	67	56.3	
	Size 3	71	29	40.8	
	Total	228	122	53.5	

Animal size groups are based on Bunn and Kroll (1986). Size 1, <50 lbs (23 kg); Size 2, 50-250 lbs (23-114 kg); Size 3, 250-750 lbs (114-341 kg). All long bone fragments include epiphyseal, near-epiphyseal, and midshaft fragments. NISP transported is the number of fragments transported at current velocities up to 40 cm/s. p values are based on the chi-square goodness-of-fit test.

Table 3.2) Proportion of specimens transported by long bone portion.

Animal Size Group	Long Bone Portion	Total NISP	NISP Transported	Percent Transported	Statistics
Size 1	Midshafts	38	26	68.4	p=.99 x^2=.01 d.f.=2
	Near-Epiphyses	9	6	66.7	
	Epiphyses	16	11	68.8	
	Total	63	43	68.3	
Size 2	Midshafts	119	67	56.3	*p=.08*
	Near-Epiphyses	7	3	42.9	
	Epiphyses	15	4	26.7	
	Total	141	74	52.5	
Size 3	Midshafts	71	29	40.8	p=.41 x^2=1.8 d.f.=2
	Near-Epiphyses	19	5	26.3	
	Epiphyses	17	5	29.4	
	Total	107	39	36.4	

See caption of table 1 for definition of animal size groups. NISP transported is the number of fragments transported at current velocities up to 40 cm/s. p values are based on chi-square goodness-of-fit statistics when 75% or more of the expected cells had a value of greater than 5. Fisher's exact probability test (*italics*) was used when less than 75% of the expected cells had a value of greater than 5.

Table 3.3) Proportion of specimens transported by maximum cortical thickness (mm).

Portion	Maximum Cortical Thickness (mm)	Total NISP	NISP Transported	Percent Transported	Statistics
All Long Bone Fragments	2	8	7	87.5	r_s=-1 r_s^2=1 p<.0001
	3	47	30	63.8	
	4	42	25	59.5	
	5	54	21	38.9	
	6	52	19	36.5	
	7	27	6	22.2	
	8	7	0	0.0	
	9	1	0	0.0	
	Total	238	108	45.4	
Midshaft Fragments	2	6	5	83.3	r_s=-.9643 r_s^2=.93 p=.0005
	3	27	17	63.0	
	4	35	22	62.9	
	5	46	17	37.0	
	6	28	12	42.9	
	7	15	5	33.3	
	8	5	0	0.0	
	9	1	0	0.0	
	Total	163	78	47.9	

All long bone fragments include epiphyseal, near-epiphyseal, and midshaft fragments. NISP transported is the number of fragments transported at current velocities up to 40 cm/s. r_s, Spearman's rank order correlation coefficient, which is based on the proportion of specimens transported for each cortical thickness value. p value indicates the significance of the correlation. The single midshaft specimen with a maximum cortical thickness of 9 mm was excluded from statistical analyses due to the small sample size of the group. The p values are significant with and without this specimen. Specimens were excluded from the table and analyses of maximum cortical thickness when cortical thickness could not be measured due to the lack of a complete cortical section (n=73 for all long bone fragments, n=65 for midshaft fragments).

Table 3.4) Proportion of specimens transported by maximum length (mm).

Portion	Length (mm)	Total NISP	NISP Transported	Percent Transported	Statistics
All Long Bone Fragments	≤20	15	11	73.3	r_s=-.9 r_s^2=.81 p=.0009
	21-30	53	31	58.5	
	31-40	39	27	69.2	
	41-50	41	21	51.2	
	51-60	39	23	59.0	
	61-70	24	11	45.8	
	71-80	20	8	40.0	
	81-90	21	6	28.6	
	>90	59	18	30.5	
	Total	311	156	50.2	
Midshaft Fragments	≤20	15	11	73.3	r_s=-.8333 r_s^2=.69 p=.005
	21-30	50	29	58.0	
	31-40	38	26	68.4	
	41-50	34	16	47.1	
	51-60	30	16	53.3	
	61-70	19	9	47.4	
	71-80	11	6	54.5	
	81-90	14	5	35.7	
	>90	17	4	23.5	
	Total	228	122	53.4	

All long bone fragments include epiphyseal, near-epiphyseal, and midshaft fragments. NISP transported is the number of fragments transported at current velocities up to 40 cm/s. r_s, Spearman's rank order correlation coefficient, which is based on the proportion of specimens transported for each length value. p value indicates the significance of the correlation.

Table 3.5) Proportion of specimens transported by maximum width (mm).

Portion	Width (mm)	Total NISP	NISP Transported	Percent Transported	Statistics
All Long Bone Fragments	≤5	13	8	61.5	r_s=-.5167 r_s^2=.27 p=.15
	6-10	87	70	80.5	
	11-15	77	43	55.8	
	16-20	55	18	32.7	
	21-25	34	6	17.6	
	26-30	14	0	0.0	
	31-35	8	3	37.5	
	36-40	6	2	33.3	
	>40	17	6	35.3	
	Total	311	156	50.2	
Midshaft Fragments	≤5	13	8	61.5	r_s=-.9429 r_s^2=.89 p=.005
	6-10	80	64	80.0	
	11-15	73	39	53.4	
	16-20	34	7	20.6	
	21-25	24	4	16.7	
	26-30	4	0	0.0	
	Total	228	122	53.4	

All long bone fragments include epiphyseal, near-epiphyseal, and midshaft fragments. NISP transported is the number of fragments transported at current velocities up to 40 cm/s. r_s, Spearman's rank order correlation coefficient, which is based on the proportion of specimens transported for each width value. p value indicates the significance of the correlation.

Table 3.6) Proportions of specimens bearing tooth, cut or percussion marks in the transported and not-transported groups for each model.

Bone Modification Type	Portion	Model	Transport Group	Total NISP	NISP Modified	Percent Modified	Bootstrap Statistics	
							Mean Percent	95% IQR
Tooth Marks	All Long Bone Fragments	CO	Not-transported	39	33	84.6	84.6	71.8-94.9
			Transported	43	31	72.1	72.1	58.1-86.1
			Total	82	64	78.0	78.0	68.3-86.6
		H-C	Not-transported	63	12	19.0	19.1	9.5-28.6
			Transported	56	13	23.2	23.2	12.5-33.9
			Total	119	25	21.0	21.0	13.5-28.6
	Midshafts	CO	Not-transported	33	27	81.8	81.8	66.7-93.9
			Transported	33	22	66.7	66.8	51.5-81.8
			Total	66	49	74.2	74.2	63.6-84.9
		H-C	Not-transported	46	2	4.3	4.4	0-10.9
			Transported	48	8	16.7	16.8	6.3-27.1
			Total	94	10	10.6	10.7	5.3-17.0
Percussion Marks	All Long Bone Fragments	HO	Not-transported	53	18	34.0	34.0	20.8-47.2
			Transported	57	16	28.1	28.0	17.5-40.4
			Total	110	34	30.9	30.9	22.7-40.0
		H-C	Not-transported	63	16	25.4	25.4	14.3-36.5
			Transported	56	9	16.1	16.0	7.1-26.8
			Total	119	25	21.0	21.0	14.3-28.6
	Midshafts	HO	Not-transported	27	4	14.8	14.7	3.7-29.6
			Transported	41	9	22.0	21.9	9.8-34.2
			Total	68	13	19.1	19.1	10.3-29.4
		H-C	Not-transported	46	10	21.7	21.7	10.9-34.8
			Transported	48	8	16.7	16.7	6.3-27.1
			Total	94	18	19.1	19.1	11.7-27.7
Cut Marks	All Long Bone Fragments	HO	Not-transported	53	29	54.7	54.7	41.5-67.9
			Transported	57	20	35.1	35.1	22.8-47.4
			Total	110	49	44.5	44.5	35.5-53.6
		H-C	Not-transported	63	11	17.5	17.5	7.9-27.0
			Transported	56	2	3.6	3.5	0-8.9
			Total	119	13	10.9	10.9	5.9-16.8
	Midshafts	HO	Not-transported	27	8	29.6	29.7	14.8-48.2
			Transported	41	7	17.1	17.0	7.3-29.3
			Total	68	15	22.1	22.0	13.2-32.4
		H-C	Not-transported	46	6	13.0	13.1	4.4-23.9
			Transported	48	1	2.1	2.1	0-6.3
			Total	94	7	7.4	7.5	2.1-12.8

All long bone fragments include epiphyseal, near-epiphyseal, and midshaft fragments. CO, Carnivore only; HO, Hammerstone Only; H-C, Hammerstone-to-Carnivore. NISP Modified is the number of specimens with at least one tooth, percussion, or cut mark. The mean and 95% interquantile range (IQR) for each sub-sample are based on bootstrap analyses with the mean representing the average of 10,000 randomized samples and the interquantile range representing all of the data between the 2.5% and 97.5% quantiles

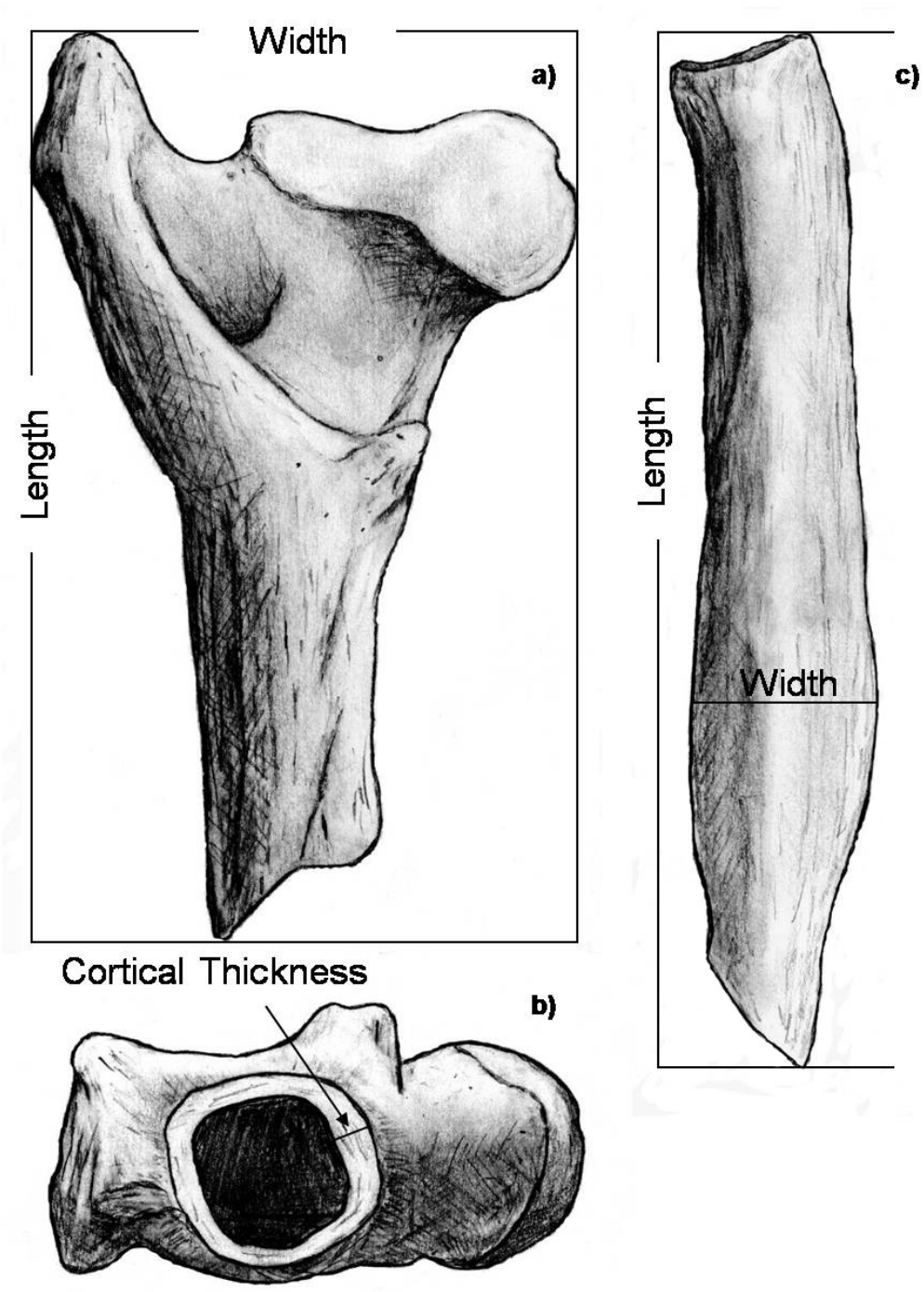


Figure 3.1) Measurements taken for length, Width, and cortical thickness illustrated using a femur epiphysis in posterior (a) and inferior (b) views, and a tibia shaft fragment in anterior view (c).

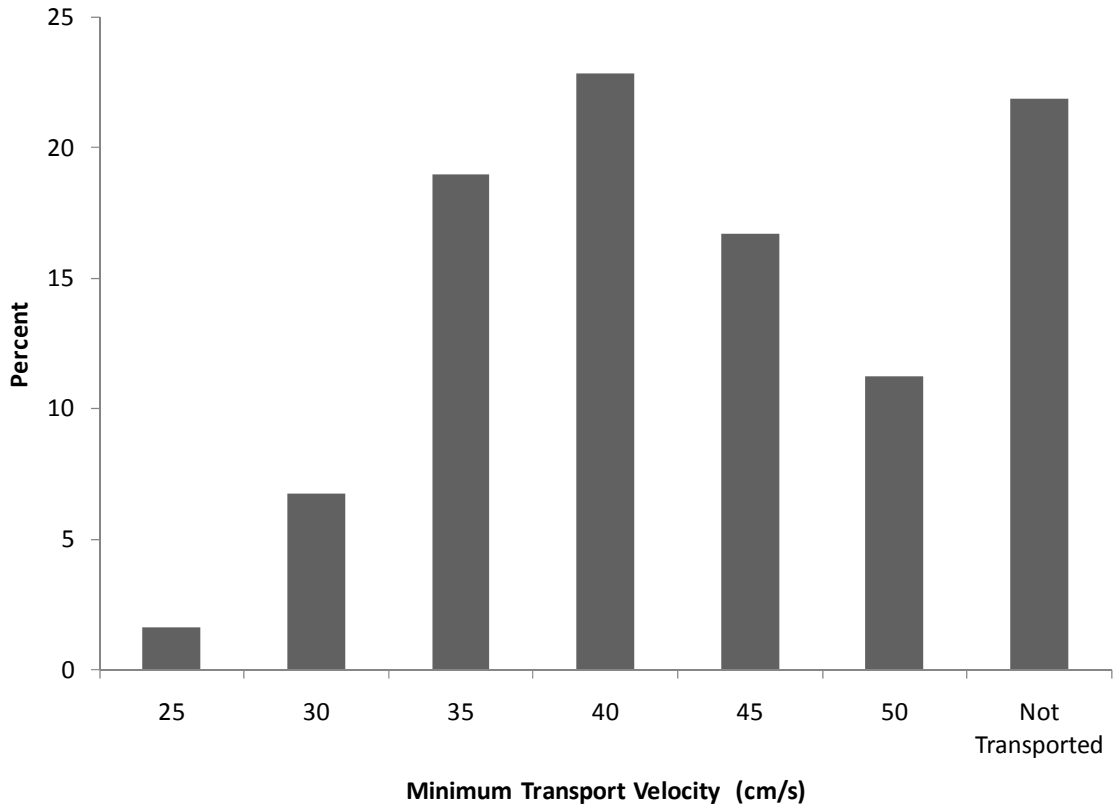


Figure 3.2) The distribution for the minimum transport velocity of individual fragments. Minimum transport velocity is based on six trials for each fragment.

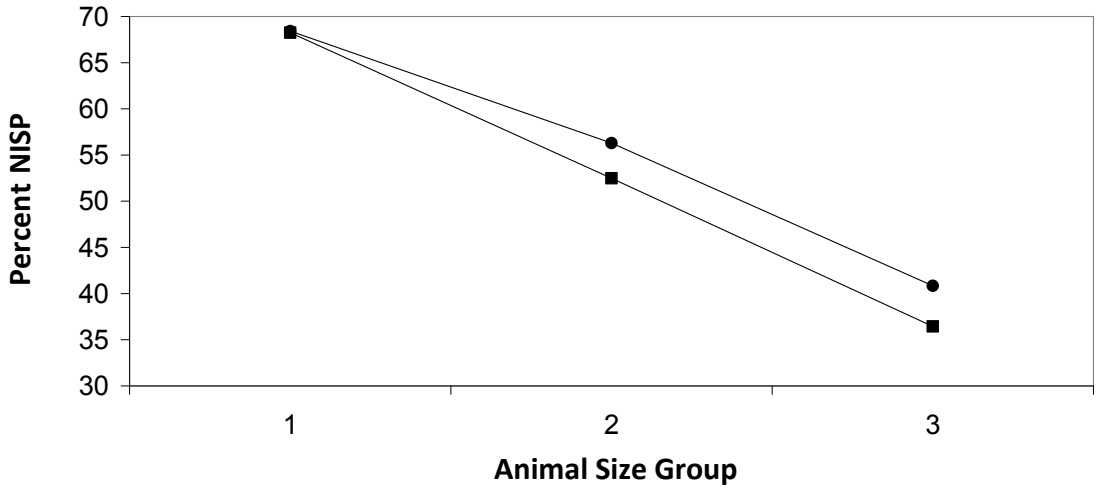


Figure 3.3) Proportion of specimens transported by animal size group. See Table 1 for definition of animal size groups. ■, all long bone portions; ●, long bone midshaft fragments

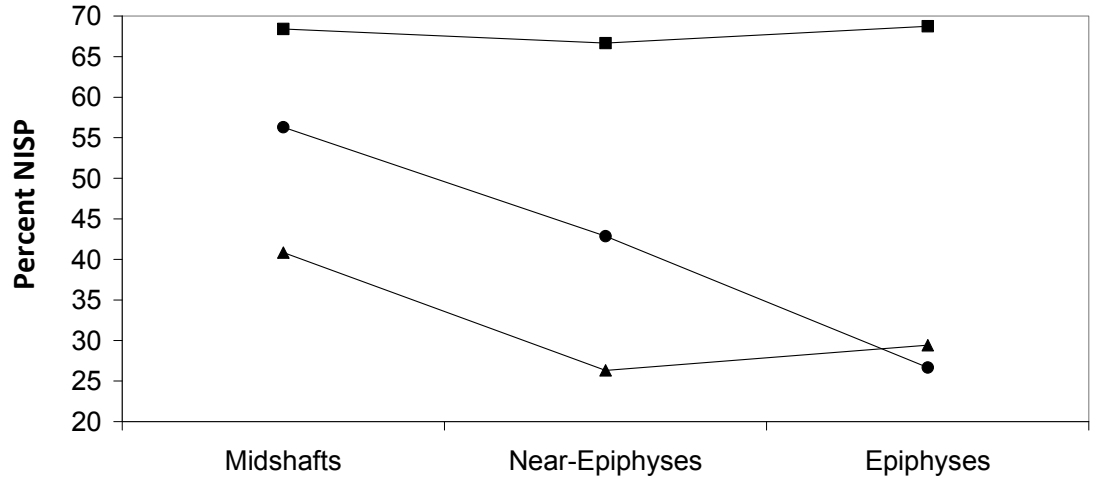


Figure 3.4) Proportion of specimens transported by long bone portion. See Table 1 for definition of animal size groups. ■, animal size group 1; ●, animal size group 2; ▲, animal size group 3.

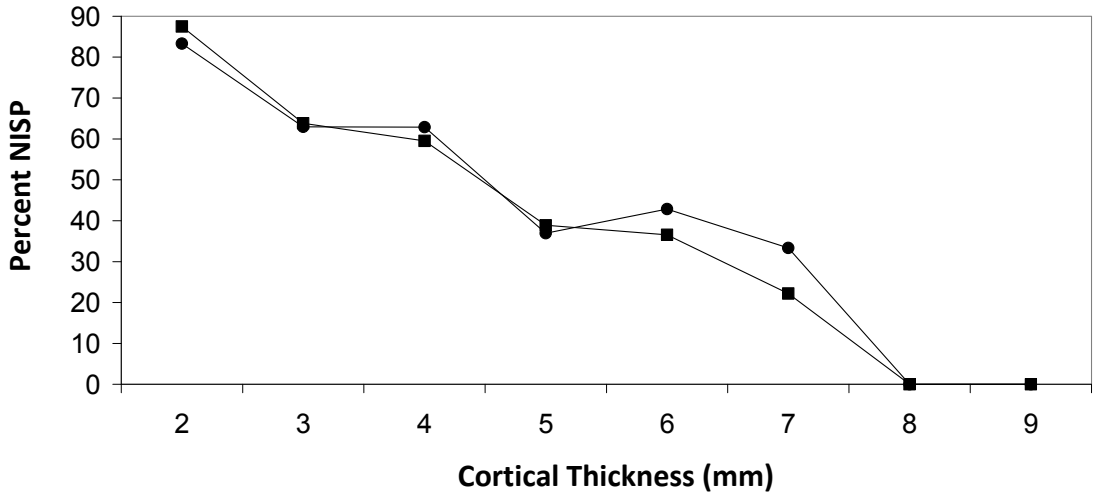


Figure 3.5) Proportion of specimens transported by maximum cortical thickness (mm). ■, all long bone portions; ●, long bone midshaft fragments.

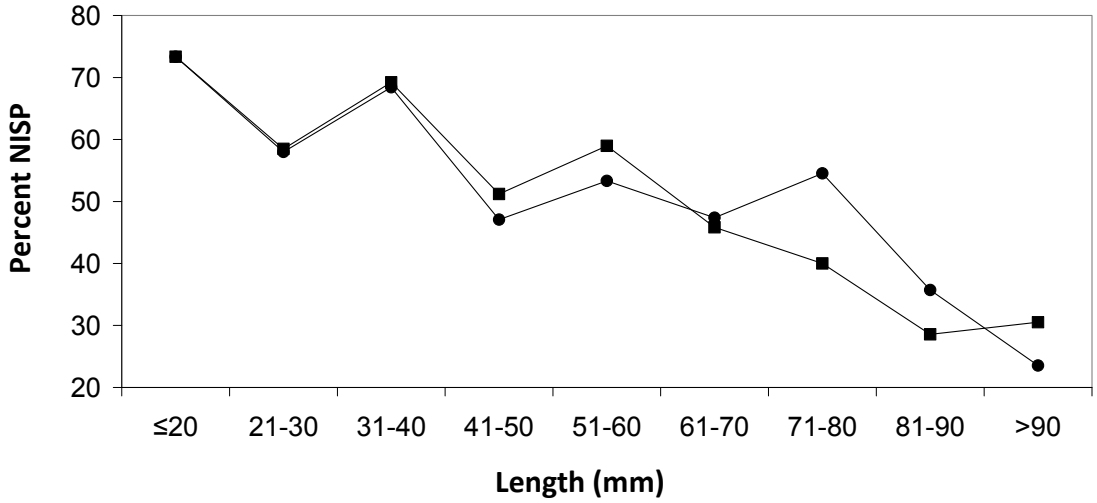


Figure 3.6) Proportion of specimens transported by maximum length (mm). ■, all long bone portions; ●, long bone midshaft fragments.

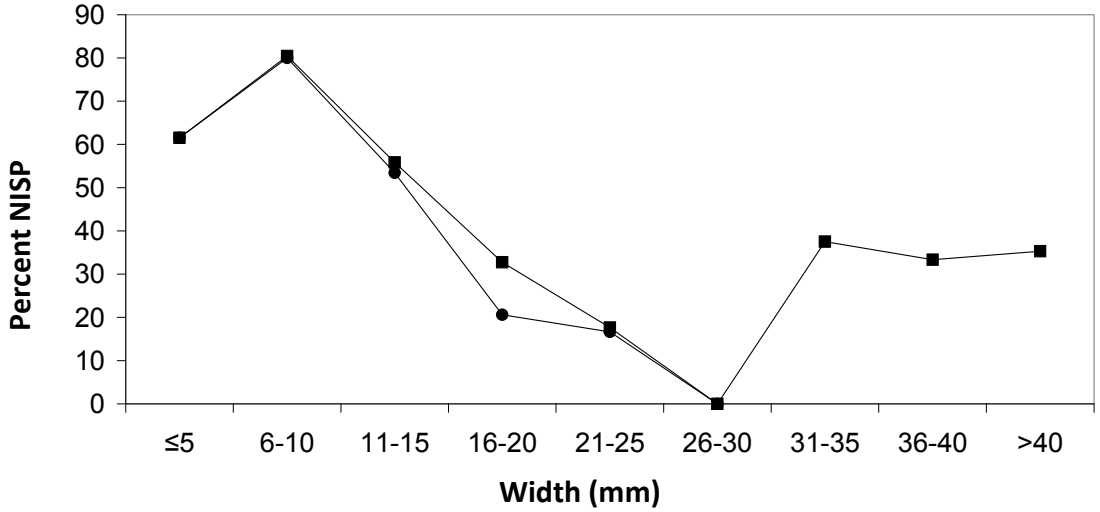


Figure 3.7) Proportion of specimens transported by maximum width (mm). ■, all long bone portions; ●, long bone midshaft fragments.

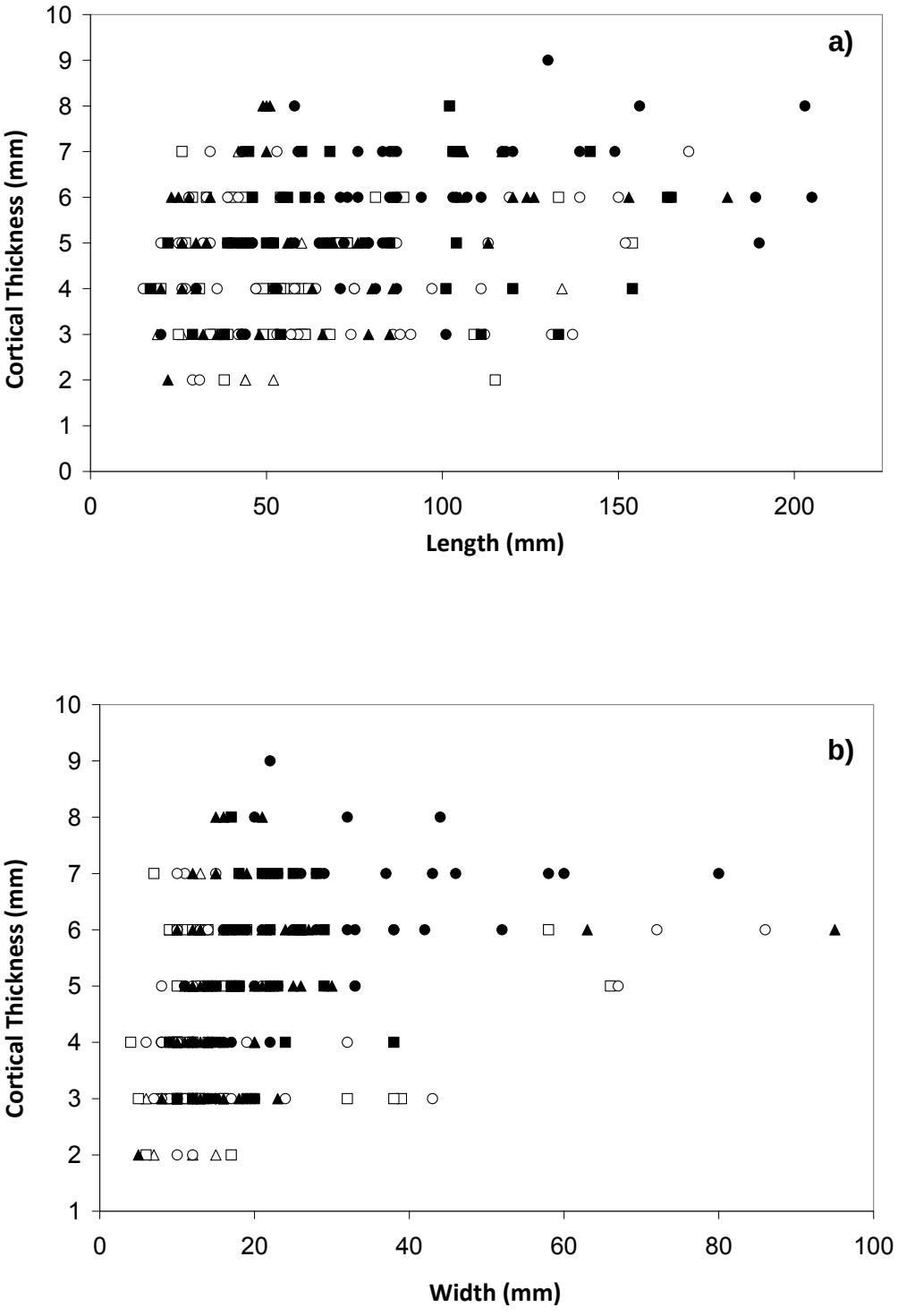


Figure 3.8) a) Maximum cortical thickness (mm) vs. maximum length (mm), and b) maximum cortical thickness (mm) vs. maximum width (mm). Specimens are distinguished by the minimum transport velocity required to move each the minimum 70 cm: Δ, 30 cm/s; □, 35 cm/s; ○, 40 cm/s; ▲, 45 cm/s; ■, 50 cm/s; ●, not transported.

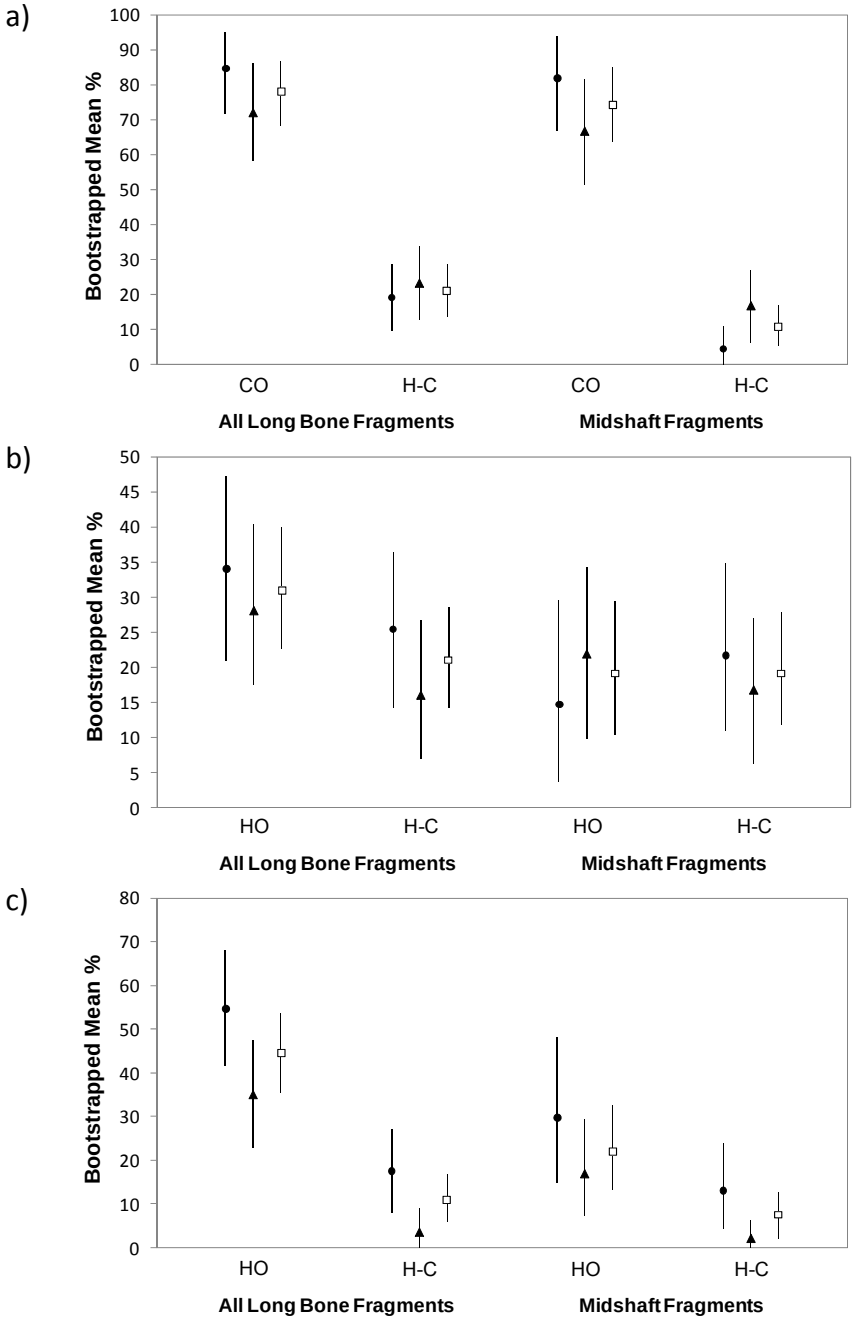


Figure 3.9) Proportions of specimens bearing tooth (a), percussion (b), or cut marks (c) in the transported and not-transported groups for each model. CO, Carnivore Only; HO, Hammerstone only; H-C, Hammerstone-to-Carnivore. The mean and 95% interquantile range for each sub-sample are based on bootstrap analyses with the mean representing the average of 10,000 randomized samples and the interquantile range representing all of the data between the 2.5% and 97.5% quantiles. □, the mean and 95% interquantile ranges for the bootstrapped fluvially-undisturbed samples; ●, the mean and 95% interquantile ranges for the bootstrapped not-transported sub-samples; ▲, the mean and 95% interquantile ranges for the bootstrapped transported sub-samples.

Chapter 4

The Taphonomy of JK2, Bed III, Olduvai Gorge

Introduction

Since the first systematic description of stone tool cut marks and the recognition of cut marks on larger mammal bones from early archaeological assemblages (Bunn; 1981; Potts and Shipman, 1981), much of the literature concerning Early Pleistocene zooarchaeology has focused on the order in which hominins and carnivores accessed carcasses at the Bed I, FLK 22 site, Olduvai Gorge (Binford, 1981; 1988; Blumenschine, 1988; 1995; Bunn, 1986; Bunn and Ezzo, 1993; Bunn and Kroll, 1988; Capaldo, 1995; 1997; 1998; Dominguez-Rodrigo; 1997; Dominguez-Rodrigo and Barba, 2006; Oliver, 1994; Selvaggio, 1994; 1998). While this vast literature has contributed to an understanding of Oldowan hominin feeding behavior, the methodologies generated by this research have yet to be applied to Acheulean-aged archaeological sites. Consequently, there is currently no way to assess the importance of carcass foods to the morphological and technological evolution of African *Homo erectus*, the first hominin species to exhibit near modern human body proportions and a larger absolute brain size (Shipman and Walker, 1989).

Feeding trace models that address the relative timing of hominin and carnivore access to carcasses were designed to interpret bone assemblages associated with Oldowan stone tools that are typically deposited in lake-margin or low-energy fluvial environments (Blumenschine, 1988; 1995; Capaldo, 1995; 1997; 1998; Dominguez-Rodrigo, 1997; Selvaggio, 1994; 1998). Acheulean fossil assemblages are most often deposited in fluvial environments and have been exposed to processes that were not considered by feeding trace modelers. Pante and Blumenschine (2010, also Chapter 3)

were the first to assess the impact of fluvial processes on the proportions of tooth, cut, and percussion marks in modern bone assemblages using a flume, concluding that the effect of low-energy hydraulic processes was not great enough to alter interpretations of hominin and carnivore carcass consumption that are based on these criteria. These results are applied here along with statistically reanalyzed feeding trace models (see Chapter 2 for details) to interpret the feeding behavior of *Homo erectus* from the fluvially-deposited JK2 fossil assemblage, Bed III, Olduvai Gorge. It is hypothesized that the hominins subsisting at JK2 would have typically acquired earlier access to carcasses than their Oldowan hominin counterparts.

JK2 History, Stratigraphy, and Archaeological Occurrences

Louis Leakey (1931-1932) discovered JK (Juma's Korongo) at the base of a reddened band believed at the time to be Bed IV, but later determined to be the only site at Olduvai Gorge which yielded concentrations of faunal and stone artifact material from Bed III (Hay, 1976; Kleindienst, 1964). Leakey called JK an occupation site in archaeological context and removed surface finds from the site when it was discovered. The site was excavated in 1962 by Maxine Kleindienst at which time she renamed the site JK2 because Louis Leakey was somewhat uncertain about whether it was the original place he called "JK" (Pers. com. Kleindienst). The only detailed account of the associated geology of the JK2 site was published by Kleindienst (1964). As such, this publication is the basis for all stratigraphic interpretations of the site.

JK2 is on the north side of the Gorge 2.2 km east of where the main and side Gorges meet. The deposits are 10-15 m below the rim of the Gorge and have been

exposed by the three branches of a side gully which converge to form one stream that joins the Olduvai River immediately south of the site. Kleindienst's 1962 excavations were originally planned to be placed only in JK2 West, but trenches were opened up in what was called JK2 East, some 100 m away to clarify the geologic setting (Figure 4.1). JK2 East and West were interpreted to have been deposited in fluvial or locally deltaic environments. Three fossil-bearing trenches were excavated by Kleindienst: Trenches A and B, were located in JK2 west where Leakey originally discovered cultural debris in 1931-1932; Trench 8 was discovered at JK2 East during Kleindienst's attempt to clarify the geology of JK2 West.

Trench A (Figure 4.2)

Artifacts including handaxes, fossil bones, and teeth were found scattered throughout grey-brown silt with the size and frequency of the fossils and artifacts increasing at the gradational contact with fine sand, continuing down to the gradational contact with the coarser sand. Large vertebrate fossils (Elephant Vertebrae) and artifacts were found at the base of the coarse sand at the contact with silty clay. The type and frequency of bone and the presence of debitage from stone-working of all size ranges indicated to Kleindienst that the finds represented debris in a hominin occupation area such as those found on earlier undisturbed occupation areas at Olduvai. Kleindienst interpreted the environment to be continuously aggrading, and she notes that finds in the silty and clayey beds, and in the fine sands may represent the remains of continuous human occupation, in disturbed context. Kleindienst regards these

materials as redeposited occupation debris which had undergone little transport and are probably a representative sample of the material from a nearby living site or sites.

Trench B

In trench B (Figure 4.3) the course sand found in Trench A thins into a medium-fine sand. Handaxes, cleavers, small artifacts, and fossil bones were found concentrated in the basal part where a minor disconformity with coarse sand and grit overlies grey silty clay. Otherwise, fossils and artifacts were found scattered throughout the trench with no other concentrations noted by Kleindienst (1964).

Trench 8

Kleindienst describes two separate archaeological occurrences in Trench 8. Scattered bones and artifacts found in the upper part of the coarse sand were designated as the upper archaeological occurrence. Concentrations designated as the lower archaeological occurrence were found immediately overlying a coarse sand/silty clay contact where the base of the coarse sand was level-bedded and within the top of the clay. In the clay, artifacts were found together with portions of two hippopotamus skeletons and a few remains of equids, suids, and bovids. Fossils and artifacts from the lower archaeological occurrence seem to have been deposited contemporaneously across the bedding contact. The environment is suggested to be continuously aggrading (i.e. sandbar or stream bank). Kleindienst believed this was a stream side butchery site in a disturbed context. No handaxes were found in these deposits and most artifacts had been worked from lava and quartzite cobbles.

All data presented here are limited to fossils excavated from Trenches A and B in JK2 West. Analysis of JK2 Trench 8 was halted due to the paucity of specimens from taxa other than Hippopotamidae, and the complete absence of hominin-induced bone surface modifications in the analyzed sample. Further, the majority of non-hippopotamid specimens from Trench 8, were exfoliated and had been extensively gnawed by rodents. It is unlikely that Trench 8 represents a stream side butchery site and the association of stone tools and fossils may be coincidental.

Methods

Experimental Controls

The experimental controls used for comparison with the JK2 assemblage represent five distinct feeding scenarios that are based on the assemblage-wide proportions of tooth, cut, and percussion marks on long bone fragments. Three of these feeding trace models were originally developed by Blumenschine (1988; 1995) including the hammerstone only (HO), carnivore only (CO), and hammerstone-to-carnivore (H-C) models. Capaldo (1995) expanded upon the H-C model and also developed the whole bone-to)-carnivore (WB-C) model. The fifth scenario, vulture-to-hominin-to-carnivore (V-H-C), was extracted from Blumenschine's H-C sample, but comprises a separate sample here due to the inclusion of cut mark frequencies not considered in his previous work. All models were reanalyzed using a bootstrap technique and Blumenschine's and Capaldo's H-C models were combined into a single sample (see Chapter 2 for details). Any reference to the models herein, are referring to the bootstrapped samples unless otherwise noted.

The JK2 Sample

Analysis of the JK2 fossil assemblage was conducted over 3 months in 2007 at the National Museums of Kenya. The study was taphonomically oriented focusing on the incidence and location of hominin- and carnivore-induced bone surface modifications within the assemblage. Taxonomic identifications are limited to the family level with the exception of bovid teeth, which were identified to tribe.

Extensive effort was invested in the curation of the JK2 assemblage. This involved cleaning all specimens with water and re-bagging using 4 mil ziplock bags. Glue was removed from the surfaces of bone fragments using acetone to allow identification of tooth, cut, and percussion marks. Trays were dusted and repaired when necessary and new trays were built to accommodate specimens that were pulled from level bags. The museums organization of the assemblage by taxonomy was maintained during and after the analysis, such that specimens that exhibited bone surface modifications were organized into separate trays, but were shelved according to their taxonomic designation.

The JK2 assemblage is the only assemblage from Beds III and IV that was excavated by Maxine Kleindienst, rather than Mary Leakey. Kleindienst's meticulous excavation and curation of the fossils and stone artifacts from the site were to a standard not often seen for Early Stone Age archaeological sites. As a result, JK2 represents the most complete assemblage from Beds III and IV as is demonstrated by the large number of fossils ranging from chips of bone less than 10 mm in maximum dimension to a complete elephant mandible (Table 4.1). Most of the smaller and

taxonomically non-identified bone fragments (n=24,962) remained in their original level bags, while 1,519 bone fragments had been organized by taxonomy and in some cases skeletal part. An additional 606 complete and/or fragmented mammal teeth are also organized by taxonomy (Table 4.2). None of these totals include surface material, which was identified, but later removed from analyses.

The taphonomically and taxonomically analyzed sample (analyzed sample throughout) includes a total of 2249 bone fragments 730 of which were pulled from the unsorted level bags, chosen for their good surface condition and/or identifiability to skeletal part. These 730 specimens along with any bone or tooth that did not have a specific identifying number were labeled to trench and given a specimen number ranging from 5000-5890 in order to allow referencing of the material. Numbers of 5000 and above were chosen because none of the originally labeled specimens had a specimen number above 4500 allowing distinction between Kleindienst's labeling system and my own. All long bone midshaft specimens from level bags that were not included in the analyzed sample (n=5400) were grouped into 10 mm size categories and counted. This data is used to describe the size distribution of all long bone midshafts excavated from JK2.

The sample used for statistical comparisons with feeding trace models (analytical sample throughout) only includes long bone specimens as they are the basis for the models. This sample was reduced to 403 long bone fragments (Table 4.3) from a total 1223 long bone fragments in the analyzed sample to maximize comparability of the JK2 assemblage with the models. Excluded specimens include those that 1) were less than

20 mm in maximum dimension, 2) had been recently broken with more than 10% of the fragment missing (inclusion of these specimens can have an unpredictable effect on mark frequencies), 3) had poor surface visibility due to mechanical rounding, exfoiliation, and/or adhering matrix covering more than 10% of the fragment, 4) were not green broken, determined by the presence of step fractures (inclusion of bones with step fractures would likely deflate mark frequencies), 5) were from an animal larger than size 4 or a taxonomic family other than bovid (feeding trace models are limited to bovids in size groups 1-4, see table 4.3 for description of size groups).

Analytical Procedure

Taxonomic, and skeletal part and portion identification was carried out using comparative collections located in the Archaeology wing of the National Museums of Kenya. Specimens that had been previously identified and labeled were independently identified for verification with only a few discrepancies being noted, most attributable to mis-located identification cards. Skeletal element portion was also recorded to tabulate more accurately the minimum number of elements (MNE) and minimum number of individuals (MNI) in the assemblage. Refitting was limited to post-curatorial breaks that had occurred during storage.

Skeletal parts were lumped into five groups for analysis following Capaldo (1995). The cranial group includes all of the cranium, the hyoid, and the mandible. The axial group includes, all vertebrae, all ribs, the clavicle, the sacrum, and the sternum. The appendicular group includes the humerus, femur, radius, ulna, tibia, fibula (for taxa other than bovidae), and metapodials (for bovidae, equidae, and giraffidae). The

compact group includes all carpals, tarsals, and phalanges, the patella, bovid fibula, and all other metapodials. The pelvis/scapula group includes all pelvis and scapula specimens.

Long bone portions were further divided into epiphyses (fragments with an articular surface, including the proximal ends of metapodials), near-epiphyses (fragments with cancellous bone on the medullary surface and no articular surface), and midshafts (fragments that do not have an articular surface or cancellous bone). Specimens that had multiple portions were identified by the most diagnostic portion, epiphyses were the most diagnostic and midshafts the least. For example, specimens identified as an epiphysis or near-epiphysis may contain a midshaft portion.

Quantitative measurements were taken to describe the size of each specimen including maximum length, maximum width, maximum thickness, and maximum cortical thickness. Each measure was taken to the nearest mm with digital calipers. Length was measured from the most proximal point to the most distal point parallel to the long-axis of the specimen, while width and thickness were measured perpendicular to length and perpendicular to each other with thickness determined to be the smaller of the two measurements. Cortical thickness was measured as the maximum thickness of bone from the outer surface to the medullary surface for long bones and the outer surface to the contact with trabecular bone for all other specimens.

Identification of tooth, cut, and percussion marks was conducted following the methods prescribed by Blumenschine et al. (1996). These include experience with bones marked under controlled conditions, and application of published morphological

and contextual criteria for distinguishing marks (see table 1 of Blumenschine et al. (1996)). The analysis of specimens was conducted in groups of ten with standard attributes recorded prior to mark analyses. The cortical surface, medullary surface, and thickness of each specimen were inspected first with the naked eye under a 100 watt table lamp and subsequently with a 16X hand lens. The orientation of the bone in relation to the light source was systematically altered to allow perception of depth for each mark, following Blumenschine (1995).

Percussion and tooth notches were identified and recorded following the methods outlined by Capaldo and Blumenschine (1994). Specifically, hammerstone percussion notches are broad and arcuate in plan form, while carnivore tooth notches approach a semi-circular plan form. Notches that fell in between these categories and were not associated with a tooth or percussion mark were considered indeterminate (N=6). Measurements taken included notch breadth, depth, and angle (obtuse, right, or acute). The location of associated tooth and/or percussion marks was also noted.

Results

Taxonomy

The JK2 assemblage is taxonomically rich, but is dominated by bovids, which represent about 70 percent of the assemblage based on the minimum number of individuals (MNI) (Figure 4.4). Equids are the second most abundant taxon at just over 11 percent. Taxonomic families representing just over 3 percent of the assemblage include Suidae, Rhinocerotidae, Hippopotamidae, Giraffidae, and Felidae. Those representing less than 2% include Hyaenidae and Elephantidae.

Further breakdown of the bovid individuals by tribe shows a dominance of Alcelaphini with Antilopini and Bovini the only other tribes represented by more than a single individual (Figure 4.5). Hippotragini, Reduncini, and Tragelaphini are also present in the assemblage.

Skeletal Group Profiles

Specimens from all five skeletal groups are represented in the JK2 assemblage (Table 4.4). The pattern observed based on the number of identified specimens (NISP) in the analyzed sample in order from most to least abundant is appendicular (54.4%)-axial (22.8%)-compact (10.3%)-cranial (6.5%)-pelvis/scapula (6.0%). The pattern based on the minimum number of elements is compact (32.7%)-appendicular (27.0%)-axial (24.7%)-pelvis/scapula (8.3%)-cranial (7.2%).

Animal Size Groups

All six animal size groups are represented in the JK2 assemblage (Table 4.4). The pattern for animal size groups is the same for both NISP and MNE estimates with size group 3 being the most abundant followed in order by size groups 2, 1, 4, 5, and 6.

Size Distribution of Long Bone Midshaft Fragments

The size distribution of long bone midshaft fragments from JK2 shows that the analyzed and analytical samples are similar to each other, but are deficient in shorter specimens when compared with the size distributions for all long bone midshaft fragments from JK2 and all five of the feeding trace models (Figure 4.6). Specifically, the analyzed and analytical samples are lacking specimens less than 40 mm in maximum length, while the size distribution for all long bone midshaft fragments from JK2 shows a

greater abundance of these specimens in the assemblage than would be expected from any of the feeding trace models.

Bone Surface Modifications

There are tooth, cut, and percussion marks on bone surfaces in the JK2 assemblage (Figures 4.7-4.10). While tooth marks are abundant, percussion and cut marks are few in the assemblage. Below is a detailed comparison of the JK2 analytical sample with the bootstrapped feeding trace models.

Percussion Marks

The incidence of percussion-marked bone in the JK2 assemblage is most similar to the V-H-C model and is below the 95% interquantile ranges for all sub-samples of the HO model (Table 4.5, Figure 4.11). For all long bone fragments, the JK2 assemblage is just within the lower 95% interquantile ranges for all size group sub-samples of the V-H-C model and the lower 95% interquantile range for the size group 3-4 sub-sample of the H-C model. For midshaft fragments, the JK2 assemblage is just within the lower ranges of the size group 1-4 and size group 3-4 sub-samples of the V-H-C model and the size group 3-4 sub-sample of the H-C model.

Tooth Marks

The incidence of tooth-marked bone in the JK2 assemblage is most similar to the V-H-C model (Table 4.6, Figure 4.12). The values for JK2 fall below all sub-samples of the CO model and above all sub-samples of the H-C model. For all long bone fragments and midshaft fragments the JK2 values fall within the 95% interquantile ranges for the size group 1-4 and size group 3-4 sub-samples of the H-C model. The value for JK2 also falls

within the relatively large 95% interquantile range for the size group 3-4 sub-sample of midshaft fragments in the WB-C model.

Cut marks

The incidence of cut-marked long bones in the JK2 assemblage is only accommodated by sub-samples that have a lower 95% interquantile range of zero (Table 4.7, Figure 4.13). These include the size group 1-4 and 3-4 sub-samples for all long bone fragments of the V-H-C model and the size group 3-4 sub-sample for midshaft fragments in the HO model. The incidence of cut-marking in the JK2 sample is below all sub-samples of the WB-C and H-C models.

Tooth and Butchery Marks

The incidence of tooth- and butchery-marked bone in the JK2 assemblage is most similar to the V-H-C model (Table 4.8, Figure 4.14). The values for JK2 fall within the 95% interquantile ranges of all sub-samples of the V-H-C model for all long bone fragments and midshaft fragments. For midshaft fragments only, the JK2 values also fall within the lower 95% interquantile ranges for the size group 1-2 sub-sample of the WB-C model and the size group 3-4 sub-sample of the H-C model. The JK2 values are below all other 95% interquantile ranges for sub-samples of the WB-C and H-C models.

Notches

The incidences of tooth and percussion notching are nearly equivalent in both the analyzed and analytical JK2 samples (Table 4.9). Both samples most closely resemble the H-C model as the assemblage bears both tooth and percussion notches. The proportions of tooth-notched bone for both JK2 samples are higher than is

predicted by the H-C model, while the proportions of percussion-notched bone are lower than is predicted by the H-C model.

Discussion

JK2 Paleoenvironment

The degree to which fluvial processes affected the JK2 assemblage holds significance for interpretations of the site. Reworking of fossils by flowing water can maximize time averaging and can cause mixing of unassociated fossil assemblages (Kidwell and Behrensmeyer, 1993). However, it is possible to overcome these challenges through interpretation of the sediments associated with the assemblage and by examining the size and skeletal part distributions of the fossils themselves.

Time Averaging in the JK2 Assemblage

Time averaging is "the process by which organic remains from different time intervals come to be preserved together." (Kidwell and Behrensmeyer, 1993:4) While time averaging affects all archaeological and paleontological assemblages, it is generally considered to have a greater influence in fluvially-deposited assemblages due to reworking of fossils by erosion and re-deposition (Kidwell and Behrensmeyer, 1993). Behrensmeyer (1982; 1988) describes two taphonomic models (Channel-fill and Channel-lag) of time averaging in fluvial systems. Generally, channel-fill sequences represent short time intervals ($<10^2$ yrs), while channel-lag sequences are associated with long intervals of time averaging (10^2-10^6 yrs), depending upon the age of the surrounding deposits from which fossils may be reworked (Behrensmeyer, 1982; 1988).

Channel-fill sequences are indicative of aggrading sediments and are associated with the abandonment of a paleochannel. The sedimentary context of channel-fill sequences is characterized as the middle to upper part of channels with discontinuous thin coarse beds and thicker fine-grained units containing mudstones, silts, clays, fine sands, and nodule conglomerates (Behrensmeyer, 1988). Fossils deposits in channel fills are usually size sorted in coarser sediments with poor sorting in finer grained sediments (Behrensmeyer, 1988). Bone edges can be fresh to rounded with fragmentation and associated skeletal parts varying with grain size (Behrensmeyer, 1988). Channel-fill sequences can be interpreted as autochthonous with bones only transported short distances if at all (Behrensmeyer, 1988).

Channel-lag sequences indicative of eroding sediments are found in the lower parts of channels or erosional troughs (Behrensmeyer, 1988). The lithology of channel-lag deposits is composed of sands, gravels, and mudclast/nodule conglomerates (Behrensmeyer, 1988). Fossils are usually well sorted and composed of larger and heavier elements with rounding on bone edges (Behrensmeyer, 1988). Fragmentation is common and associated skeletal parts are rare with bones horizontally aligned with the paleocurrent (Behrensmeyer, 1988). Bone assemblages deposited in channel-lag sequences can be interpreted as allochthonous, representing large areas of the drainage, including reworked fossils from channel banks (Behrensmeyer, 1988).

The sedimentology associated with the JK2 fossils suggests that most of the JK2 assemblage was deposited during a channel fill sequence and time averaging should be minimal ($<10^2$ yrs). Kleindienst (1964) noted that the JK2 assemblage was likely

deposited in a continuously aggrading environment and that the lack of root casts and soil development throughout the JK2 trenches suggest a fairly rapid aggradation of sediments. Kleindienst (1964) also noted that it is unlikely that materials outside of Bed III were deposited at JK2 as significant uplift would have needed to occur to transport material from even upper Bed II.

Fluvial Transport

The fossils in the JK2 assemblage also indicate low-energy channel-fill conditions at the site. The size distribution of long bone midshaft fragments for all specimens show an abundance of small specimens < 40 mm in maximum dimension. Flume experiments demonstrated that these specimens are more likely to be transported than their larger counterparts (see Chapter 3). The fact that there are actually more specimens less than 40 mm in maximum dimension than is predicted by any of the feeding trace models suggests that JK2 is an autochthonous assemblage that was likely exposed to post-depositional fragmentation. Further, the presence of size groups 1-6 and all skeletal groups in the assemblage indicate the fauna have not been sorted by fluvial processes. The dominance of size group 3 fauna likely reflects the abundance of this size group in the living population. Likewise, had the assemblage been heavily sorted it would be expected to be deficient in vertebrae, ribs, carpals/tarsals and phalanges (Voorhies, 1969). Skeletal part profiles show an abundance of these elements in the JK2 assemblage.

Taxonomy and Climate

The JK2 assemblage is dominated by grazers that thrive in dry and open habitats. The assemblage of bovids is comprised of nearly 80% Alcelaphini individuals, while the lone Tragelaphini individual is likely a member of the species *Tragelaphus strepsiceros* known for its widespread distribution in modern habitats (Gentry and Gentry, 1978). These findings are in agreement with oxygen and carbon isotope evidence from Beds III and IV that show a mean annual rainfall of less than 800 mm and a dominance of C4 grasses, which makeup between 60 and 80% of the vegetation biomass (Cerling and Hay, 1986). Together, these lines of evidence suggest open savannah habitats for Olduvai Gorge, during JK2 times.

The Feeding Behavior of Hominins and Carnivores at JK2

Results indicate the pattern of feeding traces found at JK2 cannot be accounted for by some of the models. Most clearly, the co-occurrence in the assemblage of tooth-marked specimens and butchery-marked specimens eliminates individually the CO and/or HO models as exclusive descriptors of the behavioral sequences that produced the JK2 assemblage. Likewise, individual specimens bearing both tooth and butchery marks eliminate a combination of CO and HO as exclusive descriptors.

Results also indicate the pattern of feeding traces found at JK2 can be accounted for by some of the behavioral sequences modeled by the experimental assemblages. Specifically, the proportions of tooth-, cut-, percussion-, and tooth- and butchery-marked bone in JK2 assemblage most closely resemble those for the V-H-C model.

However, in all cases the proportions of cut- and percussion-marked bone fall within the lower range or below those predicted by all models.

The proportion of percussion-marked bone in the JK2 assemblage indicates hominins may not have been the only consumers of marrow at the site. JK2 is within the 95% interquantile ranges for most sub-samples of the V-H-C model and for the size group 3-4 sub-samples of the H-C model, all of which predict primary access to marrow by hominins. However, in all cases, the JK2 values fall just within the lower ranges predicted by these models suggesting that at least some long bones were broken by carnivores at the site. This may be indicative of a CO component to the assemblage or a lack of complete processing of all long bones by hominins for marrow (i.e. the WB-C model). Both the CO and WB-C models predict significantly higher proportions of tooth-marked bone than the H-C or V-H-C model.

The proportion of tooth-marked bone in the JK2 assemblage is consistent with both hominins and carnivores having had access to flesh at the site. The values for JK2 are within the relatively large interquantile range for the size group 3-4 sub-sample of the WB-C model and the size group 1-2 and 1-4 sub-samples of the V-H-C model. It is of significance that the size group 1-2 sub-sample of the V-H-C model differs from the size group 3-4 sub-sample in that carnivores had primary access to flesh in the sole assemblage that describes the size group 1-2 sub-sample (see Chapter 2). Primary access to flesh by carnivores followed by hominin breakage of long bones for marrow removal inflates tooth mark frequencies to values that are just below those predicted by the CO model and above those predicted by the H-C model. The JK2 values fall

intermediately between all other models that predict primary access to flesh and/or marrow by carnivores (CO and WB-C) and those that predict primary access to flesh and marrow by hominins (H-C and size group 3-4 of the V-H-C model). Given the tooth mark results, it might be suggested that JK2 is best described by a carnivore-to-hominin-to-carnivore (C-H-C) model, in which carnivores were the primary consumers of flesh and hominins the primary consumers of marrow. However, the values for JK2 are still well below the 54.2% mean tooth mark frequencies for long bone midshaft fragments predicted by Selvaggio's (1994) C-H-C model. Rather, the tooth mark results for JK2 are suggestive of an assemblage that includes both, H-C and CO components or a lack of complete processing of marrow by hominins with higher proportions of cut-marked and tooth- and butchery-marked bone expected for the later scenario.

The proportion of cut-marked bone in the JK2 assemblage indicates that hominins did not extract the flesh from every carcass at the site. The incidence of cut-marking for the JK2 assemblage is lower than is predicted by all feeding trace models that do not have a lower 95% interquantile range of zero. The JK2 values are most similar to the V-H-C model where flesh was completely removed by vultures and in some cases carnivores prior to the simulation of hominin scavenging (see Chapter 2). As a result, defleshing cut marks on long bone midshaft fragments are absent in the V-H-C model. The presence of cut-marks on long bone midshaft fragments in the JK2 assemblage indicates at least some carcasses were defleshed by hominins, while the relatively low incidence of cut marking is indicative of a CO component to the assemblage.

The proportion of specimens bearing both tooth and butchery marks in the JK2 assemblage demonstrates at least some carcasses were exploited by both hominins and carnivores. However, the low incidence of specimens exhibiting both hominin and carnivore damage leaves open the possibility that a significant proportion of the assemblage is best described by HO or CO. Given the percussion, tooth, and cut mark results, CO is more likely than HO as hominin-induced modifications are in the lower ranges or below those predicted by all available feeding trace models.

Accuracy of Mark Estimates for the JK2 Assemblage

All fossil assemblages are exposed to processes not replicated by the feeding trace models. As such, it is imperative to understand the affects of these processes on proportions of tooth-, cut-, and percussion-marked bone in an assemblage. In the case of JK2, post-depositional breakage and fluvial abrasion are among the most significant processes that have potentially altered the incidences of bone surface modifications in the assemblage.

Post-depositional breakage is indicated by the abundance of small specimens in the JK2 assemblage and was accounted for by excluding specimens exhibiting step fractures that are indicative of dry-bone breakage (Johnson, 1985) and those that had been recently broken with more than 10% of the fragment missing. Partly as a result of these exclusions, both the analyzed and analytical samples of long bone midshaft fragments are depleted of specimens less than 40 mm in maximum dimension when compared with the size distributions for all long bone midshaft fragments from JK2 and for all of the feeding trace models. The lack of smaller specimens in the analytical

sample will inflate mark frequencies because the proportions of tooth- and percussion-marked bone increase with increasing specimen size (see Figure 4.15, and Blumenschine, 1995). Therefore, the results reported here may overestimate the incidences of tooth, cut, and percussion marks in the assemblage.

Fluvial processes can transport and abrade bone fragments potentially affecting the proportions of hominin and carnivore modifications in fossil assemblages. It has been demonstrated that tooth-, cut-, and percussion-marked bone fragments are not differentially transported by low-energy fluvial processes, like those that are associated with the JK2 assemblage (Chapter 3). Given these results, hydraulic transport is not likely to have had a significant effect on the proportions of hominin- and carnivore-modified bone in the JK2 assemblage. However, flowing water can also round and abrade bone potentially obscuring bone surface modifications (Shipman and Rose, 1983). Rounding was scored here as minor (not likely to obscure marks) or severe (likely to obscure marks) with only severely rounded specimens excluded from the analytical sample. This scoring is arbitrary as there is no actualistically-based method that associates degree of rounding with the obscuring of tooth, cut, and percussion marks on bone surfaces. Further, it is currently unknown whether fluvial rounding will preferentially erode one mark type over another (i.e. percussion marks over tooth marks). Given these limitations, the significance for the proportions of tooth- and percussion-notched bone in the assemblage should be emphasized in assessments of the accuracy for mark estimates as the incidences of notches are not likely to have been affected by fluvial abrasion.

Carnivore Tooth and Hammerstone Percussion notches

The incidences of tooth and percussion notching in the JK2 assemblage correspond with the bone surface modification results in suggesting a mix of CO and H-C contributed to the assemblage. The incidence of tooth notching in both the analyzed and analytical samples falls intermediately between the CO and H-C models, while the incidence of percussion notching is far less than is predicted by either the HO or H-C model. Together, these results indicate a significant CO component to the JK2 assemblage and support the bone surface modification results.

The validity of mark estimates can also be assessed by examining the proportion of percussion- and tooth-notched specimens that are percussion- and tooth-marked (Table 4.10). The proportions of percussion- and tooth- notched specimens that are also tooth-marked in the JK2 assemblage are statistically indistinguishable from those predicted by the H-C model. Conversely, the proportions of percussion- and tooth-notched specimens that are also percussion-marked are significantly different from those predicted by the H-C model. Specifically, there are more percussion-notched specimens that are also percussion-marked, but less tooth-notched specimens that are also percussion-marked in the JK2 assemblage when compared with the H-C model. This pattern may indicate that in some cases tooth marks on percussion-notched specimens were mistaken for percussion marks, an error that might occur due to hydraulic rounding, a process that may obscure the characteristic crushing that distinguishes tooth marks from percussion marks that have a smooth and featureless internal topography. (Blumenschine et al., 1996). This error would inflate percussion

mark frequencies and deflate tooth mark frequencies suggesting that the hominin signal may be overestimated by the mark analyses presented here. Therefore, it is possible that the CO component of the assemblage is more significant than the mark estimates suggest.

Conclusions

The paleoecological and taphonomic analysis of the JK2 is the first such study of a fossil assemblage associated with Acheulean stone tools in fluvial context. Application of the bootstrapped feeding trace models and the results from flume experiments, afford taphonomically informed interpretations of the site that were not previously possible. As such, the significance of this study is not only in the results reported for JK2, but also in the development of a theoretically grounded methodology for interpreting all fossil assemblages in fluvial contexts.

Skeletal part profiles and the size distribution of long bone midshaft fragments in the JK2 assemblage indicate a low-energy fluvial environment at the site. These results support Kleindienst's (1964) assertion that the assemblage had undergone minimal transport and likely represents an accumulation from a nearby living site. Therefore, the application of the feeding trace models is justified, as they have been shown to remain valid in low-energy fluvial contexts (Pante and Blumenschine, 2010).

The proportions of tooth-, cut-, and percussion-marked bones in the JK2 assemblage all indicate that both hominins and carnivores were likely acquiring early access to flesh at the site. The low incidence of percussion marking relative to the HO and H-C models indicate hominins likely did not break all long bones in the assemblage.

Tooth and cut mark frequencies independently suggest that both hominins and carnivores had access to flesh, but neither indicate hominins or carnivores as the dominant consumers of flesh. Finally, the presence of specimens that are both tooth- and butchery-marked demonstrates occasional hominin and carnivore feeding from the same carcass.

Together, the bone surface modification data are consistent with an assemblage composed of both H-C and CO components. Hominins likely had early access to flesh either through hunting or confrontational scavenging at the site. They likely exploited most bone marrow from the carcasses obtained, while remaining within-bone nutrients would have been consumed by bone-crunching carnivores (i.e. hyaenids). At least some carcasses would only have been consumed by carnivores at the site. Whether these H-C and CO components of the assemblage were deposited in a single location or in several nearby upstream locations that were later accumulated at the JK2 site is unclear. However, the evidence against fluvial transport of the assemblage suggests the former. It is possible that the site represents an area where carnivores typically ambushed prey and hominins at the site were occasionally usurping carcasses during the earliest stages of the carcass consumption sequence (Blumenschine, 1986a, b) with at least some flesh remaining intact.

The evolutionary significance of the results for the JK2 assemblage lies in the indication that *Homo erectus* likely acquired earlier access to carcasses than its Oldowan hominin ancestors at the FLK 22 site. This study contributes to a growing literature focused on tracking the increasingly pervasive role played by hominins within the

carnivore guild. The application of these methods to additional Acheulean-aged fossil assemblages will afford a greater understanding of *Homo erectus* feeding behavior and the significance of such to the evolution of our own species.

Table 4.1) Description of the JK2 sample

	All Bone Fragments	Long Bone Fragments
All Specimens	26481	6623
Analyzed Sample	2249	1223
Analytical sample	-	403

Values represent the NISP for each sample.

Table 4.2) NISP for teeth

	NISP
Bovidae	442
Carnivora	6
Equidae	65
Elephantidae	7
Hippopotamidae	45
Rhinocerotidae	8
Suidae	33
Total	606

Table 4.3) Long bone portion profile by animal size groups for the analytical sample

	Epiphyseal Fragments	Near-Epiphyseal Fragments	Midshaft Fragments	Total
Size 1-2	21	20	108	149
Size 3-4	61	53	140	254
Total	82	73	248	403

See text for definitions of long bone portions. Animal size groups are based on Bunn and Kroll (1986). Size 1, <50 lbs (23 kg); Size 2, 50-250 lbs (23-114 kg); Size 3, 250-750 lbs (114-341 kg); Size 4, 750-2000.

Table 4.4) Skeletal part profile for the analyzed JK2 sample

	Size 1		Size 2		Size 3		Size 4		Size 5		Size 6		Total	
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Cranial Fragment	1	-	7	-	16	-	4	-	1	-	0	-	29	-
Frontal	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Horn Core	1	1	10	2	29	5	3	1	0	0	0	0	43	9
Hyoid	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Maxilla	2	1	7	1	6	2	1	1	0	0	0	0	16	5
Mandible	2	2	8	2	33	17	2	1	1	1	1	1	47	24
Occipital	0	0	1	1	1	1	0	0	1	1	0	0	3	3
Temporal	0	0	1	1	3	2	0	0	2	1	0	0	6	4
Cranial Total	6	4	35	8	89	28	10	3	5	3	1	1	146	47
Atlas	1	1	1	1	2	2	1	1	0	0	0	0	5	5
Axis	0	0	1	1	6	6	1	1	0	0	0	0	8	8
Caudal Vertebra	0	0	1	1	1	1	0	0	0	0	0	0	2	2
Cervical Vertebra	0	0	5	4	15	13	0	0	1	1	1	1	22	19
Clavicle	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Lumbar Vertebra	1	1	14	11	11	7	2	1	2	1	5	4	35	25
Rib	39	2	67	14	145	22	48	6	21	3	4	1	324	48
Rib 1	1	1	2	2	2	2	0	0	1	1	0	0	6	6
Sacrum	0	0	4	3	5	5	0	0	0	0	0	0	9	8
Sternum	0	0	0	0	2	1	0	0	0	0	0	0	2	1
Thoracic Vertebra	7	5	19	15	31	14	2	2	3	1	1	1	63	38
Vertebra Fragment	5	-	8	-	15	-	3	-	1	-	4	-	36	-
Axial Total	54	10	123	53	235	73	57	11	29	7	15	7	513	161
Femur	5	3	22	5	56	9	5	2	8	4	0	0	96	23
Fibula	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Humerus	9	4	22	3	67	13	9	2	2	1	1	1	110	24
Long Bone Fragments	77	-	123	-	199	-	29	-	16	-	2	-	446	-
Metacarpal	6	1	24	5	61	12	1	1	2	2	0	0	94	21
Metapodial	3	-	35	-	62	-	0	-	0	-	0	-	100	-
Metatarsal	3	1	24	4	51	9	4	1	1	1	0	0	83	16
Radius	12	4	15	5	79	19	4	3	0	0	0	0	110	31
Tibia	9	4	24	4	112	26	7	2	2	1	0	0	154	37
Ulna	1	1	10	6	14	12	1	1	3	3	0	0	29	23
Appendicular Total	125	18	299	32	702	101	60	12	34	12	3	1	1223	176
Astragalus	2	2	6	6	13	13	3	3	0	0	0	0	24	24
Calcaneus	1	1	2	1	11	7	1	1	0	0	1	1	16	11
Carpal or Tarsal	0	-	0	-	2	-	1	-	0	-	0	-	3	-
Cuneiform	0	0	1	1	5	5	1	1	0	0	0	0	7	7
External Cuneiform	0	0	0	0	3	3	1	1	0	0	0	0	4	4
Fibula	1	1	2	2	5	5	0	0	0	0	0	0	8	8
Medial-lateral Cuneiform	0	0	3	3	6	6	0	0	0	0	0	0	9	9
Lunate	0	0	1	1	5	5	0	0	1	1	0	0	7	7
Magnum	0	0	2	2	8	8	0	0	1	1	0	0	11	11
Metapodial	0	0	2	2	2	2	0	0	2	2	0	0	6	6
Navicular-Cuboid	0	0	3	3	7	7	3	3	1	1	0	0	14	14
Patella	1	1	2	2	0	0	0	0	0	0	0	0	3	3
Phalange Proximal	1	1	3	3	32	27	0	0	0	0	0	0	36	31
Phalange Intermediate	3	3	4	3	24	21	1	1	0	0	0	0	32	28
Phalange Distal	1	1	2	2	12	12	1	1	0	0	0	0	16	16
Phalange Fragment	0	-	1	-	0	-	0	-	0	-	0	-	1	-
Pisiform	0	0	0	0	3	3	0	0	0	0	0	0	3	3
Sesamoid	0	0	5	5	10	10	5	5	0	0	0	0	20	20
Scaphoid	0	0	0	0	2	2	2	2	0	0	0	0	4	4
Unciform	0	0	3	3	4	4	0	0	0	0	0	0	7	7
Compact Total	10	10	42	39	154	140	19	18	5	5	1	1	231	213
Innominate	2	2	7	4	37	20	4	1	2	1	0	0	52	28
Scapula	2	2	15	2	59	18	5	1	2	2	1	1	84	26
Pelvis/Scapula Total	4	4	22	6	96	38	9	2	4	3	1	1	136	54
Grand Total	199	46	521	138	1276	380	155	46	77	30	21	11	2249	651

NISP is the number of identified specimens. MNE is the minimum number of elements represented and is based on skeletal part and portion data.

Table 4.5) Incidence of percussion-marked bone

		HO	H-C	V-H-C	JK2
All Long Bone Fragments	**Size 1-4**				
	Mean %	38.5	26.5	24.9	10.2
	95% I.Q.R	29.1-47.7	21.6-31.6	9.1-43.6	-
	Size 1-2				
	Mean %	36.6	30.3	17.5	6.0
	95% I.Q.R	26.3-46.2	24.3-36.6	4.4-34.8	-
	Size 3-4				
	Mean %	49.9	18.0	26.9	12.6
	95% I.Q.R	29.1-70.8	11.5-25.5	7.7-49.1	-
Midshaft Fragments	**Size 1-4**				
	Mean %	27.7	24.9	19.8	8.1
	95% I.Q.R	16.4-37.9	19.8-30.2	6.4-35.8	-
	Size 1-2				
	Mean %	26.7	29.4	23.6	4.6
	95% I.Q.R	14.0-37.8	23.6-35.8	5.9-47.1	-
	Size 3-4				
	Mean %	33.5	14.6	19.2	10.7
	95% I.Q.R	11.3-60.0	8.1-22.4	3.7-38.3	-

Incidence is measured as the proportion of specimens bearing at least one percussion mark. HO, Hammerstone Only; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where JK2 is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 4.6) Incidence of tooth-marked bone

		CO	WB-C	H-C	V-H-C	JK2
All Long Bone Fragments	**Size 1-4**					
	Mean %	83.9	73.7	20.1	23.6	31.8
	95% I.Q.R	74.6-92.1	62.3-84.5	17.4-24.6	12.2-37.0	-
	Size 1-2					
	Mean %	70.9	70.6	19.1	43.4	26.2
	95% I.Q.R	56.7-82.5	55.7-84.3	14.9-23.7	21.7-65.2	-
	Size 3-4					
	Mean %	87.6	78.9	24.9	18.5	35.0
	95% I.Q.R	77.9-95.5	61.9-95.0	19.6-30.3	9.1-28.7	-
Midshaft Fragments	**Size 1-4**					
	Mean %	82.6	65.7	14.5	11.7	26.2
	95% I.Q.R	72.5-91.9	47.8-80.8	11.4-18.1	1.3-26.2	-
	Size 1-2					
	Mean %	69.1	70.5	14.5	35.5	25.9
	95% I.Q.R	54.8-81.0	56.1-84.7	10.5-18.9	11.8-58.8	-
	Size 3-4					
	Mean %	86.5	57.3	14.8	5.6	26.4
	95% I.Q.R	75.7-95.8	18.1-89.8	7.3-23.5	0-14.4	-

Incidence is measured as the proportion of specimens bearing at least one tooth mark. CO, Carnivore Only; WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where JK2 is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 4.7) Incidence of cut-marked bone

		HO	WB-C	H-C	V-H-C	JK2
All Long Bone Fragments	**Size 1-4**					
	Mean %	29.9	27.0	18.3	6.7	4.7
	95% I.Q.R	22.2-38.3	13.7-42.8	14.8-22.3	0-15.3	-
	Size 1-2					
	Mean %	27.2	18.4	18.9	0	2.7
	95% I.Q.R	20.3-33.7	5.5-34.8	14.4-24.4	0	-
	Size 3-4					
	Mean %	45.9	41.9	16.8	8.5	5.9
	95% I.Q.R	25.0-66.7	22.1-69.5	12.1-21.9	0-18.4	-
Midshaft Fragments	**Size 1-4**					
	Mean %	11.7	25.0	14.4	0	3.6
	95% I.Q.R	4.5-19.3	9.1-44.6	11.0-18.3	0	-
	Size 1-2					
	Mean %	10.3	16.4	15.4	0	0.9
	95% I.Q.R	3.1-17.6	2.5-36.0	10.9-20.6	0	-
	Size 3-4					
	Mean %	20.1	40.0	12.2	0	5.7
	95% I.Q.R	0-40.0	13.0-80.1	7.9-16.9	0	-

Incidence is measured as the proportion of specimens bearing at least one cut mark. HO, Hammerstone Only; WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where JK2 is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 4.8) Incidence of tooth- and butchery-marked bone.

		WB-C	H-C	V-H-C	JK2
All Long Bone Fragments	**Size 1-4**				
	Mean %	19.7	8.4	9.6	2.7
	95% I.Q.R	9.5-32.2	6.0-11.4	2.0-19.7	-
	Size 1-2				
	Mean %	11.6	8.6	8.7	0.7
	95% I.Q.R	3.3-22.4	5.4-12.5	0-21.7	-
	Size 3-4				
	Mean %	33.7	8.0	9.9	3.9
	95% I.Q.R	16.7-57.5	5.5-10.9	1.6-22.3	-
Midshaft Fragments	**Size 1-4**				
	Mean %	9.7	4.9	4.4	1.2
	95% I.Q.R	3.0-18.0	2.9-7.4	0-12.2	-
	Size 1-2				
	Mean %	8.2	5.9	11.6	0.9
	95% I.Q.R	0-19.7	3.2-9.4	0-29.4	-
	Size 3-4				
	Mean %	12.3	3.2	2.5	1.4
	95% I.Q.R	2.6-24.4	1.3-5.8	0-10.0	-

Incidence is measured as the proportion of specimens bearing at least one tooth and one percussion and/or cut mark. WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where JK2 is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 4.9) Incidences of carnivore tooth-notched and hammerstone percussion-notched bone in the JK2 assemblage and feeding trace models.

	Carnivore Tooth Notching	Hammerstone Percussion Notching	Tooth and/or Percussion Notching
Carnivore Only	19.1	-	19.1
Hammerstone Only	-	26	26
Hammerstone-to-Carnivore	2.2	16.4	18.1
JK2 (Analyzed Sample)	3.5	3.5	7.2
JK2 (Analytical Sample)	7.7	7	15.4

Incidence is measured as the proportion of specimens bearing at least one notch. The tooth and or percussion notching category includes specimens with notches that were considered indeterminate. Data for the feeding trace models taken from Blumenschine (1995).

Table 4.10) Incidence of percussion- and tooth-notched specimens that are also percussion- and tooth-marked.

	% Percussion-Marked			**% Tooth-Marked**		
	JK2	H-C	Statistics	JK2	H-C	Statistics
Percussion-Notched	85.7	59.4	p=.02 d.f.=1 x^2=5.53	7.1	22.9	*p=.11*
Tooth-Notched	0	23.1	*p=.02*	83.9	92.3	*p=.65*

Incidence is measured as the proportion of specimens bearing at least one percussion or tooth mark. H-C, Hammerstone-to-Carnivore (data taken from Blumenschine and Selvaggio (1991). Statistics are based on the number of notched specimens that are or are not marked. Chi-square statistics were used when no cells had a value < 5. Fisher's exact probability test (marked by italics) used when at least one cell had a value < 5.

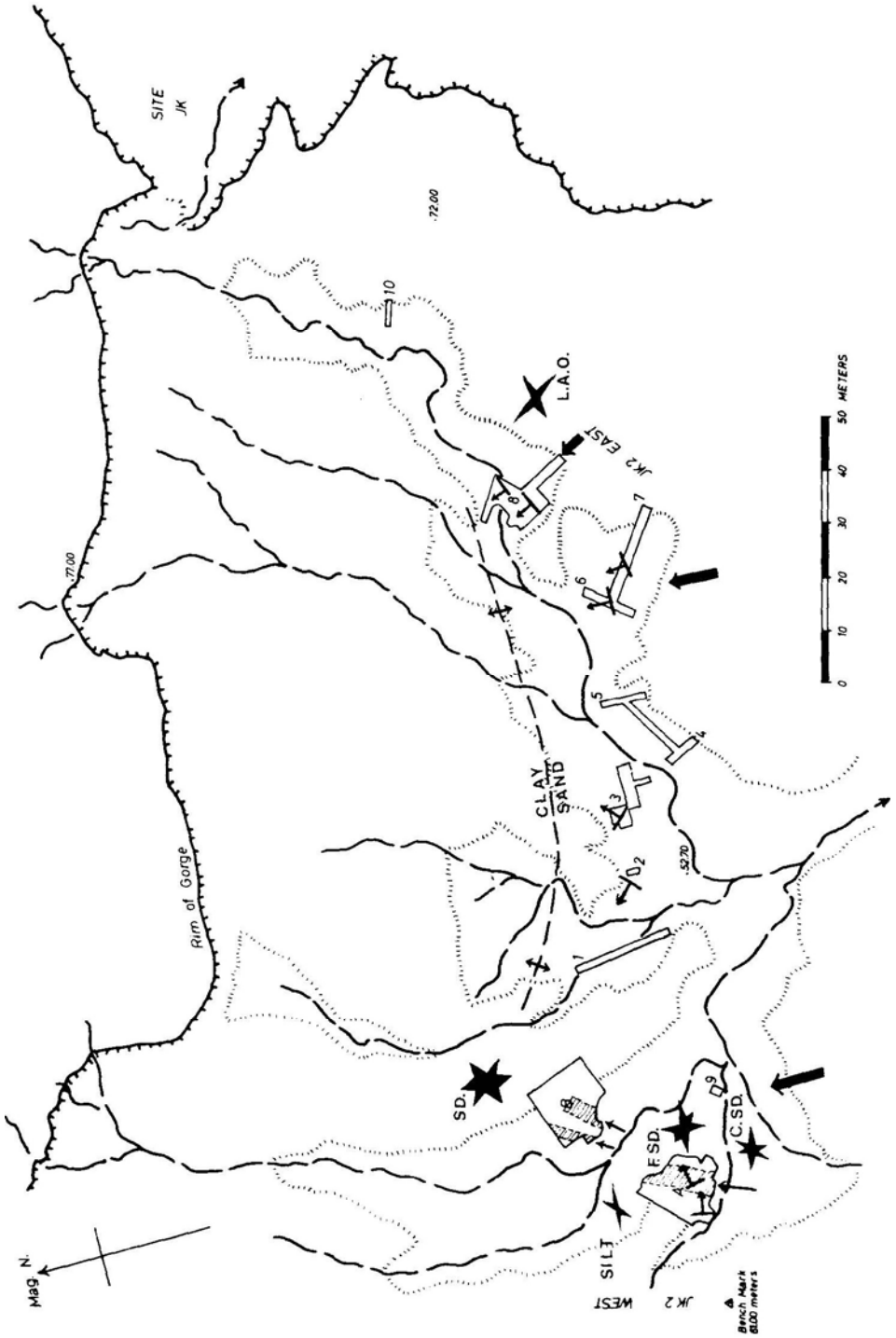


Figure 4.1) Image reproduced from Figure 14 (Kleindienst, 1964). Site map showing trenches A and B in JK2 West, and trenches 1-10 in JK2 East.

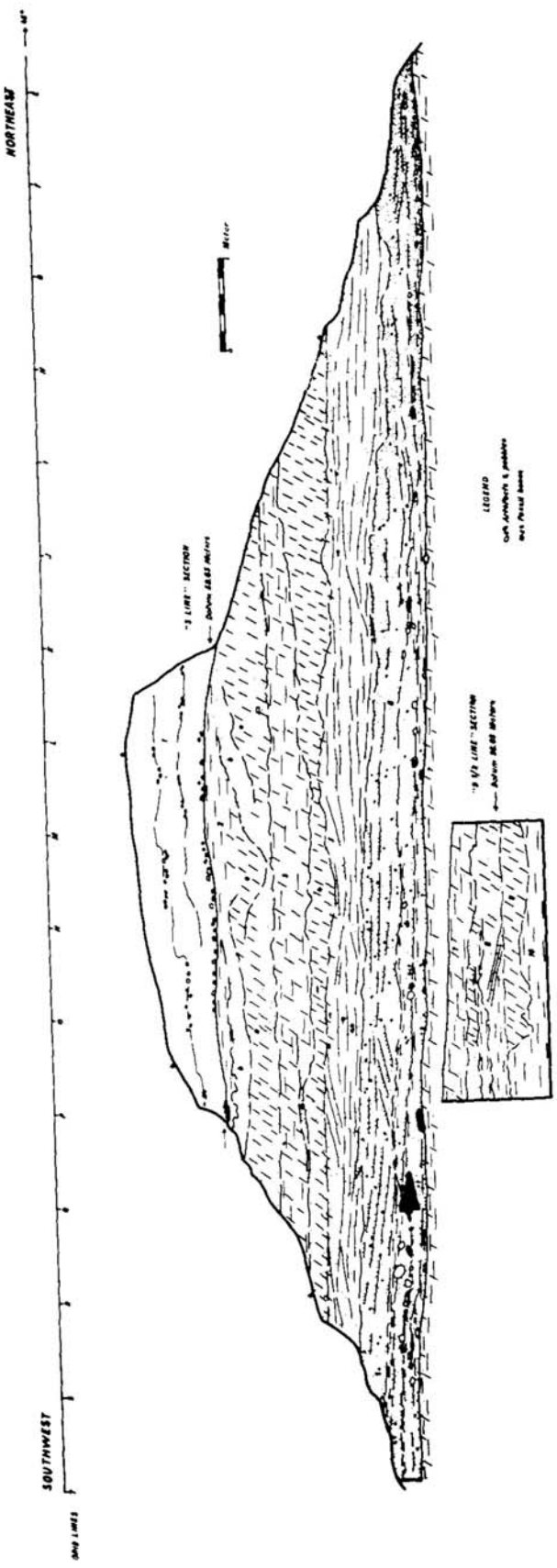


Figure 4.2) Image reproduced from Figure 10 (Kleindienst, 1964). Stratagraphic section from Trench A, JK 2 West.

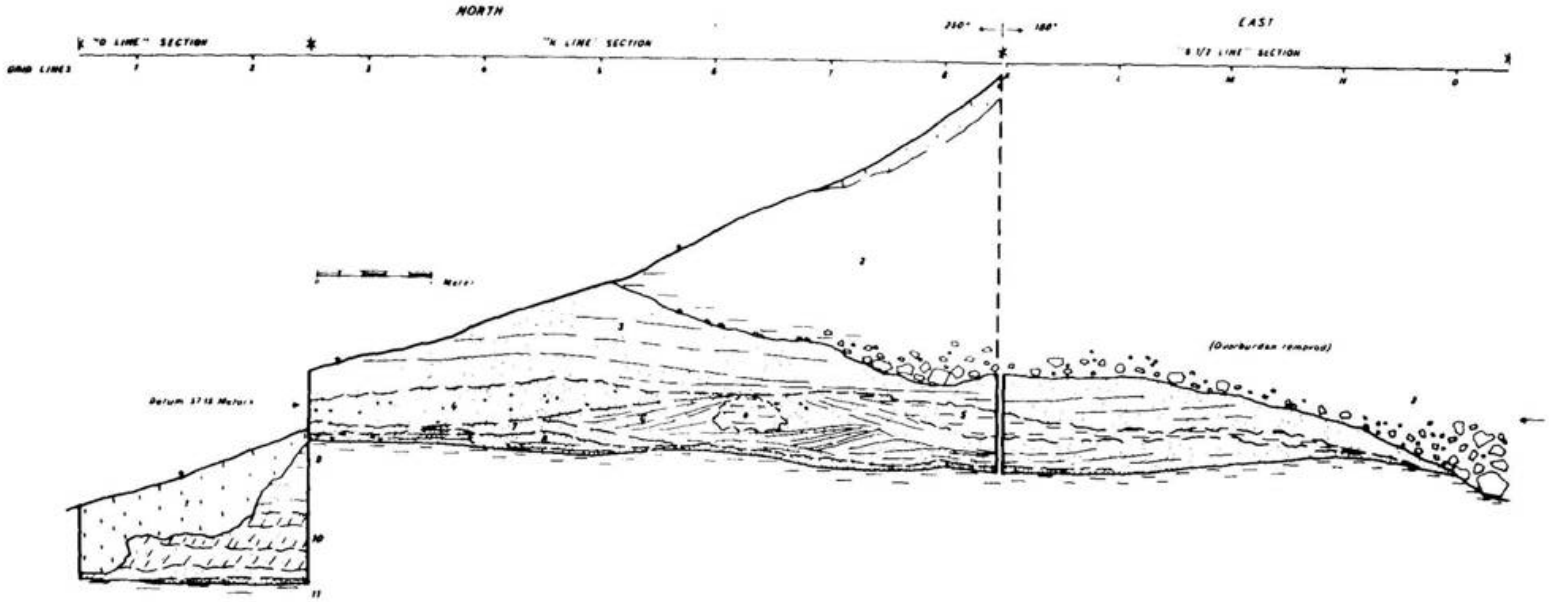


Figure 4.3) Image reproduced from Figure 11 (Kleindienst, 1964). Stratagraphic section from Trench B, JK2 West

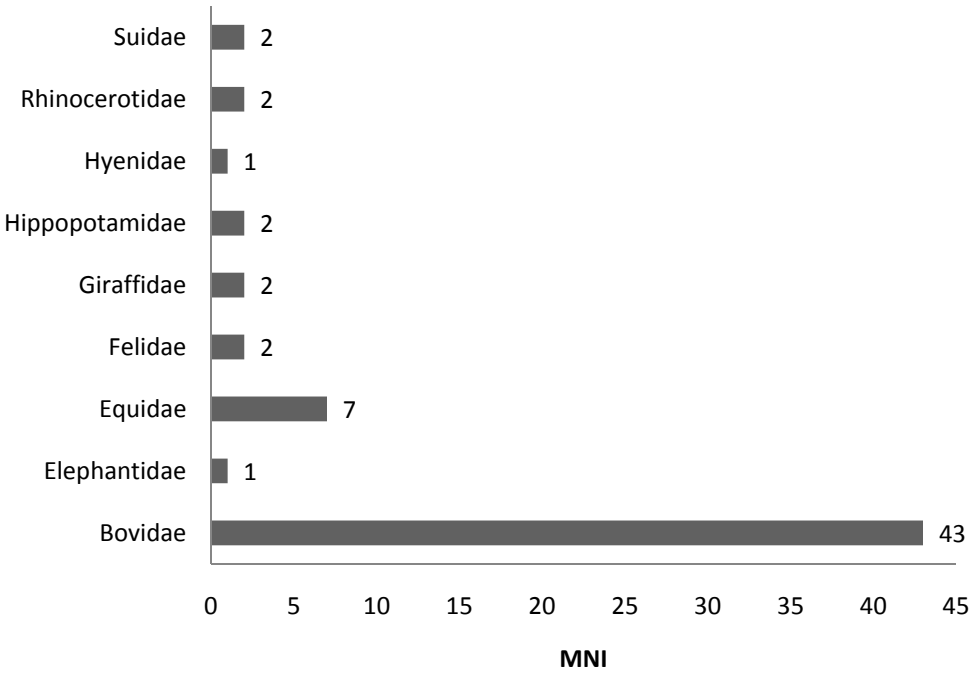


Figure 4.4) Minimum number of individuals based on all identified bone and teeth specimens.

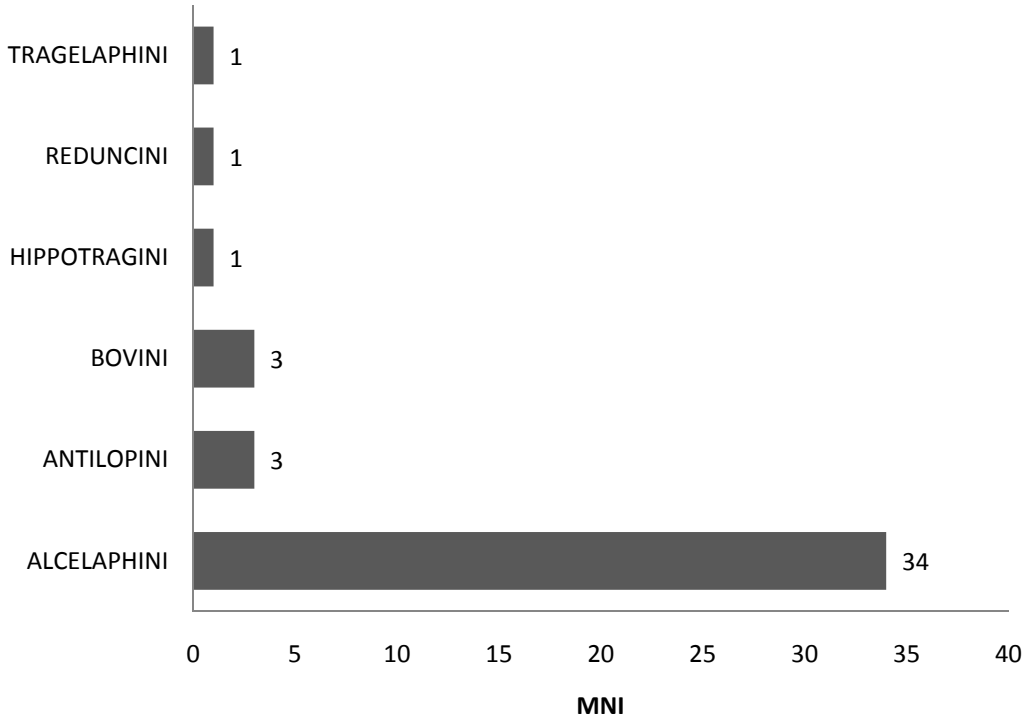


Figure 4.5) Minimum number of bovid individuals by tribe. Estimates are based on bovid teeth.

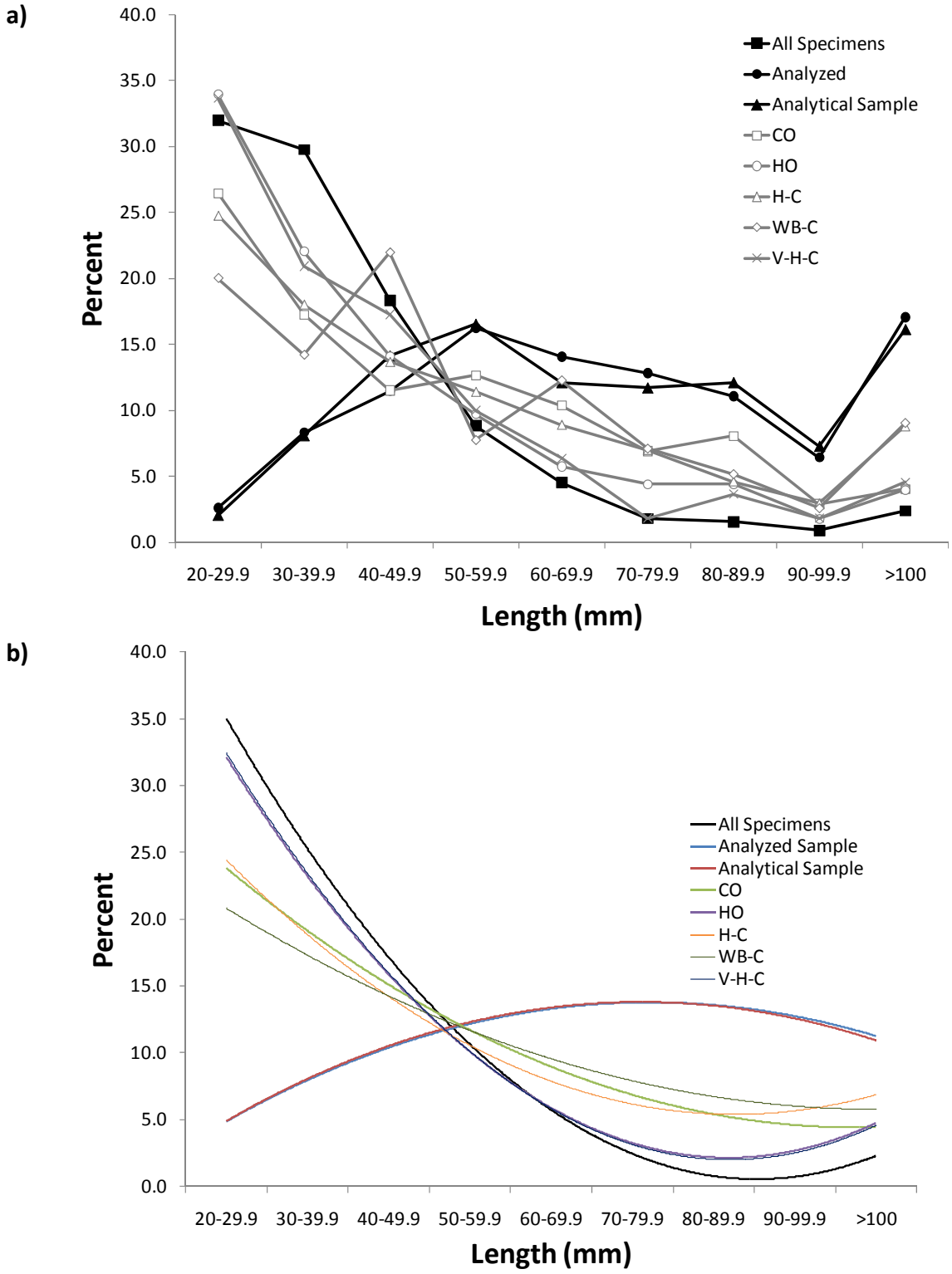


Figure 4.6) Size distribution of long bone midshaft fragments in feeding trace models and JK2 sub-samples a) actual values, b) polynomial trend lines. Data for the feeding trace models is based on the non-bootstrapped sample.

Figure 4.7) Percussion-marked specimens from JK2. Scale = 1 cm. a) Battered anterior surface of a size 3 bovid metatarsal distal epiphyseal fragment. b, c) Pits and microstriations on anterior surface of a size 4 bovid radius midshaft fragment.

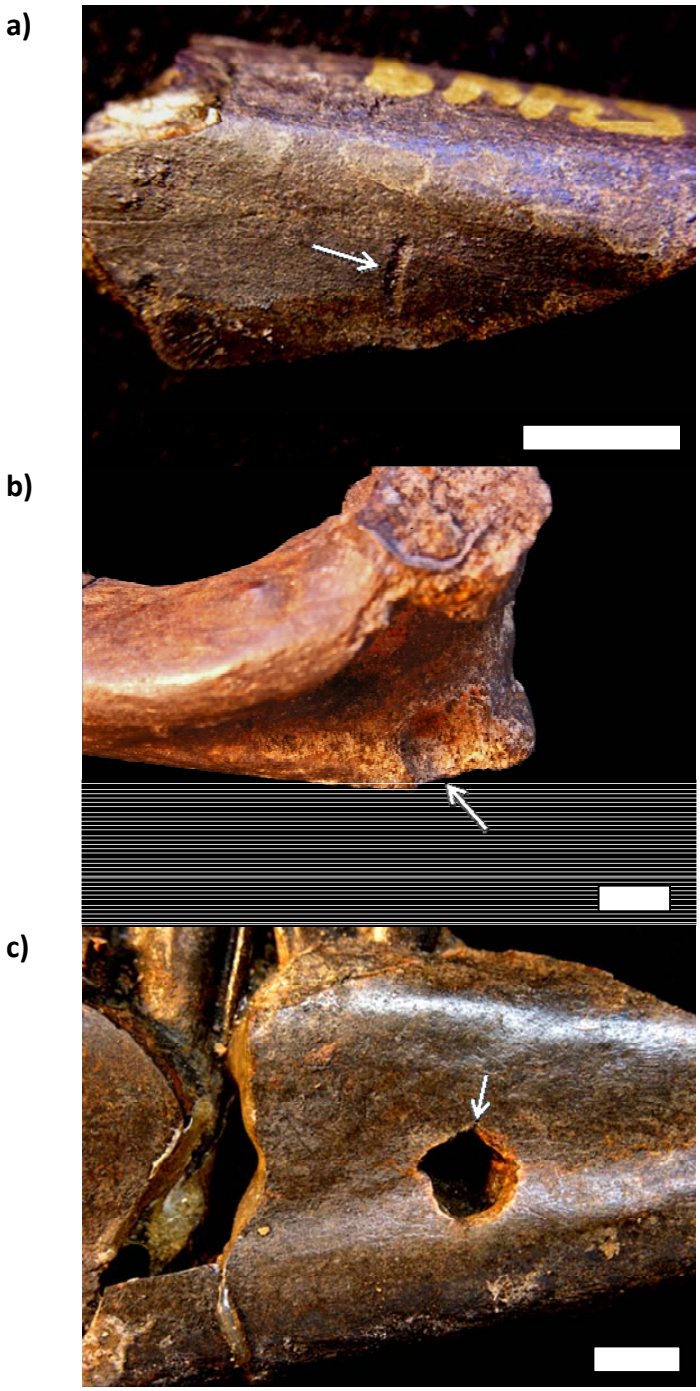


Figure 4.8) Tooth-marked specimens from JK2. Scales = 1 cm. a) Classic carnivore tooth score on a size 3 long bone midshaft fragment. b) Carnivore tooth pit on anterior size 3 bovid distal humerus epiphyseal fragment. c) Possible bisected crocodile tooth pit on size 3 bovid mandible. Arrow points to a bisection that may have been left by the carina of a crocodile tooth (Njau and Blumenschine, 2006).

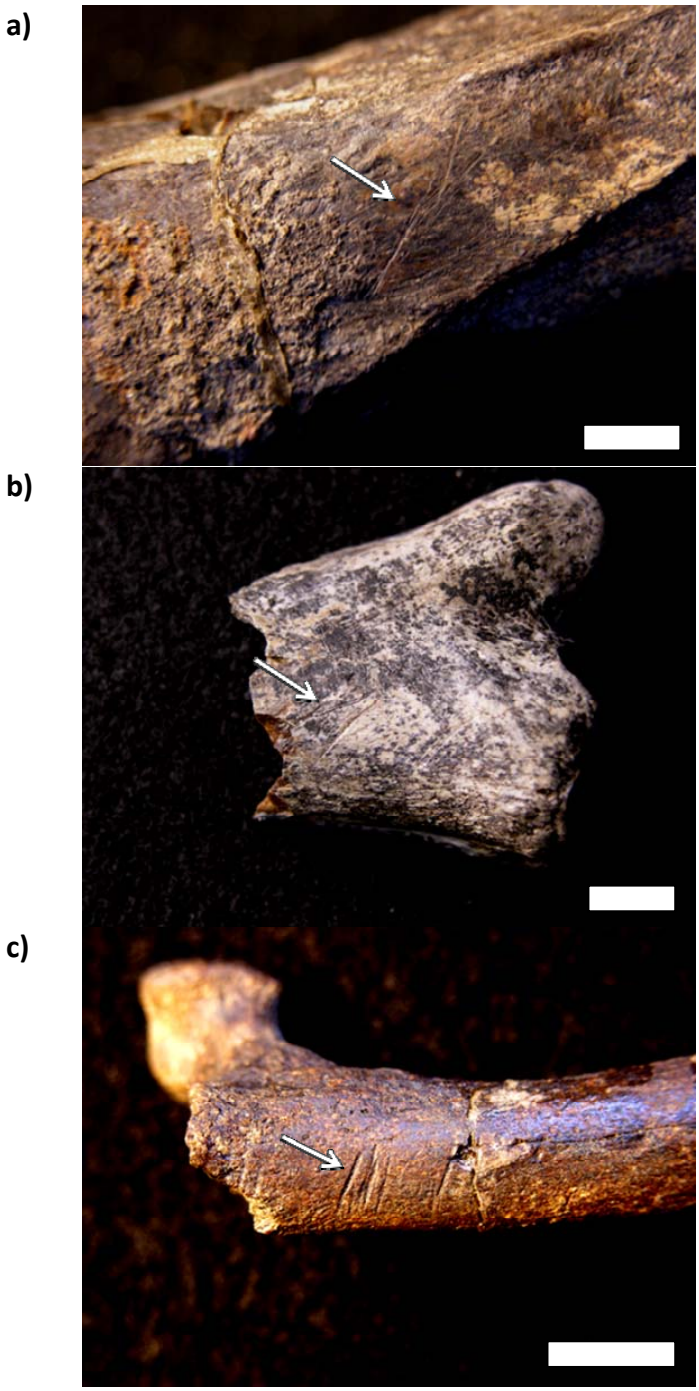


Figure 4.9) Cut-marked specimens from JK2. Scales = 1 cm. a) Stone tool cut marks on posterior surface of a size 3 bovid femur epiphyseal fragment. b) Stone tool cut marks on a size 3 bovid tibia distal epiphyseal fragment. c) Stone tool cut marks on a size 2 bovid nearly complete 1st rib.

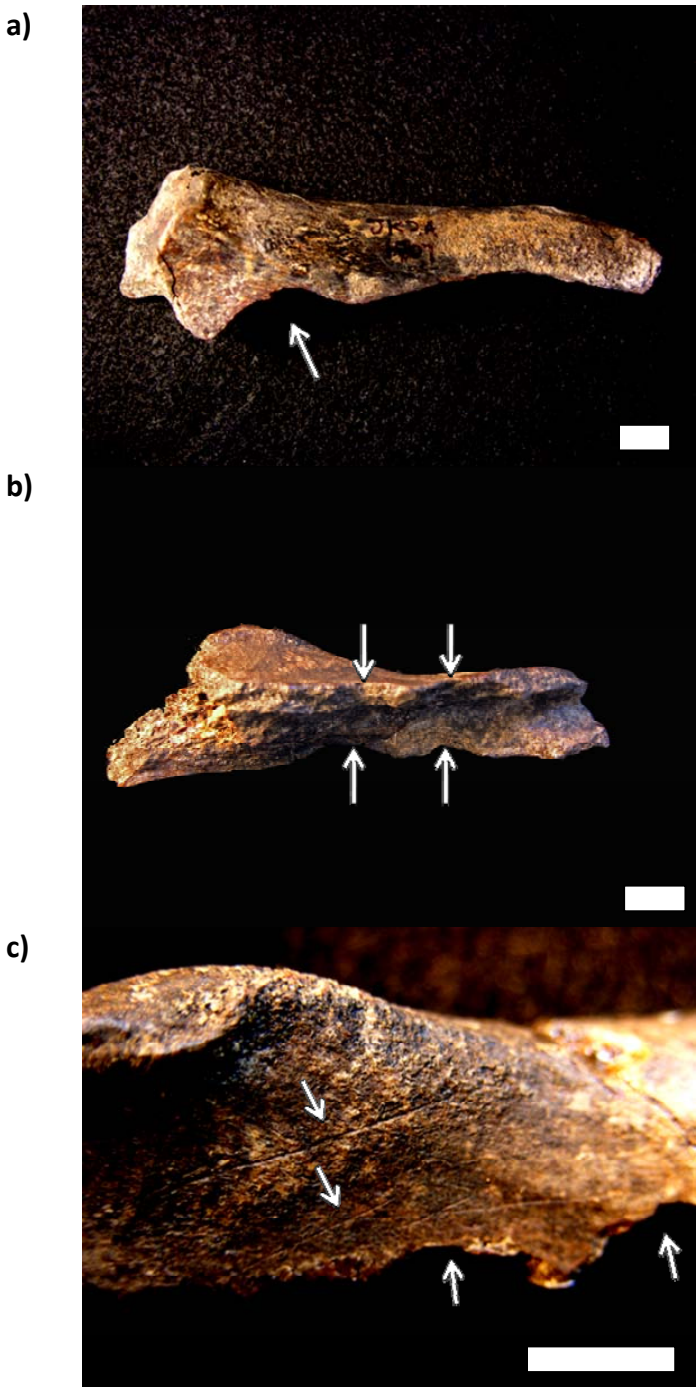


Figure 4.10) Percussion- and tooth-notched specimens from JK2. Scales = 1 cm. a) Percussion notch on a size 3 bovid proximal radius epiphyseal fragment. b, c) Carnivore tooth notches and stone tool cut marks on a size 2 bovid femur third trochanter.

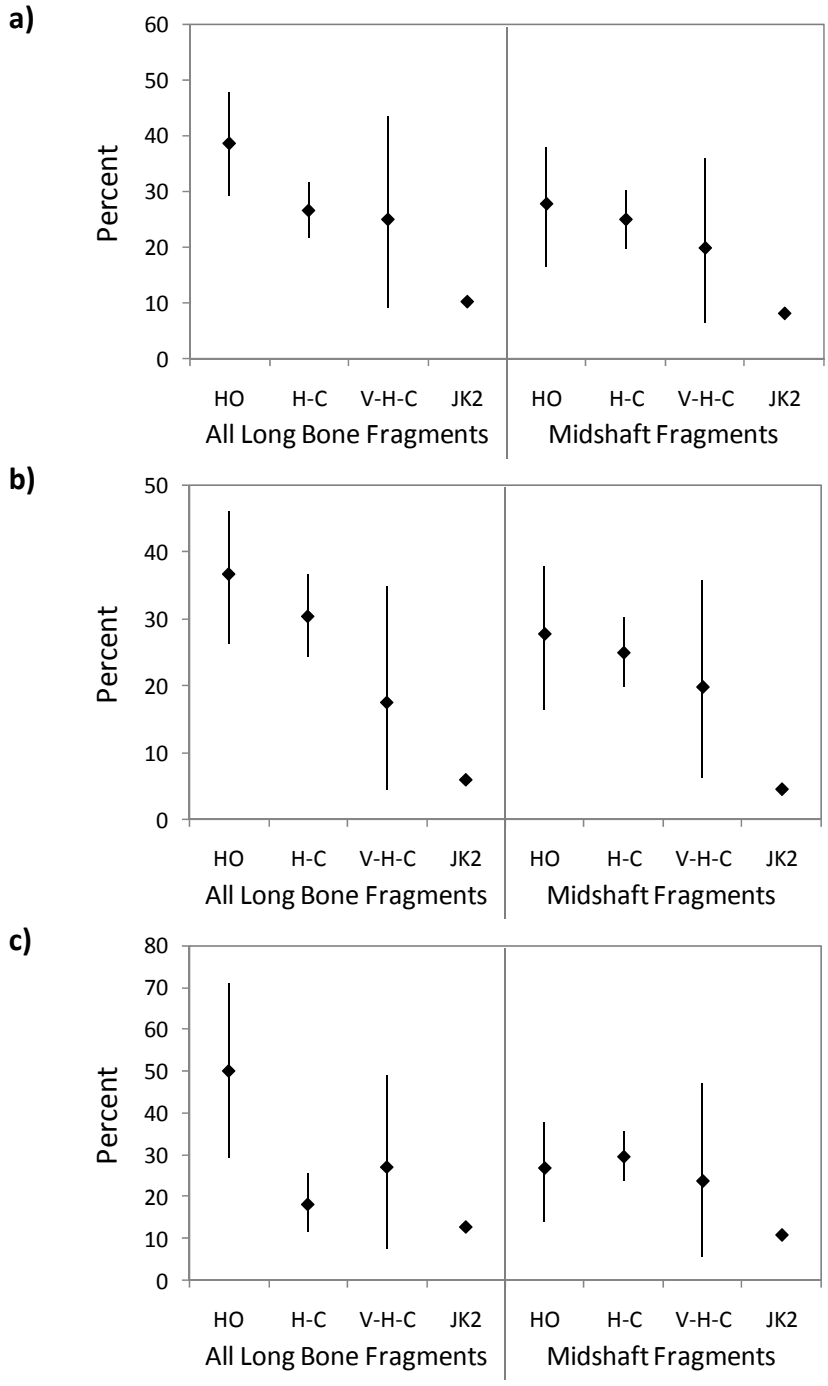


Figure 4.11) Incidence of percussion-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. HO, Hammerstone-Only; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for JK2 represents the proportion of percussion-marked bone.

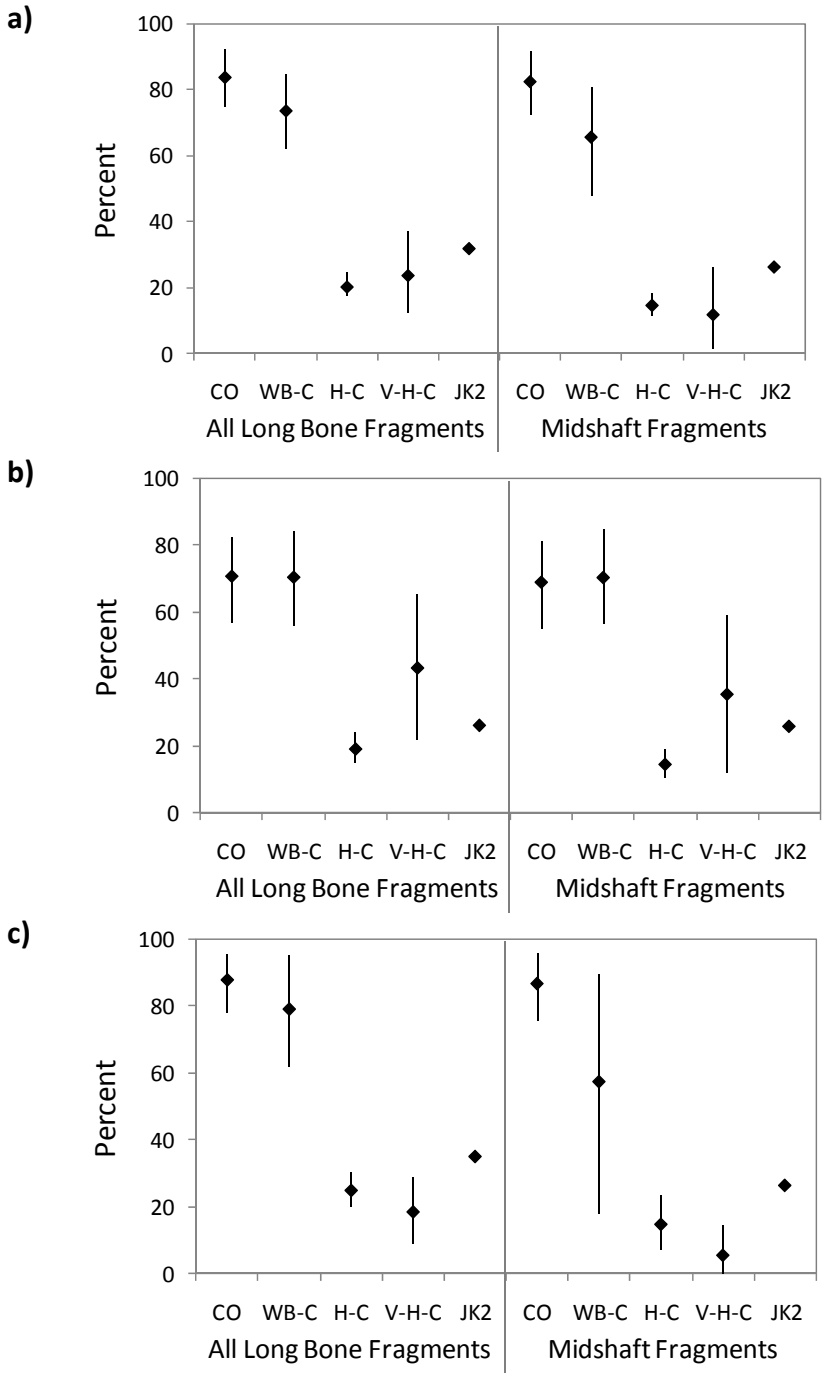


Figure 4.12) Incidence of tooth-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. CO, Carnivore Only; WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for JK2 represents the proportion of tooth-marked bone.

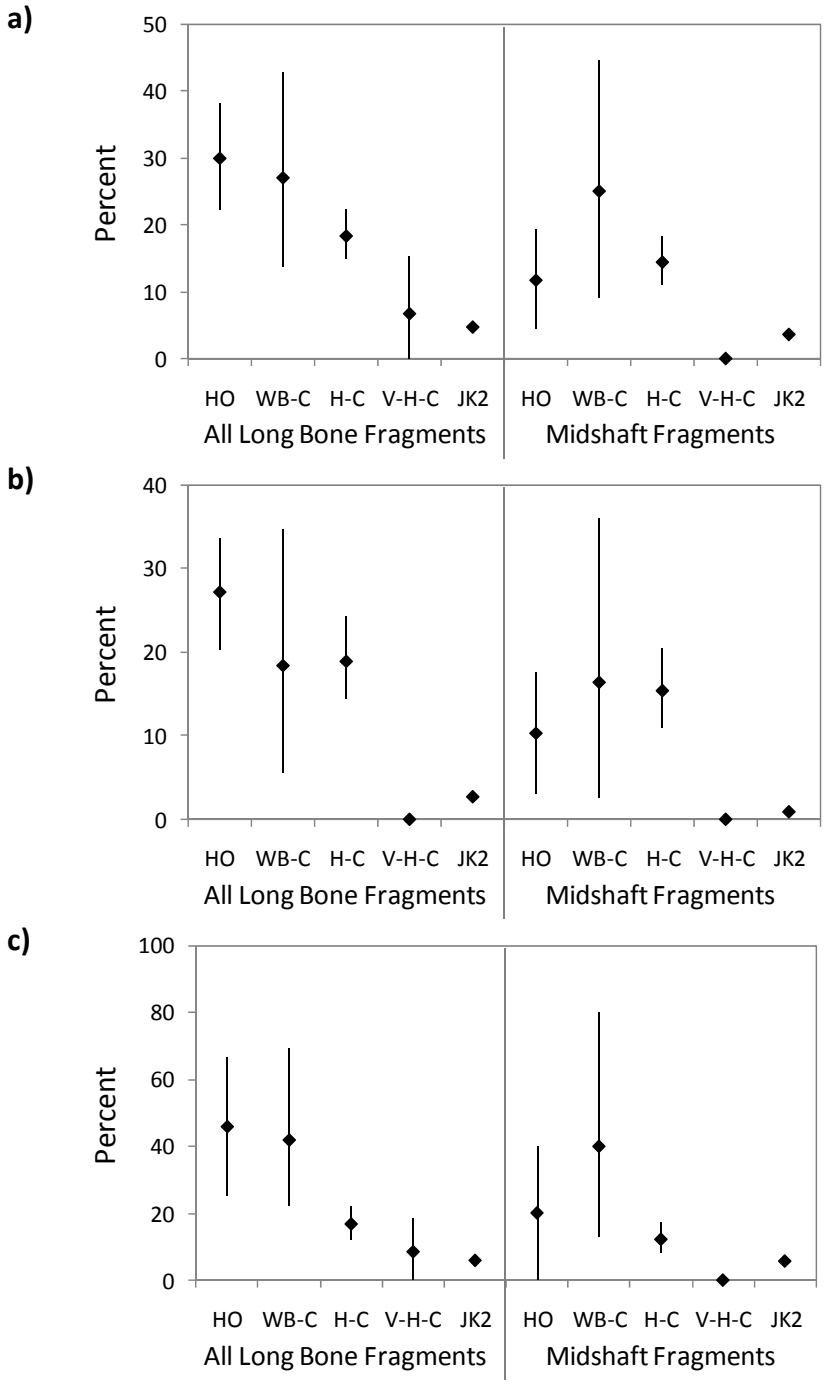


Figure 4.13) Incidence of cut-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. HO, Hammerstone-Only; WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for JK2 represents the proportion of cut-marked bone.

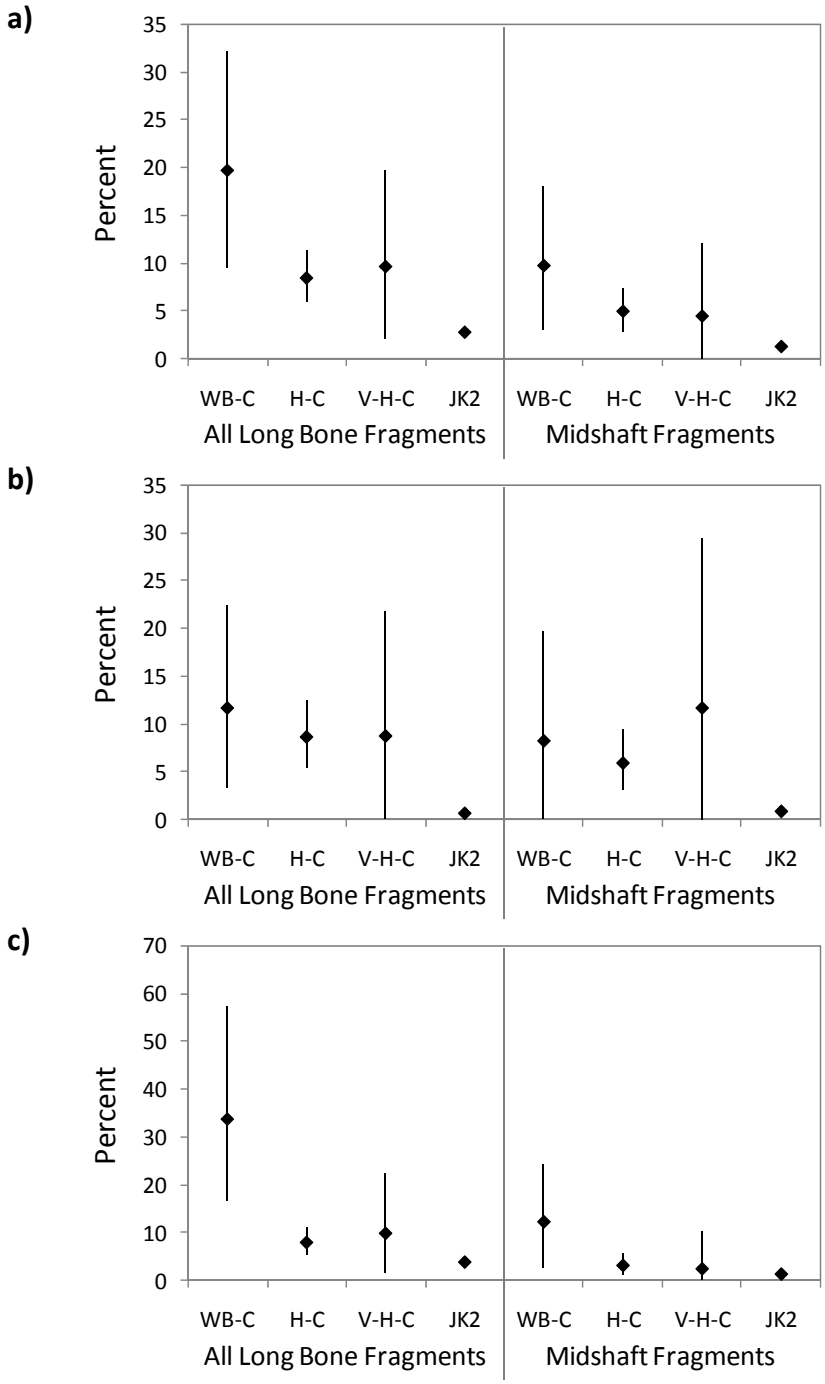


Figure 4.14) Incidence of tooth- and butchery-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for JK2 represents the proportion of tooth- and butchery-marked bone.

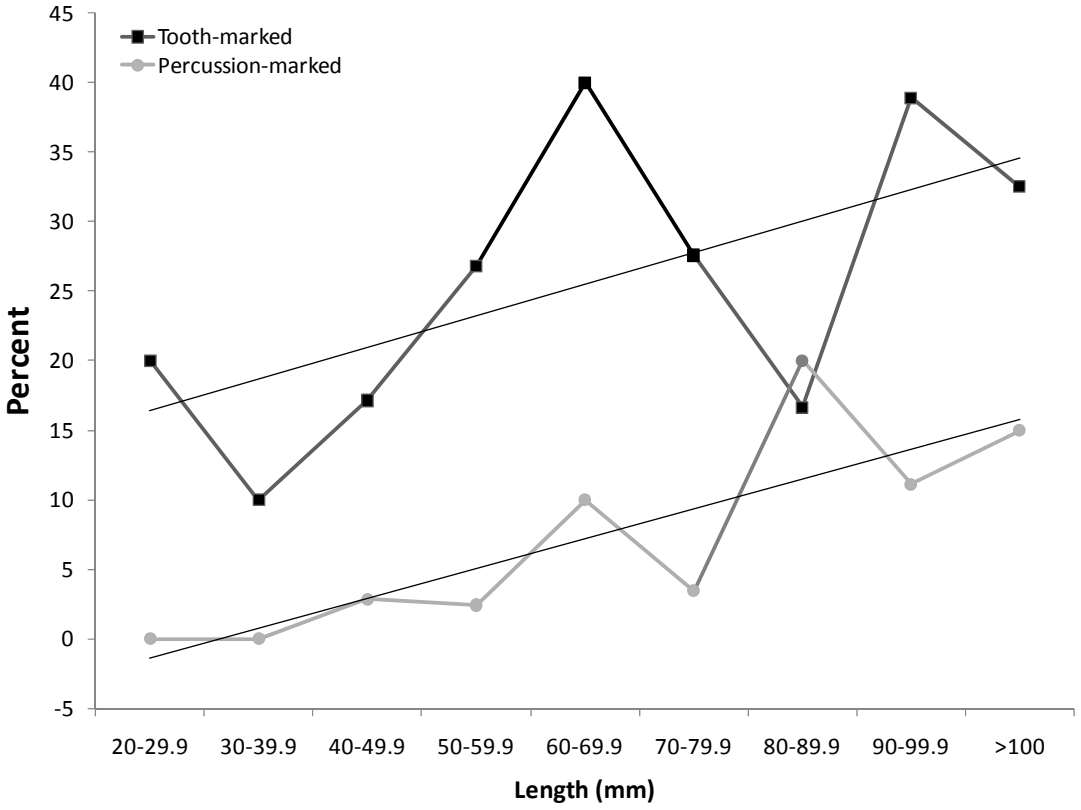


Figure 4.15) Size distribution of tooth- and percussion-marked bone.

Chapter 5

The Taphonomy of WK, Bed IV, Olduvai Gorge

Introduction

The larger mammal fossil and stone artifact collections from Beds III and IV, Olduvai Gorge are significant in representing a time period for which *Homo erectus* was the only hominin known to exist. These collections and the behavioral interpretations that are based upon them can therefore be confidently associated with the species. The collections from Beds III and IV were excavated by Mary Leakey from 1968-1971 and represent seventeen archaeological occurrences that span roughly 500 ky. In stark contrast to the Bed I and II collections (Leakey, 1971a), all of the Bed III and IV collections were found in fluvially-disturbed contexts and were largely ignored after descriptive data were recorded. Further, the collections are kept in a lab located at the Leakey Camp on site at Olduvai Gorge, as opposed to the material excavated from most Bed I and II sites, which are stored and maintained by the National Museums of Kenya in Nairobi. Unfortunately, these and other factors have led to the neglect of the Bed III and IV collections, which were allowed to deteriorate for nearly four decades.

This chapter depicts the curation and describes the condition of the fossils that were excavated by Mary Leakey from Beds III and IV. It also features a detailed taphonomic analysis of the larger mammal fossil assemblage excavated from the Bed IV, WK site. The goals for this chapter are to: 1) provide a catalog of the Bed III and IV material that is located at Olduvai Gorge in hopes that other researchers will study the vast collections of stone artifacts and fossils; and 2) interpret the feeding behavior of *Homo erectus* from the WK fossil assemblage.

Curation of the Bed III and IV Fossils

The fossil and artifact assemblages from Beds IV that are stored in the Olduvai Laboratory include those from PDK I-IV; WK; WK East A, B, C, and Hippo Cliff; and HEB, HEB East and HEB West. The collection from Mary Leakey's excavation of JK, the only Bed III site from Olduvai Gorge is also in the lab. Assemblages not from Beds III and IV that are stored in the lab include SC, a Bed I assemblage and HWK EE, a Bed II assemblage, along with artifacts from Nasera rock shelter and Mumba cave. HWK EE was the only assemblage outside of those from Beds III and IV that underwent extensive curation. The following is intended to provide a brief summary of the condition of the fossil assemblages in the Olduvai Lab.

The initial curation of the Bed III and IV material housed in the Olduvai lab began in July, 2007. The first step in this process was to remove all non-archaeological material from the lab (Figures 5.1 and 5.2). Two Tanzanian assistants and I spent 3 days removing old equipment, chemicals and other materials that had accumulated in the lab. Materials that were disposable were taken to a waste dump in Karatu, the nearest town to Olduvai Gorge. Once cleared of debris, we began to repair the shelves in the lab by replacing termite-infested wood and installing additional support beams for shelves that had collapsed. Shelves were also dusted, cleaned with water, and allowed to dry. Many of the fossils and artifacts in the lab had been left on the concrete floor, which resulted in the deterioration of the cardboard boxes in which they were stored. These materials were repackaged, labeled, and placed on the newly repaired shelves. Fortunately, the majority of stone artifacts from Bed III and IV remained in excellent

condition as they were all stored in wooden trays on shelves that had not collapsed. Thus the majority of curatorial efforts were focused on the fossil material.

The Bed III and IV fossil assemblages were curated using the 5th Volume of the Olduvai Monograph to guide the process. This part of the curation was complicated by the deterioration of plastic bags and cards that were used to organize fossils by archaeological location, trench, spit, stratigraphic context, and skeletal part. In order to minimize the loss of the above information the following steps were taken: 1) I worked alone to minimize the possibility of misplacing identification cards or specimens; 2) A single box or tray of fossils was removed from the lab at a time to avoid mixing of the material; 3) Fossils were individually removed from bags taking care to look for a card or label. In most cases, rodents had completely destroyed the plastic bags and/or I. D. cards; 4) Fossils were cleaned using only water and a tooth brush, they were placed on a screen, organized by the bag they were removed from or according to labeling on the surface of the fossil, and allowed to dry in the sun; 5) Once dry, fossils were re-bagged using 4 mil plastic zip lock bags. The outside of the bags were labeled with a sharpie according to the most detailed level of organization that was available for the fossil, and a card with the same information was placed inside the bag; 6) Bags were placed in new cardboard boxes or trays that were cleaned and labeled according to archaeological site. In some cases, trench number and taxonomic information were also included. The condition of each of the assemblages and further details of their curation is discussed below.

JK

Curation of the Bed III and IV fossil material began with the JK site because it was in the worst condition of the above mentioned material. The JK site designation should not be confused with JK2 as the two represent separate assemblages excavated a decade apart, with the latter being excavated by Maxine Kleindienst (see Chapter 4). Still, it is likely that the two excavations represent different samples of the same occupation, rather than two distinct sites. The JK assemblage was the only Bed III and IV assemblage stored completely in wooden trays rather than cardboard boxes (taxonomically identified bone for all of the Bed III and IV assemblages were also stored in wooden trays). These trays organized the assemblage by stratigraphic context and placed the fossils into one of four categories, coarse grey sand, fine grained ferruginous sand, pink siltstone, and clay above the pink siltstone, (Leakey, 1994). The trays, which were stacked one on top of the other, had been damaged by termites and rodents causing fossils from several trays to become mixed together. Many of the plastic bags had also deteriorated and some of the fossils could not be identified to stratigraphic context. This was problematic because in most cases the surfaces of the fossils were only labeled to trench and spit and Mary Leakey had started a new set of spits every time there was a change in the sedimentary context. She noted that, "In describing the archaeological and faunal material the spits have been disregarded since it was impossible to correlate accurately the spits in different trenches" (Leakey, 1994:17). As a result, some of the stratigraphic information for the JK assemblage may be permanently lost unless excavation catalogs can be located. I contacted both Maxine

Kleindienst and Meave Leakey in search of the excavation notes and catalogs for the Bed III and IV collections. Some were located in the archives of the National Museums of Kenya, but others appear to have been lost. Dr. Leakey kindly supported my photocopying of the catalogs that were located by writing a letter to the Archives Department of the National Museums of Kenya.

The condition of the roughly 1900 JK fossils that are stored in the lab ranges from pristine to heavily rounded and weathered. Almost all of the fossils are stained black (a unique feature among all fossil material from Olduvai Gorge) and are not distinguishable from those excavated by Kleindienst from JK2. An analysis of the JK fossils has potential to provide important behavioral information. However, the available sample for the JK assemblage is biased as Mary Leakey had dumped the majority of taxonomically non-identified, but taphonomically informative material on site prior to labeling the specimens (based on personal observation of the JK site). This is a persistent problem for all of the Bed III and IV fossil assemblages excavated by Mary Leakey, as the importance of long bone shaft specimens in analyses of fossil assemblages had not been established until two decades after the sites had been excavated (Marean and Spencer, 1991).

Taxonomically Identified Bone for All Sites

The taxonomically identified fossils were organized by family and included Proboscidea, Giraffidae, Rhinocerotidae, Hippopotamidae, Equidae, Suidae, and Bovidae. These trays do not represent all of the taxonomically identifiable material from Beds III and IV as some remained organized by archaeological sites. Most of the

specimens that were organized by taxonomy were stored in wooden trays with the exception of those from size 5 and 6 animals, which were kept in cardboard boxes or placed directly on the shelves without protection. Unlike the JK assemblage the trays, bags, and labels that organized the taxonomically identified fauna remained intact. Great care was taken in the cleaning and re-labeling of this material to preserve as much information as possible. Once cleaned and re-bagged the original organization of the taxonomically identified fossils was maintained.

WK East A, B, C and Hippo Cliff

Nearly all the WKE fossils, with the exception of those that were taxonomically identified, were organized by trench. The fossil assemblages from all four trenches were scattered throughout the lab in cardboard boxes that had deteriorated. Almost all of the plastic bags and identification cards that were in the boxes were destroyed by rodents. In such cases, fossils were individually removed from the box and cleaned, while taking notice of any identifying cards that remained intact. After cleaning, fossils were placed in new 4 mil zip lock bags and cardboard boxes labeled as either bone for identification, which included all the material that I felt could be identified to skeletal element, but in most cases was not taxonomically diagnostic, or as indeterminate bone, which mainly comprised long bone midshaft specimens and rib shafts. Indeterminate bone was further separated into fossils with good surface preservation and those with poor surface preservation on the basis of the likelihood that tooth, cut, and/or percussion marks might be visible. This would have allowed for a more efficient taphonomic analysis of the material had I had time to do so.

The majority of fossils from the WK East site are heavily rolled and poorly preserved. The coloration of individual fossils in the assemblage is mottled with a mix of red, orange, white, and black staining. This coloration is dominant in other Bed IV sites including, WK and PDK. Many of the fossils appear to have been green broken, but a taphonomic analysis focusing on hominin- and carnivore-induced bone surface modifications would be hindered by the poor bone surface preservation in the assemblage. It is also unlikely that the entire excavated assemblage was kept by Leakey, introducing excavator bias to any analysis of the material.

PDK I-IV

The PDK fossil assemblages are limited in size, comprising only 219 specimens between the four excavated trenches. Fossils from PDK were curated in a manner identical to the previously described sites. Most of the PDK fossils could not be identified to the trench from which they were excavated. This is significant as trenches I-III are stratigraphically located in Upper Bed IV, while trench IV is located at the base of Bed IV. Additionally, PDK trench IV was the only site from Beds III and IV believed to be in primary context by Leakey (1994) based on the fresh condition of the artifacts and lack of a conglomerate layer at the site. The fossils from PDK exhibit similar preservation and coloration to the WK East material. Despite Mary Leakey's assertion that the site was in primary context, most of the fossils including those from trench IV are mechanically rounded.

HEB, HEB East, and HEB West

The HEB assemblages are also limited in size (n=269 in the Olduvai Lab) with an unknown number of specimens stored at the National Museums of Kenya in Nairobi. Fossils from the three HEB sites were mixed together in several boxes. However, specimens were individually labeled to one of the three sites, allowing their distinction. Curation methods were consistent with those for the above mentioned sites.

The fossils from all three sites are well preserved with a white to tan coloration similar to that which is typical for those excavated from Bed I and II sites. The impact of fluvial process on the assemblage appears to have been minimal as many of the fossils from the site are not mechanically rounded. Still, the assemblage is incomplete and scattered between Kenya and Tanzania.

HWK EE

Most of the HWK EE fossils were stored in unlabeled wooden trays on shelves in the Olduvai Lab. There were also several cardboard boxes that contained fossils from the site. Leakey had organized the HWK EE assemblage by stratigraphic context, as she had done with the JK assemblage. However, unlike the JK assemblage boxes and trays were largely intact allowing the fossils to be organized into two different stratigraphic categories; sandy conglomerate or clay. Leakey had further organized the fossils within the trays by taxonomy and skeletal part, but the plastic bags that had separated the fossils according to these criteria had deteriorated. During the cleaning, re-bagging and labeling of the assemblage I was able to re-organize many of the fossils by the taxonomic and skeletal part categories that Leakey had used.

The HWK EE assemblage is beautifully preserved rivaling Bed I material with its pristine bone surfaces. Like other Bed I and II assemblages, bone surfaces are white to tan in color. There are over 1200 bone fragments that comprise the assemblage and over 500 of these fragments are long bone midshafts, suggesting Mary Leakey was more meticulous in her excavation of the HWK EE material than she had been with that from Beds III and IV. Still, it is likely that a large portion of the assemblage was dumped on site. Hominin- and carnivore-induced bone surface modifications appear to be prevalent in the assemblage. A detailed analysis of the material and further excavation of the site are currently underway (see Chapter 6).

WK

The initial curation of the WK assemblage mirrored that of the WK East assemblages. The assemblage was stored in cardboard boxes and fossils from different trenches were only separated by plastic bags that were no longer intact. However, unlike all other Bed III and IV material, every fossil within the WK assemblage was labeled to trench and spit. As a result, no identifying information was lost due to the deterioration of the boxes and bags that the fossils were stored within.

The WK fossils were subjected to additional curatorial procedures to prepare the assemblage for the detailed taphonomic analysis. Specifically, glue that covered all of the fossils obscuring bone surfaces was removed using acetone and cotton cloths. The process of removing the glue was carried out by a representative from the Tanzanian Department of Antiquities who was given explicit instructions including to write down all information that was on each specimen before beginning the removal of glue and to

avoid using acetone on parts of the fossils that were labeled. I also had him alert me when labels had been obscured or removed by the process. I periodically checked his work to ensure that he was writing down the correct information.

Stratigraphic Context for the WK Assemblage

The WK site was discovered in 1931 by Louis Leakey and was later excavated in 1969 by Mary Leakey (Leakey, 1994). It is located on the south side of the Eastern Gorge and spans the entire Bed IV sequence dating between 800 and 600 ka. Ten adjacent trenches were excavated at the site with three separate archaeological occurrences found in conglomerates or channel fillings (Leakey, 1994). These occurrences were divided into the lower, intermediate, and main or upper channels (Leakey, 1994). Only trench 10 was dug to the lowest level, while trenches 1, 2, and 5 were dug down to the intermediate channel. The remainder of the trenches did not go below the main channel where Leakey (1994) found the largest concentration of artifacts and fossils.

The stratigraphy for WK as described by Leakey (1994) is as follows. 9 m of overburden spanning from the Ndutu Bed to the top of Bed IV was above the eroded 1 m thick sandy conglomerate of the upper archaeological occurrence or main channel. 1.5 m of root-marked siltstone separated the upper archaeological occurrence from the intermediate occurrence. The intermediate channel conglomerate was 30 cm thick cutting into a 1.7 m thick grey siltstone that was above a 1 m thick sandy claystone. The lower channel was 50 cm thick and was found in what Leakey (1994) described as a grit and pebble conglomerate below a sandy claystone with grit lenses. The occurrence in

the lower channel is just above the junction of Beds III and IV. The occurrence in the intermediate channel was found 2.7 m above the Bed III/IV junction and was at the same stratigraphic level as tuff IVb in places where it had not been incised by the channel. The occurrence in the upper channel was another 1.5 m higher and contained blocks of tuff IVb.

Methods for the Analysis of the WK Assemblage

Analysis of the WK fossil assemblage was conducted over 6 weeks in 2007 at Olduvai Gorge. The study was taphonomically oriented focusing on the incidence and location of hominin- and carnivore-induced bone surface modifications within the assemblage. Taxonomic identifications are limited to the family level with the exception of bovid teeth, which were identified to tribe. The methods employed closely follow those used for the JK2 assemblage (see Chapter 4). Those that are unique for the WK assemblage are described below.

<u>The WK Sample</u>

The WK assemblage comprises 1423 bone fragments (Table 5.1) and 273 complete and fragmented teeth that were excavated from trenches 1-10 (Table 5.2). The sample for which the proportions of tooth-, cut-, and percussion-marked specimens are based (analytical sample throughout) only includes long bone specimens from trenches that were not excavated below the level of the main channel (trenches 3, 4, 5, 7, 8, and 9). This measure was taken to minimize the effect of time averaging on the results. Specimens were also excluded from the analytical sample using the same criteria employed in analyses of the JK2 assemblage with one exception; bones that

exhibited transverse breaks were not excluded. This was unavoidable as nearly half (46.5% of the analytical sample) of the WK assemblage exhibited step fractures indicative of dry-bone breakage. Excluded specimens include those that 1) are less than 20 mm in maximum dimension, 2) have been recently broken with more than 10% of the fragment missing (inclusion of these specimens can have an unpredictable effect on mark frequencies), 3) have poor surface visibility due to mechanical rounding, exfoiliation, and/or adhering matrix covering more than 10% of the fragment, 4) are from an animal larger than size 4 or a taxonomic family other than bovid. Application of the criteria for the exclusion of specimens reduced the analytical sample to 284 long bone fragments (Table 5.3) from a total 964 long bone fragments in the analyzed sample.

Analytical Procedure

Taxonomic, and skeletal part and portion identification was carried out using the limited comparative collections located at the Leakey Camp, Olduvai Gorge. Skeletal element portion was also recorded to more accurately tabulate the minimum number of elements (MNE) and minimum number of individuals (MNI) in the assemblage. Refitting was limited to post-curatorial breaks that had occurred during storage. Methods for the identification of skeletal parts and details on the quantitative measurements recorded can be found in Chapter 4.

Identification of tooth, cut, and percussion marks was conducted following the methods prescribed by Blumenschine et al. (1996). However, due to overall poor surface condition of WK fossils including many of those that are part of the analytical

sample, confident mark identifications were often limited to conspicuous marks including gross gnawing or multiple tooth scores for carnivore damage, battering (i.e. several deep and adjacent indentations) for hammerstone breakage, and multiple parallel and overlapping striations for cut mark identification (see Figure 5.3). This will always reduce the assemblage-wide frequencies of bone surface modifications (see Chapter 2).

Results for the Analysis of the WK Assemblage

Taxonomy

The WK assemblage is taxonomically diverse (Figure 5.4). Suidae represent the most common taxonomic family followed closely by Bovidae, and then Equidae. Taxonomic families represented by two or fewer individuals in the assemblage include Hippopotamidae, Rhinocerotidae, Giraffidae, and Elephantidae.

Further breakdown of the bovid individuals by tribe shows Alcelaphini and Antilopini are the most common tribes (Figure 5.5). Bovini, Hippotragini, Reduncini, and Tragelaphini are also present in the assemblage.

Skeletal Group Profiles

Specimens from all five skeletal groups are represented in the WK assemblage (Table 5.4). The pattern observed based on the number of identified specimens (NISP) in the analyzed sample in order from most to least abundant is appendicular (67.7%)-axial (15.6%)-pelvis/scapula (6.3%)-cranial (6.1%)-compact (4.2%). The pattern based on the minimum number of elements is appendicular (43.1%)-compact (24.9%)-axial (12.2%)-cranial (10.4%)-pelvis/scapula (9.4%).

Animal Size Groups

All six animal size groups are represented in the WK assemblage (Table 5.4). The pattern for animal size groups is the same for both NISP and MNE estimates with size group 3 the most abundant followed in order by size groups 2, 4, 5, 1, and 6.

Size Distribution of Long Bone Midshaft Fragments

The size distribution of long bone midshaft fragments from WK shows that the analyzed and analytical samples are similar to each other, but are deficient in shorter specimens when compared to the size distributions for all five of the feeding trace models (Figure 5.6). Specifically, the analyzed and analytical samples are both depleted of specimens less than 40 mm in maximum length.

Bone Surface Modifications

There are tooth, cut, and percussion marks on bone surfaces in the WK assemblage (Figures 5.7-5.9). While tooth marks are abundant, percussion and cut marks are lacking in the assemblage. Below is a detailed comparison of the WK analytical sample with the bootstrapped feeding trace models.

Percussion Marks

The incidence of percussion-marked bone in the WK assemblage is most similar to the V-H-C model (Table 5.5, Figure 5.11). The values for WK are within the 95% interquantile ranges for all sub-samples of the V-H-C model. They fall within the 95% interquantile ranges of the size group 3-4 sub-samples for all long bone fragments and midshaft fragments of the H-C model and for midshaft fragments of the HO model. The WK values are below all other sub-samples of the HO and H-C models

Tooth Marks

The incidence of tooth-marked bone in the WK assemblage is most similar to the H-C and V-H-C models (Table 5.6, Figure 5.12). The values for WK fall below the 95% interquantile ranges for all sub-samples of the CO model and all but the relatively large size group 3-4 sub-sample of the WB-C model. The WK values fall within the 95% interquantile ranges for the size group 1-4 sub-samples of the H-C and V-H-C models. With the exception of the midshaft fragment sub-sample of the V-H-C model, the WK values are within the 95% interquantile ranges for all other size group 3-4 sub-samples of the V-H-C and H-C models. The WK values are below all size group 1-2 sub-samples for both models.

Cut Marks

The proportion of cut-marked long bones in the WK assemblage is only accommodated by sub-samples that have a low incidence of cut marking (Table 5.7, Figure 5.13). These include the size group 1-4 and 3-4 sub-samples for all long bone fragments of the V-H-C model, the size group 1-2 and 3-4 sub-samples for midshaft fragments of the HO model, and the size group 1-2 sub-sample for midshaft fragments of the WB-C model. The incidence of cut marking in the WK sample is below the 95% interquantile ranges for all other sub-samples of the models.

Tooth and Butchery Marks

The incidence of tooth- and butchery-marked bone in the WK assemblage is most similar to the V-H-C model (Table 5.8, Figure 5.14). The values for WK fall within the 95% interquantile ranges for all sub-samples of midshaft fragments from the V-H-C

model, but only the size group 1-2 subsample for all long bone fragments of the model. For midshaft fragment only, the WK value also falls within the lower 95% interquantile ranges for the size group 1-2 sub-sample of the WB-C model. The WK values are below all other 95% interquantile ranges for sub-samples of the models

Notches

Together, the proportions of tooth- and percussion-notched long bone fragments in the WK analytical sample do not match any one model (Table 5.9). The proportion of tooth-notched long bone fragments in the WK sample is nearly identical to that of the H-C model. However, the proportion of percussion-notched bone is well below those predicted by both the HO and H-C models.

Discussion

WK Paleoenvironment

Paleoenvironmental indicators are not as clear for the WK site as they are for the JK2 site. This is in part the result of a low resolution description of the WK stratigraphy and the incomplete nature of the assemblage. Still, a basic assessment of time averaging and fluvial transport is necessary to provide context for behavioral interpretations of the assemblage.

Time Averaging

The effect of time averaging on the WK assemblage has been minimized by limiting the analytical sample to the main channel. All fossils excavated from trenches that reached the levels of the intermediate and lower channels were excluded from the analytical sample. Despite this precaution, specimens from the main channel may

represent a time range of 10^3 or 10^4 years because the channel had cut into older sediments and was later eroded before being covered and preserved by the overlying younger sediments. The possibility that some of the fossils were transported from an upstream location where the channel had incised into sediments as old as Bed I cannot be discounted in which case the assemblage could represent a time range on the order of 10^7 years. However, fossils from Beds I and II are typically white in color, a feature that was not observed on any of the WK fossils suggesting that material older than Bed III was not incorporated into the assemblage.

Fluvial Transport

The effect of fluvial transport on the WK assemblage cannot be confidently ascertained from the fossils or Leakey's (1994) stratigraphic sections. Both the analyzed and analytical samples are depleted of specimens smaller than 40 mm in maximum length indicating that the smaller specimens may have been transported from the site by fluvial processes (see Chapter 3). However, it is also likely that Leakey preferentially discarded fossils in this size category over larger more complete specimens. The WK assemblage is also deficient in size group 1 fossils, which are less abundant than all but size group 6 specimens indicating that bones from smaller animals may have been winnowed from the site. Again, excavator bias may have produced this result. The stratigraphic section for the main channel shows a 1 m deep channel filled with a sandy conglomerate. However, the clast size of the conglomerate is not provided by Leakey (1994) preventing an estimate of the flow velocity associated with the channel. Clearly, the fossils and artifacts are not in primary context as the majority of specimens were

found at the base of the channel. Whether, the assemblage represents a single nearby occupation area or a collection of bones and artifacts from multiple upstream locations cannot be ascertained from the available data.

Taxonomy and Climate

The WK assemblage is taxonomically diverse. Suidae represents the most common taxonomic family, but their abundance in the assemblage is solely the result of teeth that had been previously identified to species affording more precise MNI estimates. The species identifications are not presented here because they could not be verified without a comparative sample. Bovids are also abundant with Alcelaphini and Antilopini the most common tribes in the assemblage. Equids are common in the assemblage as well. Together, the equids and bovids suggest an open grassland habitat for the site, and support additional independent lines of evidence that indicate dryer conditions during Bed III and IV times (see Chapters 1 and 4).

The Feeding Behavior of Hominins and Carnivores at WK

Results indicate the pattern of feeding traces found at WK cannot be accounted for by some of the models. Most clearly, the co-occurrence of tooth-marked specimens and butchery-marked specimens in the assemblage eliminates individually the CO and/or HO models as exclusive descriptors of the behavioral sequences that produced the WK assemblage. Likewise, individual specimens bearing both tooth and butchery marks eliminate a combination of CO and HO as exclusive descriptors.

Results also indicate the pattern of feeding traces found at WK can be accounted for by some of the behavioral sequences modeled by the experimental assemblages.

Specifically, the proportions of tooth-, cut-, percussion-, and tooth- and butchery-marked bone in WK assemblage most closely resemble those for the H-C and V-H-C models.

The proportion of percussion-marked bone in the WK assemblage indicates hominins may not have been the only consumers of marrow at the site. JK2 is within the 95% interquantile ranges for all sub-samples of the V-H-C model and for the size group 3-4 sub-samples of the H-C model, all of which predict primary access to marrow by hominins. However, in all cases, the WK values fall just within the lower ranges predicted by these models suggesting that at least some long bones were broken by carnivores at the site or that the more conservative criteria used here for identifying percussion marks has underestimated the impact of hominin marrow removal on the assemblage (see methods). The former scenario may be indicative of a CO component to the assemblage or a lack of complete processing of all long bones by hominins for marrow (i.e. the WB-C model). Both the CO and WB-C models predict significantly higher proportions of tooth-marked bone than the H-C or V-H-C model.

The proportion of tooth-marked bone in the WK assemblage suggests hominins had primary access to flesh at the site. The WK values for the size group 3-4 sub-samples are within the 95% interquantile ranges predicted by the H-C and V-H-C models, both of which simulate hominins having had primary access to flesh. The WK values for the size group 1-2 sub-samples fall below those predicted by all models, suggesting that the carcasses in this category were not heavily ravaged after hominins had exploited the flesh and marrow. Lupo (1995) noted that bones that were roasted

and discarded by the Hadza were less ravaged by Hyenas, resulting in lower tooth mark frequencies than are predicted by the H-C model. Specifically, the proportions of tooth-marked long bone midshaft specimens from impala (size group 2) carcasses in the Hadza assemblages were well below 10%, while those from the larger alcelaphine (size group 3) carcasses were tooth-marked at rates between 15 and 30% (proportions of tooth-marked bone estimated from Figure 6, Lupo, 1995). The proportions of tooth-marked midshaft fragments from the size group 1-2 (5.9%) and size group 3-4 (19.4%) sub-samples of the WK assemblage fall within the ranges reported for the Hadza butchery sites suggesting the possibility that hominins at the site were roasting meat, while it remained on the bone. This process would strip bones of grease rendering them unattractive to scavengers. Lower cut mark frequencies might also be expected had hominins been cooking their meals because flesh can be more easily separated from bone after it has been cooked.

The proportion of cut-marked bone in the WK assemblage also suggests hominins at the site may have been using fire to prepare their meals. The incidence of cut marking for the WK assemblage is only accommodated by models that have a lower 95% interquantile range of less than 4%. The overall low incidence of cut marking in the WK assemblage is suggestive of hominins having removed flesh after cooking. Cooking allows flesh to be removed more easily from bones than would otherwise be possible with uncooked flesh (personal observation). It is possible that cooking afforded the removal of flesh without the use of stone tools at the site. Although the presence of cut

marks on long bone midshafts suggests at least some flesh was removed with the aid of a stone knife.

The proportion of tooth- and butchery-marked bone in the WK assemblage demonstrates at least some carcasses were exploited by both hominins and carnivores. However, the low incidence of specimens exhibiting both hominin and carnivore damage leaves open the possibility that some carcasses were only exploited by hominin and some only by carnivores. Given the proportion of tooth-marked bone in the assemblage, a HO component to the assemblage is more likely than CO as cooking may have reduced ravaging of hominin refuse by removing grease from long bones that would have otherwise remained attractive to scavengers.

Burnt Bone?

Thermal alteration of bone is not easily recognizable on fossils. The effects of heat on bone, which include discoloration and cracking, closely mimic those that are produced naturally through diagenesis (Brain and Sillen, 1998; Nicholson, 1993). As such, thermal alteration was not directly observed and was likely not observable on any of the WK fossils. Cooking also removes the organic and flexible collagen component of bone resulting in greater fragmentation and step fractures that are also indicative of dry-bone breakage (Shipman et al., 1984; Stiner, 1995). The abundance of dry-broken fossils in the WK assemblage (46.5% of the analytical sample) suggests the possibility that hammerstone breakage had occurred after the organic and flexible collagen component of bone had been removed through cooking.

Carnivore Tooth and Hammerstone Percussion Notches

The incidences of tooth and percussion notching in the WK assemblage support interpretations that are based upon the bone surface modification results. The incidence of tooth notching in the analytical sample is almost identical to that predicted by the H-C model suggesting hominins had first access to marrow at the site. However, the incidence of percussion notching in the WK analyzed sample is far less than predicted by either the H-C or HO models. As noted above, the removal of collagen through cooking prior to hammerstone breakage may have caused the high number of step fractures in the assemblage. This may have also limited the number of percussion notches in the assemblage. The dynamic force that is applied through hammerstone-on-anvil percussion is not likely to have produced the diagnostic arcuate notches that characterize hammerstone breakage (Capaldo and Blumenschine, 1994) on thermally altered bones that are also more brittle than their unheated counterparts. The results for percussion notching are consistent with the interpretation that *Homo erectus* was cooking flesh on the bone and subsequently extracting marrow using a hammerstone-on-anvil technique.

Accuracy of Mark Estimates for the WK Assemblage

The accuracy of estimates for the proportions of tooth-, cut-, and percussion-marked bones in the WK assemblage are subject to uncertainty due to the fluvial context of the assemblage. As was noted in Chapters 3 and 4, hydraulic processes can round bones obscuring bone surface modifications in unknown ways (Shipman and Rose, 1983). For the WK assemblage, impact marks created during transport of bones

may have been identified as percussion marks in some cases, and rounding of bone surfaces may have obscured all three mark types in others. More importantly, the conservative criteria used here for mark identification likely resulted in underestimates for the proportions of tooth, cut, and percussion marks in the assemblage. Still, the results for tooth and percussion notches, which are not likely to have been altered by fluvial processes, agree with those for the bone surface modifications suggesting the affects of such on the estimates reported are minimal.

Conclusion

The stratigraphy, skeletal part profiles, and the size distribution of long bone midshaft fragments for the WK assemblage indicate the site is in disturbed context. However, poor resolution in the description of the stratigraphy and the discarding of bone fragments from the site prevent a more detailed assessment of the paleoenvironmental conditions that are associated with the deposition and preservation of the assemblage. As such, it cannot be confidently ascertained whether the assemblage represents a single nearby occupation area or a collection of bones and artifacts from multiple upstream locations.

The proportions of tooth-, cut-, and percussion-marked fossils in the WK assemblage all indicate hominins having had primary access to both flesh and marrow at the site. The incidence of percussion marking indicates hominins broke the majority of bones at the site while tooth and cut mark frequencies suggest hominins may have been cooking flesh while it remained on the bone. Finally, the presence of specimens that are

both tooth- and butchery-marked demonstrates occasional hominin and carnivore feeding from the same carcass.

The proportion of hammerstone percussion-notched and carnivore tooth-notched specimens in the WK assemblage support the bone surface modification results. Tooth notches occur in frequencies that are nearly identical to the H-C model, while percussion notches occur less frequently than is predicted by either the HO or H-C model. It is suggested that the paucity of percussion notches may be the result of hominins exposing bones to heat through cooking prior to breaking them open for marrow removal; a process that would leave bones brittle and unlikely to exhibit the features typical of hammerstone breakage.

Together, the bone surface modification and notch data are consistent with hominins having typically acquired primary access to carcasses and possibly cooking flesh while it was on the bone, prior to consumption. Hominins likely had early access to flesh and marrow either through hunting or confrontational scavenging at the site. They may have cooked the flesh while it remained on the bone and removed it with stone tools in some cases or without in others. Marrow would typically have been exploited after cooking and consumption of flesh. Bone-crunching carnivores (i.e. hyaenids) likely scavenged the resulting bone fragments from which grease had not been depleted after cooking. Of course, these interpretations apply with the caveat that there are currently no available feeding trace models that systematically identify the effects of cooking on the proportions of tooth, cut, and percussions marks in experimentally controlled assemblages.

The WK assemblage may represent the earliest evidence for the controlled use of fire and cooking at Olduvai Gorge. This technical innovation would have provided significant advantages to the foraging capabilities of *Homo erectus* and may have been developed in the roughly 500 ky time span that separates the JK2 and WK sites. Cooking would not only have made the consumption of flesh more feasible, but would also have afforded resources from plants that would otherwise have been toxic including leaves, roots, tubers, and several species of seeds (Stahl, 1984, Wrangham et al., 1999). Fire could also have been used as a defense against predators or a weapon to aggressively usurp carcasses from large carnivores (Bellamo, 1994). Ultimately, the controlled use of fire may have been the most significant technological innovation developed by any hominin species making the results for WK invaluable in understanding the evolution of our own species.

Table 5.1) Description of the WK Sample

	All Bone Fragments	Long Bone Fragments
Analyzed Sample	1423	964
Analytical sample	-	284

Values represent the NISP for each sample.

Table 5.2) NISP for teeth for the WK sample

	NISP
Bovidae	67
Equidae	77
Elephantidae	10
Giraffidae	4
Hippopotamidae	43
Rhinocerotidae	25
Suidae	47
Total	273

Table 5.3) Long bone portion profile by animal size groups for the analytical sample

	Epiphyseal Fragments	Near-Epiphyseal Fragments	Midshaft Fragments	Total
Size 1-2	10	19	51	80
Size 3-4	19	61	124	204
Total	29	90	175	284

See methods in Chapter 4 for definitions of long bone portions. Animal size groups are based on Bunn and Kroll (1986). Size 1, <50 lbs (23 kg); Size 2, 50-250 lbs (23-114 kg); Size 3, 250-750 lbs (114-341 kg); Size 4, 750-2000.

Table 5.4) Skeletal part profile for the analyzed WK sample

	Size 1		Size 2		Size 3		Size 4		Size 5		Size 6		Total	
	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE	NISP	MNE
Cranial Fragment	0	-	3	-	22	-	1	-	0	-	0	-	26	-
Horn Core	2	2	6	1	5	1	1	1	0	0	0	0	14	5
Maxilla	0	0	0	0	5	1	1	1	1	1	0	0	7	3
Mandible	2	1	10	2	20	4	4	1	1	1	0	0	37	9
Occipital	0	0	0	0	2	1	1	1	0	0	0	0	3	2
Total	4	3	19	3	54	7	8	4	2	2	0	0	87	19
Atlas	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Axis	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Caudal Vertebra	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Cervical Vertebra	0	0	1	1	2	1	1	1	3	3	0	0	7	6
Lumbar Vertebra	0	0	1	1	3	2	1	1	0	0	0	0	5	4
Rib	4	-	30	-	112	-	29	-	13	-	0	-	188	-
Sacrum	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Sternum	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Thoracic Vertebra	0	0	0	0	5	2	0	0	1	1	0	0	6	3
Vertebra Fragment	0	-	2	1	6	1	4	2	0	0	0	0	12	4
Total	4	0	36	5	130	8	35	4	18	5	0	0	223	22
Femur	4	1	10	2	25	3	16	1	2	1	0	0	67	8
Fibula	0	0	1	1	0	0	0	0	0	0	0	0	1	1
Humerus	2	2	8	2	39	7	8	1	5	3	1	1	63	16
Long Bone Fragments	18	-	118	-	325	-	100	-	16	-	1	-	578	-
Metacarpal	3	2	5	2	13	3	3	2	2	1	0	0	26	9
Metapodial	7	2	9	1	25	2	11	1	1	1	0	0	53	7
Metatarsal	2	2	7	1	23	4	4	1	1	1	0	0	37	9
Radius	1	1	15	2	28	3	3	1	0	0	0	0	47	7
Tibia	2	1	19	3	43	5	17	4	2	1	1	1	84	15
Ulna	0	0	1	1	4	2	1	1	2	2	0	0	8	6
Total	39	11	193	15	525	29	163	12	31	10	3	2	964	78
Astragalus	0	0	1	1	7	7	0	0	0	0	0	0	8	8
Calcaneus	0	0	4	1	4	2	1	1	1	1	0	0	10	5
Carpal or Tarsal	0	-	5	-	3	-	1	-	0	-	1	-	10	-
External Cuneiform	1	1	0	0	1	1	0	0	0	0	0	0	2	2
Fibula	0	0	0	0	0	0	1	1	0	0	0	0	1	1
Lunate	0	0	0	0	0	0	1	1	0	0	0	0	1	1
Magnum	0	0	1	1	2	2	1	1	0	0	0	0	4	4
Metapodial	0	0	2	2	0	0	0	0	0	0	0	0	2	2
Patella	0	0	1	1	1	1	0	0	0	0	0	0	2	2
Phalange Proximal	1	1	1	1	1	1	1	1	0	0	0	0	4	4
Phalange Intermediate	1	1	1	1	0	0	0	0	0	0	0	0	2	2
Phalange Distal	0	0	2	2	1	1	0	0	0	0	0	0	3	3
Phalange Fragment	0	0	2	2	0	0	2	2	0	0	0	0	4	4
Pisiform	0	0	2	2	1	1	1	1	0	0	0	0	4	4
Scaphoid	1	1	0	0	0	0	1	1	0	0	0	0	2	2
Unciform	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Total	4	4	22	14	22	17	10	9	1	1	1	0	60	45
Innominate	0	0	4	1	27	3	6	1	2	1	0	0	39	6
Scapula	0	0	15	4	26	3	5	1	4	3	0	0	50	11
Total	0	0	19	5	53	6	11	2	6	4	0	0	89	17
Grand Total	51	18	289	42	784	67	227	31	58	22	4	2	1423	181

NISP is the number of identified specimens. MNE is the minimum number of elements represented and is based on skeletal part and portion data.

Table 5.5) Incidence of percussion-marked bone

		HO	H-C	V-H-C	WK
All Long Bone Fragments	**Size 1-4**				
	Mean %	38.5	26.5	24.9	12.3
	95% I.Q.R	29.1-47.7	21.6-31.6	9.1-43.6	-
	Size 1-2				
	Mean %	36.6	30.3	17.5	10.0
	95% I.Q.R	26.3-46.2	24.3-36.6	4.4-34.8	-
	Size 3-4				
	Mean %	49.9	18.0	26.9	13.2
	95% I.Q.R	29.1-70.8	11.5-25.5	7.7-49.1	-
Midshaft Fragments	**Size 1-4**				
	Mean %	27.7	24.9	19.8	13.1
	95% I.Q.R	16.4-37.9	19.8-30.2	6.4-35.8	-
	Size 1-2				
	Mean %	26.7	29.4	23.6	11.8
	95% I.Q.R	14.0-37.8	23.6-35.8	5.9-47.1	-
	Size 3-4				
	Mean %	33.5	14.6	19.2	13.7
	95% I.Q.R	11.3-60.0	8.1-22.4	3.7-38.3	-

Incidence is measured as the proportion of specimens bearing at least one percussion mark. HO, Hammerstone Only; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where WK is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 5.6) Incidence of tooth-marked bone.

		CO	WB-C	H-C	V-H-C	WK
All Long Bone Fragments	**Size 1-4**					
	Mean %	83.9	73.7	20.1	23.6	20.8
	95% I.Q.R	74.6-92.1	62.3-84.5	17.4-24.6	12.2-37.0	-
	Size 1-2					
	Mean %	70.9	70.6	19.1	43.4	11.3
	95% I.Q.R	56.7-82.5	55.7-84.3	14.9-23.7	21.7-65.2	-
	Size 3-4					
	Mean %	87.6	78.9	24.9	18.5	24.5
	95% I.Q.R	77.9-95.5	61.9-95.0	19.6-30.3	9.1-28.7	-
Midshaft Fragments	**Size 1-4**					
	Mean %	82.6	65.7	14.5	11.7	15.4
	95% I.Q.R	72.5-91.9	47.8-80.8	11.4-18.1	1.3-26.2	-
	Size 1-2					
	Mean %	69.1	70.5	14.5	35.5	5.9
	95% I.Q.R	54.8-81.0	56.1-84.7	10.5-18.9	11.8-58.8	-
	Size 3-4					
	Mean %	86.5	57.3	14.8	5.6	19.4
	95% I.Q.R	75.7-95.8	18.1-89.8	7.3-23.5	0-14.4	-

Incidence is measured as the proportion of specimens bearing at least one tooth mark. CO, Carnivore Only; WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where WK is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 5.7) Incidence of cut-marked bone.

		HO	WB-C	H-C	V-H-C	WK
All Long Bone Fragments	**Size 1-4**					
	Mean %	29.9	27.0	18.3	6.7	4.6
	95% I.Q.R	22.2-38.3	13.7-42.8	14.8-22.3	0-15.3	-
	Size 1-2					
	Mean %	27.2	18.4	18.9	0	5.0
	95% I.Q.R	20.3-33.7	5.5-34.8	14.4-24.4	0	-
	Size 3-4					
	Mean %	45.9	41.9	16.8	8.5	4.4
	95% I.Q.R	25.0-66.7	22.1-69.5	12.1-21.9	0-18.4	-
Midshaft Fragments	**Size 1-4**					
	Mean %	11.7	25.0	14.4	0	4.0
	95% I.Q.R	4.5-19.3	9.1-44.6	11.0-18.3	0	-
	Size 1-2					
	Mean %	10.3	16.4	15.4	0	3.9
	95% I.Q.R	3.1-17.6	2.5-36.0	10.9-20.6	0	-
	Size 3-4					
	Mean %	20.1	40.0	12.2	0	4.0
	95% I.Q.R	0-40.0	13.0-80.1	7.9-16.9	0	-

Incidence is measured as the proportion of specimens bearing at least one cut mark. HO, Hammerstone Only; WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where WK is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 5.8) Incidence of tooth- and butchery-marked bone.

		WB-C	H-C	V-H-C	WK
All Long Bone Fragments	**Size 1-4**				
	Mean %	19.7	8.4	9.6	1.7
	95% I.Q.R	9.5-32.2	6.0-11.4	2.0-19.7	-
	Size 1-2				
	Mean %	11.6	8.6	8.7	2.5
	95% I.Q.R	3.3-22.4	5.4-12.5	0-21.7	-
	Size 3-4				
	Mean %	33.7	8.0	9.9	1.5
	95% I.Q.R	16.7-57.5	5.5-10.9	1.6-22.3	-
Midshaft Fragments	**Size 1-4**				
	Mean %	9.7	4.9	4.4	0.5
	95% I.Q.R	3.0-18.0	2.9-7.4	0-12.2	-
	Size 1-2				
	Mean %	8.2	5.9	11.6	0
	95% I.Q.R	0-19.7	3.2-9.4	0-29.4	-
	Size 3-4				
	Mean %	12.3	3.2	2.5	0.8
	95% I.Q.R	2.6-24.4	1.3-5.8	0-10.0	-

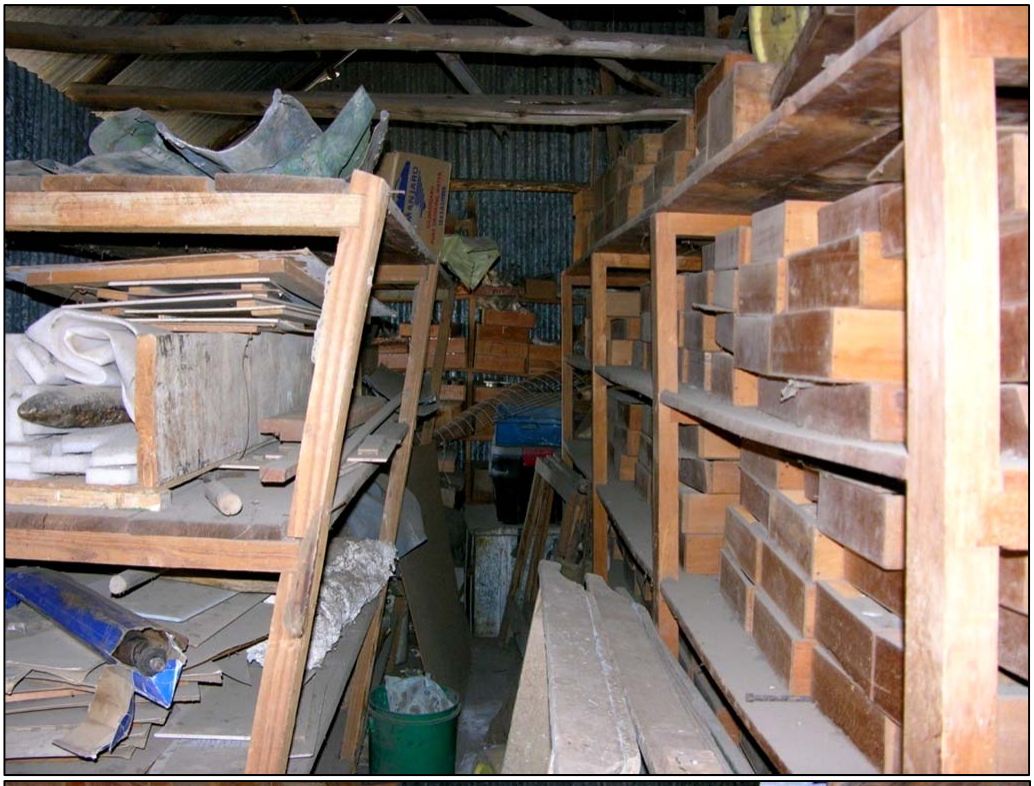
Incidence is measured as the proportion of specimens bearing at least one tooth and one percussion and/or cut mark. WB-C, Whole-Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. 95% I.Q.R. (Interquantile range), values between the 2.5% and 97.5% quantiles. Highlighted boxes indicate where WK is within the 95% interquantile ranges and therefore, statistically indistinguishable from the model.

Table 5.9) Incidence of carnivore tooth-notched and hammerstone percussion-notched bone for the WK assemblage and the feeding trace model.

	Carnivore Tooth Notching	Hammerstone Percussion Notching	Tooth and/or Percussion Notching
CO	19.1	-	19.1
HO	-	26	26
H-C	2.2	16.4	18.1
WK	2.8	6.7	11.6

Incidence is measured as the proportion of specimens bearing at least one notch. The tooth and or percussion notching category includes specimens with notches that were considered indeterminate. Data for WK represents the analytical sample. Data for the feeding trace models taken from Blumenschine (1995).

a)



b)

Figure 5.1) The Olduvai Lab prior to curation a) collapsing shelving system, b) debris which was later removed from the lab.

Figure 5.2) The Olduvai Lab after curation. Repaired shelves can be seen on the left, stone artifact collections are on the right.

Figure 5.3) Photograph showing a sample of bone fragments excavated from trench 9, main channel, WK. Scale = 10 cm. Observe the mottled coloring, rounded edges and transverse breaks on the fossils

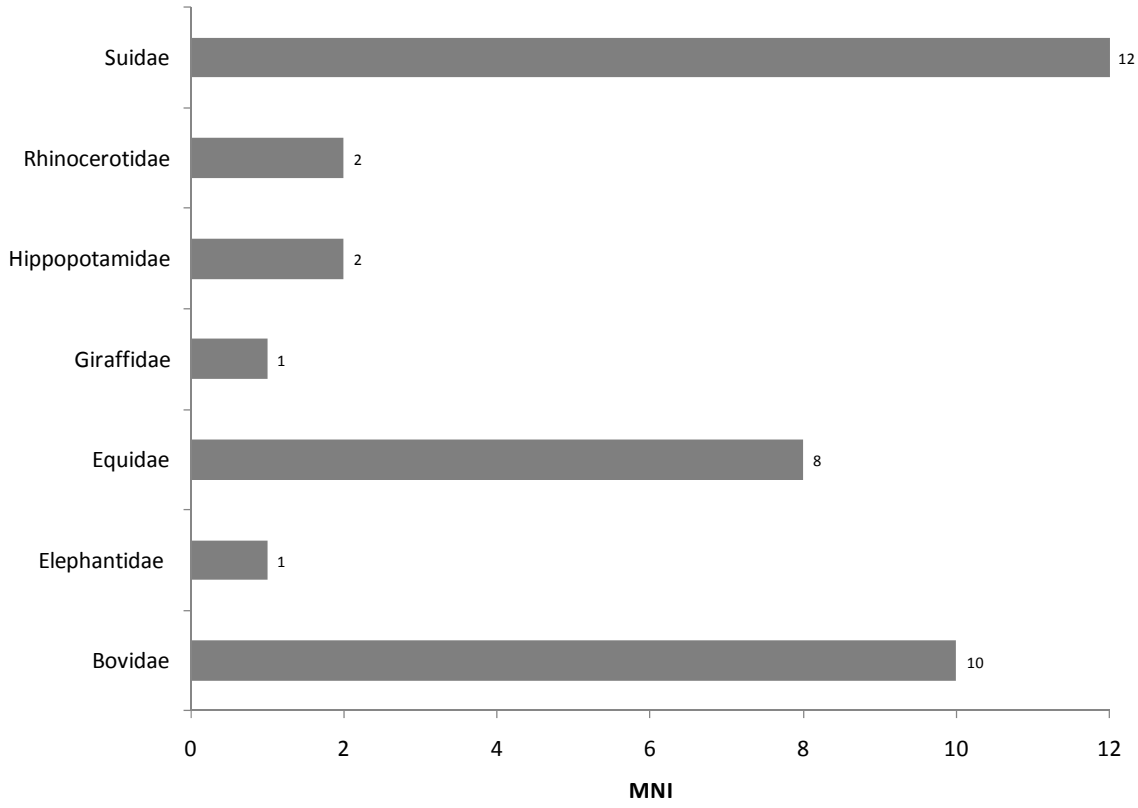


Figure 5.4) Minimum number of individuals based on all identified bone and teeth specimens. Note: carnivore specimens are located at the National Museums of Kenya in Nairobi and were not included in this study.

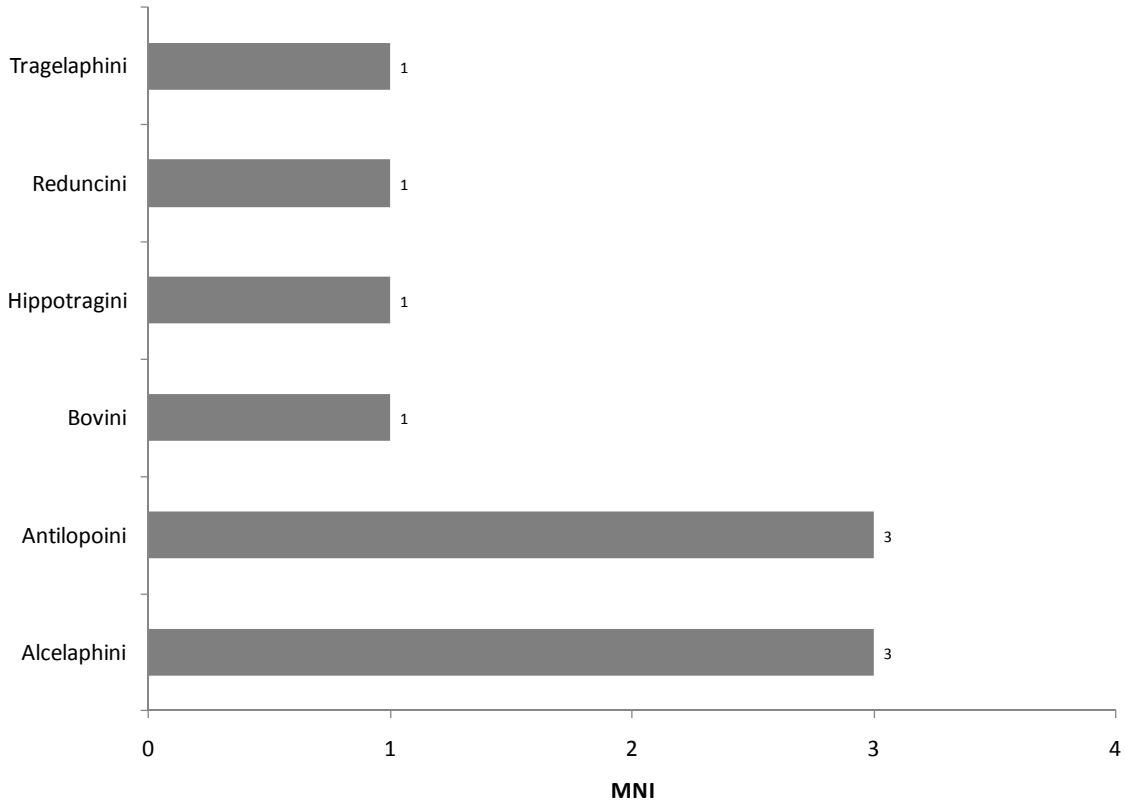


Figure 5.5) Minimum number of bovid individuals by tribe. Estimates are based on bovid teeth.

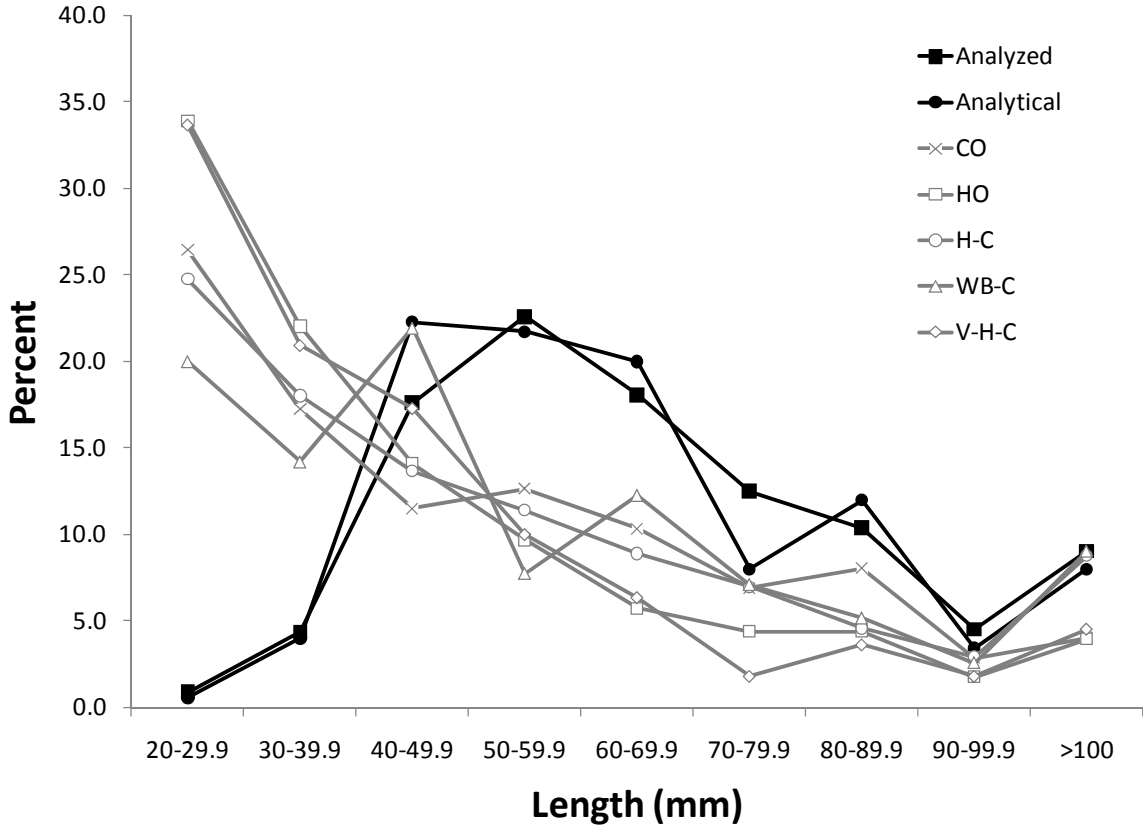


Figure 5.6) Size distribution of long bone midshaft fragments in feeding trace models and the analyzed and analytical WK samples. Data for the feeding trace models is based on the non-bootstrapped sample.

Figure 5.7) Possible percussion pits on size 3 long bone midshaft fragment. Scale = 1 cm.

Figure 5.8) Tooth marks on a size 3 equid mandible fragment. Scale = 1 cm.

Figure 5.9) Cut marks on a size 5 rib shaft fragment. Scale = 1 cm.

a)

b)

Figure 5.10) a) tooth notches on size 3 long bone midshaft fragment. Scale = 1 cm. b) Percussion notches on a size 4 long bone midshaft fragment. Scale = 5 cm.

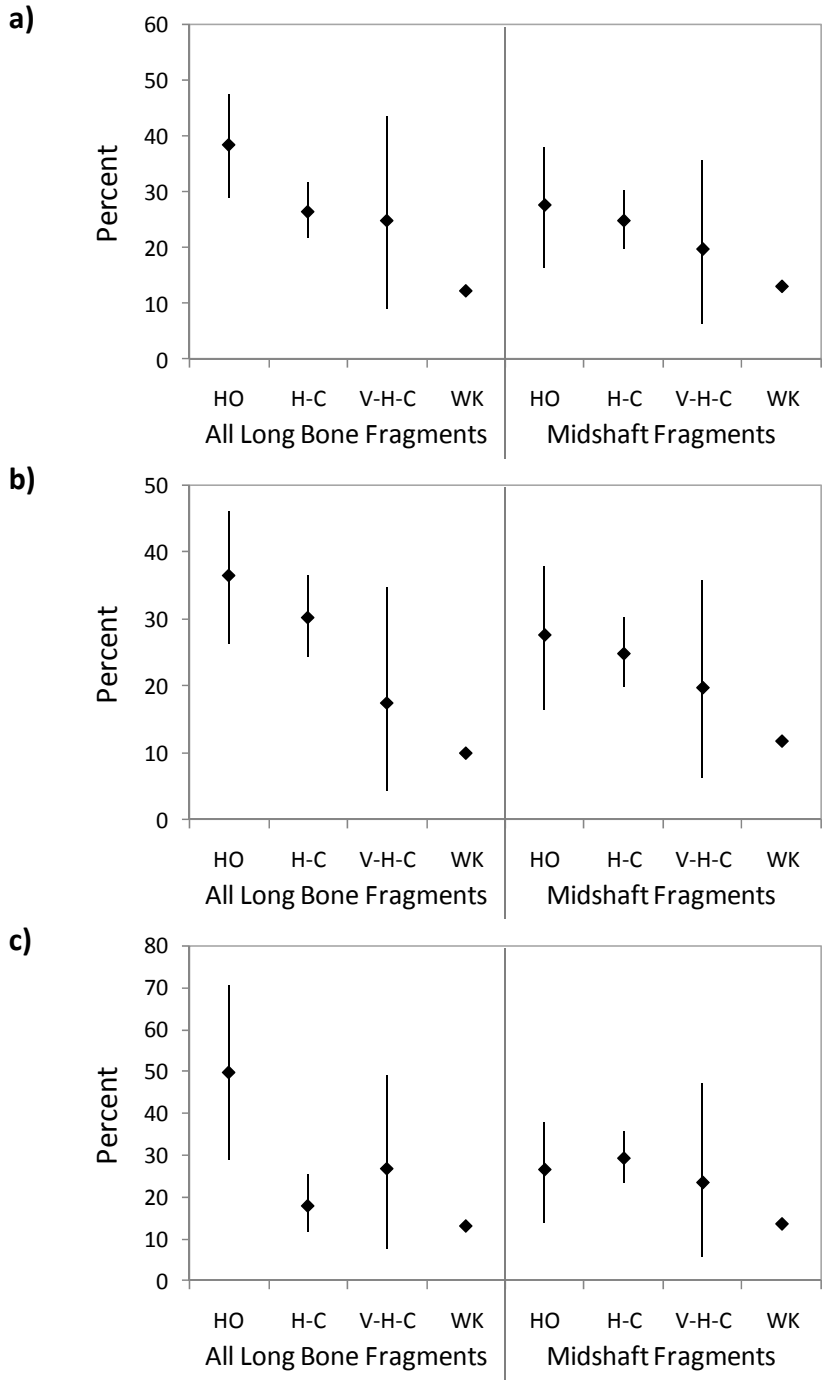


Figure 5.11) Incidence of percussion-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. HO, Hammerstone-Only; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for WK represents the proportion of percussion-marked bone.

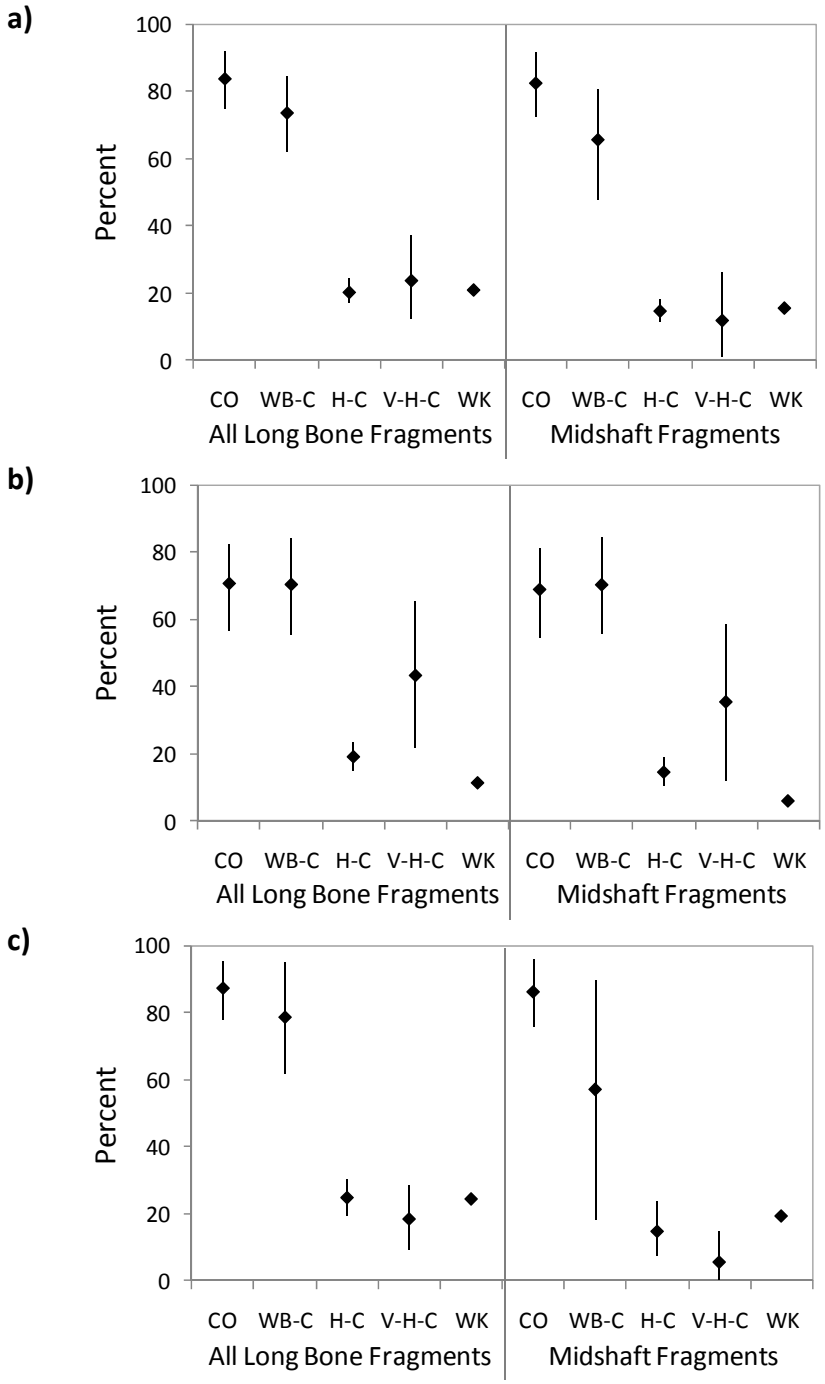


Figure 5.12) Incidence of tooth-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. CO, Carnivore Only; WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for WK represents the proportion of tooth-marked bone.

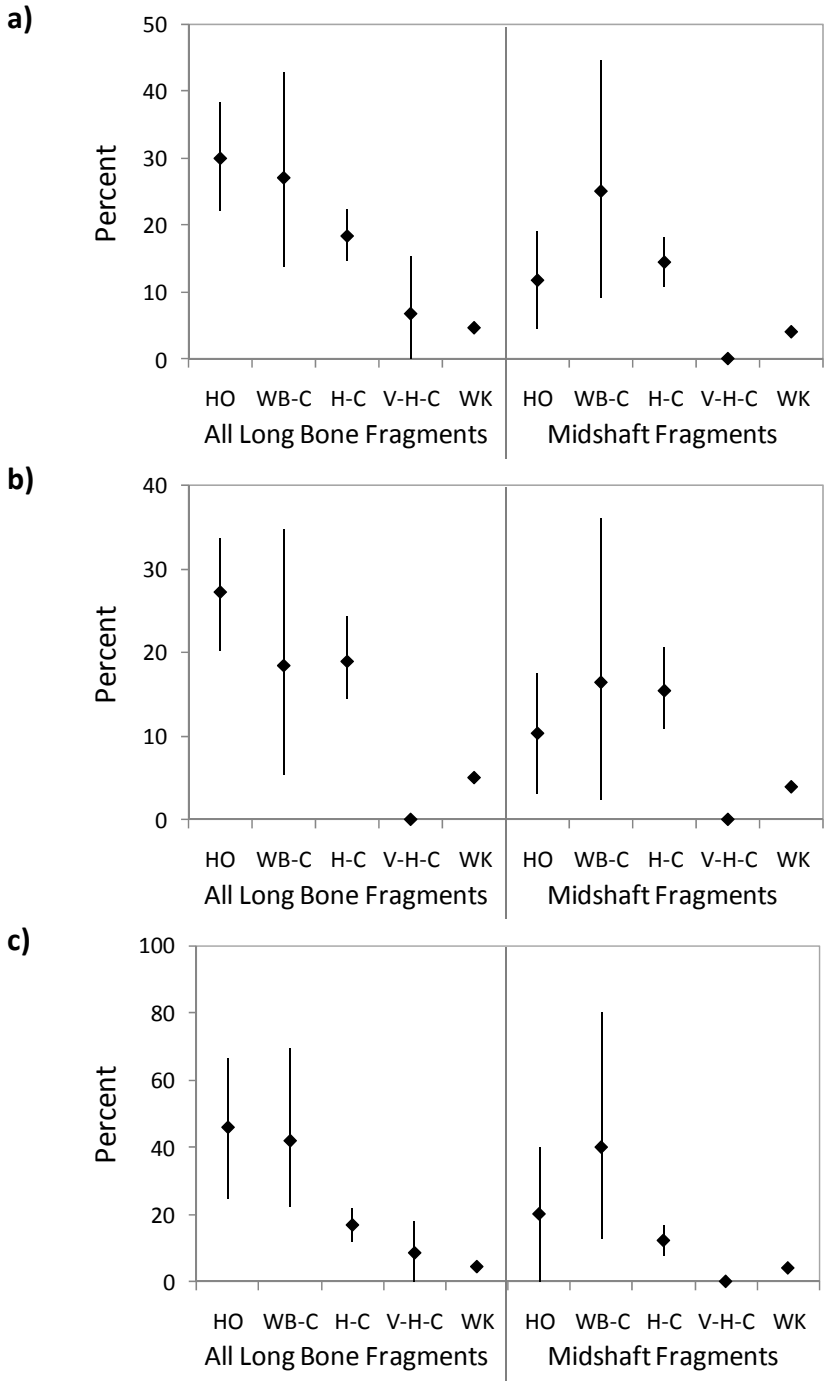


Figure 5.13) Incidence of cut-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. HO, Hammerstone-Only; WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for WK represents the proportion of cut-marked bone.

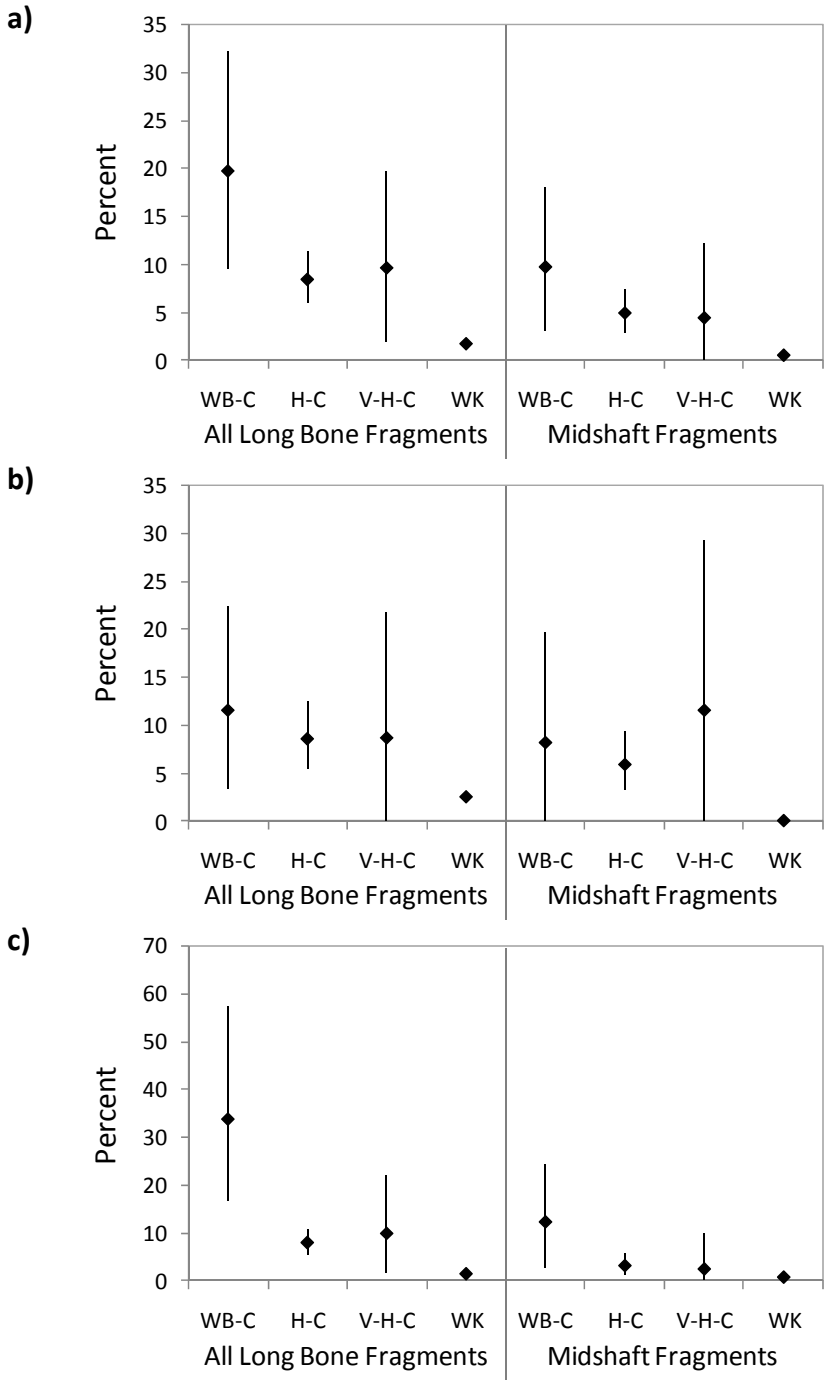


Figure 5.14) Incidence of tooth- and butchery-marked bone for (a) animal size group 1-4, (b) animal size group 1-2, and (c) animal size group 3-4. WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore**.** Data shown for feeding trace models is based on the bootstrap analysis and include the mean and 95% interquantile range. Data shown for WK represents the proportion of tooth- and butchery-marked bone.

Chapter 6

Conclusions and Future Directions

Introduction

This dissertation represents the first systematic analysis of larger mammal fossil assemblages from Beds III and IV, Olduvai Gorge, Tanzania and the first taphonomically informed assessment of the feeding behavior of *Homo erectus.* The paucity of similar analyses of fossil assemblages deposited after the emergence of Acheulean stone technology underscores the importance of this contribution to paleoanthropology. The significance of this research lies not only in the results reported for the Bed III and IV fossil assemblages, but also in the methodology that was developed to interpret the results, which is broadly applicable to archaeological sites regardless of age or geographic location. The methodologies and conclusions based on this research are a significant contribution to the larger goal of understanding the feeding behavior of *Homo erectus* and the impact of such on the evolution of the species. This final chapter will discuss the broader significance of the results and outline future research, some of which has already begun.

Methodological Contributions

This dissertation has contributed to a theoretically grounded body of research that seeks to understand the past through observations in the present. The contributions made are two-fold, serving to validate the primacy of feeding trace models in understanding the feeding behavior of Early Stone Age hominins and to reaffirm the applicability of these models to fossil assemblages deposited in fluvial contexts. It is in these methodological contributions that research presented in this dissertation becomes broadly applicable. Below is a summary of the methodological

contributions of this dissertation along with suggested future directions for actualistic research.

Validation of the Feeding Trace Models

The methodology developed by Blumenschine (1988; 1995) for interpreting the feeding behavior of Early Stone Age hominins from the assemblage-wide proportions of tooth and percussion marks was novel in emphasizing an ecological perspective in interpretations of fossil assemblages. This method was later expanded upon by his students Capaldo (1995) and Selvaggio (1998) and was the inspiration for the research presented in this dissertation. However, the validity of the feeding trace models had been called into question, threatening to undermine any application of the method. It has been shown here that published criticisms of these models are unfounded and that the models can be used to test hypotheses about hominin subsistence ecology. Still, the models are limited in sample size and require further development to provide greater specificity in interpretations of hominin and carnivore feeding behavior. Below are suggestions for future directions for feeding trace modelers.

There is a need for greater accuracy in feeding trace models. Currently, the models are limited to the general distinction of early access vs. secondary access to carcasses by hominins. The models cannot reliably identify the type and amount flesh (bulk vs. scrap) hominins were acquiring or the precise timing of hominin carcass acquisition relative to the carcass consumption sequence (Blumenschine, 1986a, b). The above issues can be addressed with actualistic studies that vary the timing of human access to carcasses relative to the amount of flesh that has been consumed by

carnivores. Such experiments would require acquiring carcasses from carnivores prior to the complete consumption of bulk flesh.

It has been suggested that tree-stored leopard kills may have provided reliable scavenging opportunities for hominins (Cavallo and Blumenschine, 1989). Leopards regularly return to specific trees to cache carcasses, temporarily abandoning them with varying amounts of flesh intact (Cavallo and Blumenschine, 1989). This behavior can be exploited to simulate early access to carcasses by hominins by baiting trees leopards are known to frequent and acquiring carcasses after they have been temporarily abandoned. I have successfully employed this method in a pilot study which demonstrated that assemblage-wide proportions of cut-marked bones increase with the amount of bulk flesh available to hominins, while the proportions of tooth-marked bones decrease. These results are promising and merit further investment in the modeling of hominin access to carcasses with variable amounts of bulk flesh remaining intact. The apparent indirect relationship between the incidences of tooth and cut marks in such experimentally generated assemblages will be key in identifying patterning that is sensitive to the type and amount of flesh exploited by hominins. Further development of the feeding trace models might also focus on the effects of cooking on the incidences of tooth, cut, and percussion marks in archaeological bone assemblages.

Models that highlight the effects of cooking on the proportions of tooth-, cut-, and percussion-marked specimens are needed to investigate the feeding behavior of hominins that were capable of controlling fire. Lupo's (1995) work represents the first

step in this research. She demonstrated that cooking reduces the degree of carnivore ravaging as measured by long bone epiphyseal:shaft fragment ratios and the proportion of carnivore tooth-marked specimens in bone assemblages (Blumenschine and Marean, 1993). However, one is left to infer the effects of cooking on the incidences of cut and percussion marks in fossil assemblages that have been thermally-altered. Systematic feeding observations following the methods prescribed by Blumenschine (1988) are needed to establish a new class of feeding trace model that is defined by its focus on the effects of cooking. This new class would parallel the HO and H-C models. However, the experiments would replicate the preparation of flesh in a manner that might be expected from hominins exploiting carcass foods after the advent of controlled fire, but before the innovation of boiling technology. Additional experiments might include the use of boiling technology for extracting grease from long bone epiphyses. However, initially the models would be limited to simulations of roasting flesh while it remained on the bone, a culinary method that may have been employed by the individuals that contributed to the accumulation of the WK fossil assemblage (see Chapter 5). These new models will prove to be invaluable in tracking the evolution of hominin feeding behavior as technological advancements facilitated the exploitation of new food resources, and will be essential to understanding the transition between *Homo erectus* and our own species.

Flume Experiments

Prior to the work conducted for this dissertation little was known about the effect of fluvial processes on bone fragments, particularly those that were fragmented

by the feeding activities of hominins and carnivores. The results reported here show that the transportability of bone fragments is inversely related to the size of bone fragments as measured by length, width, cortical thickness, and indirectly by the size group of the carcass from which the fragments were generated. Specifically, larger bone fragments are less likely to be transported than their smaller counterparts. More importantly, results have shown that fluvial processes should not significantly alter the assemblage-wide proportions of tooth, cut, and percussion marks in low-energy fluvial environments. Together, these results have provided a methodology for assessing the effects of fluvial transport on fossil bone assemblages and a basis for interpreting hominin and carnivore feeding behavior from these assemblages. Still, this research failed to anticipate the need for greater precision in identifying the effects of mechanical rounding and abrasion on bone surface modifications.

Hydraulic processes can round bones, obscuring surface modifications in currently unknown ways as was noted in Chapters 3, 4, and 5. However, this problem can be overcome with controlled experiments that simulate the rounding and polishing of bone that occurs during fluvial transport. The use of a rock tumbler would allow control over the experiments and accurately simulate the effects of fluvial transport on bone surfaces. Bones could be placed in the tumbler for preset time intervals and removed for observation at the end of each interval. The experiments would first need to develop a scale capable of describing with accuracy and precision the degree of rounding on bones. This scale might focus on the location of rounding (i.e. on edges or

cortical surface) and the appearance of features such as polishing or abrasion striae. Pilot work is necessary to identify potential criteria for the scale.

The next stage would relate the degree of rounding to the obscuring of the morphological criteria that are used to describe tooth, cut, and percussion marks on bone surfaces (Blumenschine et al., 1996). This step would require placing specimens with all three mark types into the tumbler and observing the morphological changes that occur describing them in relation to the rounding scale. The suggested experimental protocol would provide a basis for the exclusion of specimens from mark analyses according to the degree which they have been rounded. It may also provide a new set of criteria to be employed in the identification of bone surface modifications that have been partially obscured by fluvial processes.

The methodological contributions of this dissertation along with suggested future directions for this research pave the way for further development and refinement of the currently available feeding trace models. The models if more broadly applied will allow us to track the increasingly pervasive role played by hominins in the larger carnivore guild. Application of the models to the Bed III and IV fossil assemblages has already proven rewarding.

The Significance of Fossil Assemblages from Beds III and IV

The Bed III and IV fossil assemblages are important in representing a time period for which little is known about the behavior of hominins. The study of Acheulean fossil and stone artifact assemblages is complicated by poorly constrained dates and the fluvial context of most sites. These issues have been recognized for decades and are

underscored by Isaac's (1975) use of the phrase "the muddle in the middle" in noting our ignorance of the Middle Pleistocene. While dating methods have improved since Isaac's assessment, little progress has been made in the development of interpretive tools that can overcome the challenges posed by the study of Acheulean fossil assemblages. As a result, the Bed III and IV fossil assemblages have been ignored for nearly forty years despite the rich literature that has accumulated concerning Oldowan sites from Olduvai Gorge (Blumenschine, 1988; 1995; Bunn and Kroll, 1986; Binford, 1988; Capaldo, 1995; 1997; 1998; Dominguez-Rodrigo, 1997; Oliver, 1995; Selvaggio, 1994; 1998). This alone lends to the importance of the work presented here. However, the results reported are also broadly significant in what they have revealed about the feeding behavior of *Homo erectus*.

The Feeding Behavior of *Homo erectus*

The evolutionary significance of the results for the JK2 and WK assemblages lies in the indication that *Homo erectus* likely acquired earlier access to carcasses than its Oldowan hominin ancestors. The reanalysis of the FLK 22 fossil assemblage supports earlier interpretations of the site that suggest the role played by *Homo habilis* in the larger carnivore guild was in the form of a scavenger (Binford, 1988; Blumenschine, 1995; Capaldo, 1995; 1997; 1998; Selvaggio, 1994; 1998). Results for the JK2 and WK assemblages suggest *Homo erectus* may have been a more formidable opponent for large carnivores than was *Homo habilis*, obtaining earlier access to carcasses through either hunting or confrontational scavenging.

The feeding behavior of *Homo erectus* is not only likely to have evolved from that of earlier hominin species, but also during its own existence. The hammerstone-to-carnivore model best describes the pattern of feeding traces exhibited by both the JK2 and WK fossil assemblages. Whether *Homo erectus* was obtaining earlier access to carcasses through hunting or by aggressively usurping carcasses prior to their abandonment by carnivores cannot yet be ascertained from the feeding trace models. Still, both behaviors would indicate that the foraging capabilities of *Homo erectus* were more advanced than those of its Oldowan ancestors. These results are not surprising given the morphological characteristics and technological advancements that separate the two species (Shipman and Walker, 1989). Results also indicate that the subsistence capabilities of *Homo erectus* may have evolved substantially in the roughly 500 ky that separates the JK2 and WK sites. While both assemblages indicate early access to carcasses by *Homo erectus*, only the results for WK suggest the possibility that the species was capable of not only controlling fire, but also cooking its meals.

Homo erectus is a species that is characterized by its more human-like morphology, which includes increased brain and body size, reduced body-size dimorphism between males and females, and smaller jaws and dentition (Kappelman, 1996; Walker and Leakey, 1993; Wood, 1992). It has been argued that these traits evolved in response to or were facilitated by an increase in nutritional intake through the consumption of higher quality foods (Aiello and Wheeler, 1995; Milton, 1987; Ruff and Walker, 1993; Shipman and Walker, 1989; Washburn and Lancaster, 1968), with some researchers suggesting that cooking would have afforded hominins nutrient-rich

food resources that would have otherwise been toxic and inedible (Stahl, 1984, Wrangham et al., 1999). Wrangham et al. (1999) go so far as to suggest the morphological traits exhibited by *Homo erectus* are the direct result of the adoption of cooking by its ancestor, discounting meat eating alone as being responsible for the adaptive suite associated with the species. The authors acknowledge that the one test of this hypothesis is to produce evidence for the controlled use of fire dating to around 1.9 ma.

Evidence for the controlled use of fire in the Early Pleistocene is limited and unreliable. The earliest such evidence comes in the form of burnt sediments from the FxJj 20 main site, Koobi Fora, Kenya, dated at 1.6 Ma (Bellomo, 1994; Harris, 1978). Baked clay was also identified at Chesowanja in Kenya dated to 1.4 Ma (Harris and Gowlett, 1978; Gowlett et al., 1981). However, natural brush fires and burned out tree stumps may have produced these traces, and neither is evidence for cooking as there is no evidence of burning on the associated faunal remains. The earliest evidence for cooking may come in the form of burnt bones at the Swartkrans site in South Africa, dated to 1.4 Ma (Brain, 1993). While thermal-alteration was confirmed for some of the fossils at the site through chemical analyses (Brain and Sillen, 1988), there is no way to ascertain whether hominins or natural fires were responsible for the burning. Still, evidence for the controlled use of fire in the Early Pleistocene is rare and none of the above mentioned sites are as old as 1.9 Ma. The available evidence suggests the technological innovation of cooking did not occur until much later in time, possibly

contributing to the dramatic encephalization seen in the descendents of *Homo erectus* rather than the morphological characteristics exhibited by the species itself.

When put into context, evidence for cooking at WK becomes highly significant. The site may represent not only the earliest evidence for the controlled use of fire at Olduvai Gorge, but perhaps the earliest evidence of cooking for any archaeological site. Clearly, these results emphasize the need for the new class of feeding trace models proposed above. For it is only with a greater understanding of the effects of cooking on modern, controlled bone assemblages that credibility can be lent to the identification of such in the archaeological record. Tracking the role of cooking in the diet of *Homo erectus* has become crucial to understanding the evolution of our own species.

Future Directions

The results for the analyzed Bed III and IV fossil assemblages justify the expansion of this research to the unstudied assemblages excavated by Leakey. Such a study is now possible because of the curation of the fossil assemblages that were excavated by Leakey and stored in the Olduvai Lab. Fossil and stone artifact assemblages excavated from JK, PDK, WK east, HEB, and HWK EE in Bed II have yet to be subjected to detailed analyses. It has been demonstrated that these assemblages have the potential to provide invaluable information about the behavior and technological capabilities of *Homo erectus*, despite their fluvial contexts. While such analyses of these sites have yet to be planned, I hope to continue my work with the Bed III and IV material and encourage other researchers to do the same.

New excavations in Beds II, III, and IV are needed to collect complete and unbiased assemblages. The most significant shortcoming for interpretations of the WK site was an inability to account for excavator bias that was introduced into the assemblage by Mary Leakey when she selectively discarded specimens. This issue would complicate the analysis of any fossil assemblage that was excavated by Leakey from Beds II, III, and IV. Clearly, new excavations are warranted as unbiased samples will more accurately reflect the behavior of the hominins that they are associated with. The Olduvai Geochronology and Acheulean Paleoanthrology Project (OGAPP) with which I am a collaborator has already begun to carry out this task by opening excavations in Bed II with the goal of redefining the Oldowan/Acheulean boundary at Olduvai Gorge.

OGAPP excavations of the HWK EE site in Bed II will produce an unbiased sample of Developed Oldowan stone artifacts and fossils from which the behavior of *Homo erectus* can be inferred. An informal analysis of the HWK EE fossils that were excavated by Mary Leakey identified tooth, cut, and percussion marks on bone surfaces, indicating that new excavations of the site may also produce hominin- and carnivore-modified bone fragments. The assemblage excavated by OGAPP will be complete and include detailed analyses of the associated stratigraphy. Analyses of the HWK EE fossil assemblage will mirror those conducted for JK2 and WK as the stratigraphy indicates a low-energy fluvial context for the site. The stone artifacts from the site are strictly Developed Oldowan as not a single biface has been found on the surface or *in situ*. Still, at an age of roughly 1.5 ma traces of hominin activity can be confidently attributed to *Homo erectus*. The inferred feeding behavior for *Homo erectus* based on the HWK EE

fossil assemblage will lend well to comparisons with that of the species as inferred from fossil assemblages associated with Acheulean technology. Future survey and excavation will seek to recover material from sites deposited after the emergence of Acheulean stone technology. Ultimately, tracking the subsistence capabilities of *Homo erectus* along with the advent of technological innovations such as more advanced stone tools and the controlled use of fire will provide invaluable insights into the often assumed relationship between morphological and technological adaptations (Shipman and Walker, 1989).

Summary

This dissertation contributes to an understanding of the feeding behavior of *Homo erectus*. The development of methods tailored for analyses of Acheulean fossil assemblages has afforded new opportunities for interpreting the behavior of the *Homo* lineage as it encroached upon the larger carnivore guild. Continued research will seek to expand this contribution with the hopes of tracking the evolution of the feeding behavior of *Homo erectus* along with its relation to the morphological and technological adaptations with which it coincides. For it is through this research that the social behavior of the species may ultimately be revealed and a greater understanding of our own behavior and societies can be obtained.

Bibliography

Aiello, L. C., Wheeler, P. 1995. The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. Current Anthropology 36(2):199-221.

Behrensmeyer, A. K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. Bulletin of the Museum of Comparative Zoology 146, 473-578.

Behrensmeyer, A. K, 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4:150-162.

Behrensmeyer, A. K., 1982. Time resolution in fluvial vertebrate assemblages. Paleobiology 8, 211-227.

Behrensmeyer, A. K., 1988. Vertebrate preservation in fluvial channels. Paleogeography, Paleoclimatology, Paleoecology 63,183-199.

Behrensmeyer, A. K., Gordon, K. D., Yanagi, G.T., 1986. Trampling as a cause of bone surface damage and pseudo-cut marks. Nature 319:768-771.

Binford, L.R., 1981. Bones Ancient Men and Modern Myths. New York Academic Press, New York.

Binford, L.R., 1986. Comment on "Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge". Current Anthropology 27, 444-446.

Binford, L.R., 1988. Fact and Fiction about the *Zinjanthropus* Floor: Data, Arguments, and Interpretations. Current Anthropology 29, 123-135.

Blumenschine, R.J., 1986a. Carcass consumption sequences and the archaeological distinction of scavenging and hunting. Journal of Human Evolution 15, 639-659.

Blumenschine, R.J., 1986b. Early Hominid Scavenging Opportunities. B.A.R., Oxford.

Blumenschine, R.J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. Journal of Archaeological Science 15, 483-502.

Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. Journal of Human Evolution 29, 21-51.

Blumenschine, R.J., Caro, T.M., 1986. Unit flesh weights of some East African bovids. Journal of Human Evolution 24, 273-286.

Blumenschine, R.J., Madrigal, T.C., 1993. Variability in Long Bone Marrow Yields of East African Ungulates and its Zooarchaeological Implications. Journal of Archaeological Science 20, 555-587.

Blumenschine, R.J., Marean, C.W., 1993. A carnivore's view of archaeological bone assemblages. In: Hudson, J. (Ed.), From Bones to Behavior. Carbondale, The Center for Archaeological Investigations at Southern Illinois University, pp 273-300.

Blumenschine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. Journal of Archaeological Science 23, 493-507.

Blumenschine, R.J., Peters, C.R., Capaldo, S.D., Andrews, P., Njau, J.K., Pobiner, B.L., 2007b. Vertebrate Taphonomic Perspectives on Oldowan Hominin Land Use in the Plio-Pleistocene Olduvai Basin, Tanzania. In: Pickering, T., Schick, K., Toth, N.T. (Eds.), Breathing Life into Fossils: Taphonomic Studies in Honor of CK (Bob) Brain. Stone Age Institute, Gosport, IN, pp 161-179.

Blumenschine, R.J., Pobiner, B.L., 2007. Zooarchaeology and the ecology of Oldowan hominin carnivory. In: Unger, P.S. (Ed.), Evolution of the Human Diet: The Known, the Unknown, and the Unknowable. Oxford University Press, New York, pp 167-190.

Blumenschine, R.J., Prassack, K.A., Kreger, C.D., Pante, M.C., 2007a. Carnivore tooth-marks, microbial bioerosion, and the invalidation of Dominguez-Rodrigo and Barba's (2006) test of Oldowan hominin scavenging behavior. Journal of Human Evolution 53, 420-426.

Blumenschine, R. J., Selvaggio, M. M., 1991. On the marks of marrow bone processing by hammerstones and hyenas: Their anatomical patterning and archaeological implications: In Clark, J. D. (Eds.), Cultural Beginnings, Bonn: Dr. R. Habelt GMBH, pp. 17-32.

Blumenschine, R.J., Stanistreet, I.G., Njau, J.K., Bamford, M.K., Masao, F.T., Albert, R.M., Stollhofen, H., Andrews, P., Prassack, K.A., McHenry, L.J., Fernández-Jalvo, Y., Camilli, E.L., Ebert, J.I., In Review. Environments and hominin activities across the FLK Peninsula during *Zinjanthropus* times (1.84 Ma), Olduvai Gorge, Tanzania. Journal of Human Evolution (in review).

Boaz, N. T., Behrensmeyer, A. K., 1976. Hominid taphonomy: Transport of human skeletal parts in an artificial fluviatile environment. American Journal of Physical Anthropology 45, 53-60.

Brain, C.K., 1993. The occurrence of burnt bones at Swartkrans and their implications for the control of fire by early hominids. In Brain, C.K. (eds), Swartkrans: A cave's chronicle of early man. Transvaal Museum Monograph 8. pp. 229–42.

Brain, C.K., Sillen, A., 1988. Evidence From the Swartkrans Cave for the Earliest Use of Fire. Nature 336,464-466.

Bramble, D.M, Lieberman, D.E., 2004. Endurance and the Evolution of *Homo.* Nature 432:345-352.

Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. Nature 291, 574-577.

Bunn, H.T., Ezzo, J.A., 1993. Hunting and Scavenging by Plio-Pleistocene Hominids: Nutritional Constraints, Archaeological Patterns, and Behavioural Implications. Journal of Archaeological Science 20, 365-398.

Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio-Pleistocene hominids at Olduvai Gorge, Tanzania. Current Anthropology 27, 431-452.

Bunn, H.T., Kroll, E.M., 1988. Fact and Fiction about the *Zinjanthropus* Floor: data, arguments, and interpretations. Current Anthropology 29, 135-149.

Callow, P., 1994. The Olduvai bifaces: technology and raw materials. In Leakey, M.D. and Roe, D.A. (Eds.) Olduvai Gorge Excavations in Beds III, IV, and the Masek Beds *1968-1971*. Cambridge University Press. pp. 235-253.

Capaldo, S.D., 1995. Inferring Hominid and Carnivore Behavior from Dual-Patterned Archaeofaunal Assemblages. Ph.D. Dissertation, Rutgers University.

Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (*Zinjanthropus*), Olduvai Gorge, Tanzania. Journal of Human Evolution 33, 555-597.

Capaldo, S.D., 1998. Simulating the Formation of Dual-Patterned Archaeofaunal Assemblages with Experimental Control Samples. Journal of Archaeological Science 25, 311-330.

Carlos Díez, J., Fernández-Jalvo, Y., Rosell, J., Caceres, I., 1999. Zooarchaeology and taphonomy of Aurora Stratum (Gran Dolina, Sierra de Atapuerca, Spain. Journal of Human Evolution 37, 623-652.

Cavallo, J.A., Blumenschine, R.J., 1989. Tree-stored leopard kills: expanding the hominid scavenging niche. Journal of Human Evolution 18, 393-399.

Cerling, T. E., Hay, R. L. , 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. Quaternary Research 25:63-78.

Coard, R., 1999. One bone, two bones, wet bones, dry bones: Transport potentials under experimental conditions. Journal of Archaeological Science 26, 1369-1375.

Coard, R., Dennell, R. W., 1995. Taphonomy of some articulated skeletal remains: Transport potential in an artificial environment. Journal of Archaeological Science 22, 441-448.

Cruze-Uribe, K., 1991. Distinguishing hyena from hominid bone accumulations. Journal of Field Archaeology 18, 467-486.

Cruz-Uribe, K, Klien, R. G., Avery, G., Avery, M., Halkett, D., Hart, T., Milo, G., Sampson, C. G., Volman, T. P., 2003. Excavation of buried Late Acheulean (Mid-Quaternary) land surfaces at Duinefontein 2, Western Cape Province, South Africa. Journal of Archaeological Science 30:559-575.

De Heinzelin, Jean, Desmond Clark, J., Schick, K. D., Gilbert, W. H., 2000. The Acheulean and the Plio-Pleistocene deposits of the Middle Awash Valley, Ethiopia. Musee Royal De L'Afrique Centrale, Tervuren, Belgique Annales, Sciences Geologiques, Vol. 104.

Dodson, P., 1973. The significance of small bones in paleoecological interpretation. University of Wyoming Contributions to Geology 12, 15-19.

Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22 *Zinjanthropus* site, Olduvai Gorge (Tanzania): an experimental approach using cut-mark data. Journal of Human Evolution 33, 669-690.

Dominguez-Rodrigo, M., 1999. Distinguishing between apples and oranges: the application of modern cut-mark studies to the Plio-Pleistocene (a reply to Monahan). Journal of Human Evolution 37, 793-800.

Domínguez-Rodrigo, M., Barba, R., 2006. New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore-hominid-carnivore hypothesis falsified. Journal of Human Evolution 50, 170-194.

Domínguez-Rodrigo, M., Barba, R., 2007. Five more arguments to invalidate the passive scavenging version of the carnivore-hominid-carnivore model: a reply to Blumenschine et al. (2007). Journal of Human Evolution 53, 427-433.

Dominguez-Rodrigo, M., de la Torre, I., de Luque, L., Alcala, L., Mora, R., Serrallonga, J., Medina, V., 2002. The ST Site Complex at Peninj, West Lake Natron, Tanzania: Implications for Early Hominid Behavioural Models. Journal of Archaeological Science 29:639-665.

Dominguez-Rodrigo, M., Serrallonga, J., Jaun-Tresserras, J., Alcala, L., Luque, L., 2001. Woodworking activities by early humans: a plant residue analysis on Acheulean stone tools from Peninj (Tanzania). Journal of Human Evolution 40:289-299.

Efron, B., 1979. Bootstrap Methods: Another Look at the Jackknife. The Annals of Statistics 7, 1-26.

Efron, B., Tibshirani, R., 1993. An Introduction to the Bootstrap. Chapman and Hall, New York.

Egeland, C.P., Pickering, T.R., Domínguez-Rodrigo, M., Brain, C.K., 2004. Disentangling Early Stone Age palimpsests: determining the functional independence of hominid- and carnivore-derived portions of archaeofaunas. Journal of Human Evolution 47, 343-357.

Faith, J.T., 2007. Sources of variation in carnivore tooth-mark frequencies in a modern spotted hyena (*Crocuta crocuta*) den assemblage, Amboseli Park, Kenya. Journal of Archaeological Science 34, 1601-1609.

Fernández-Jalvo, Y., 2003. Experimental effects of water abrasion on bone fragments. Journal of Taphonomy 1(3), 145-162.

Fernández-Jalvo, Y., Carlos-Díez, J., Cáceres, I., Rosell, J., 1999. Human cannibalism in the Early Pleistocene of Europe (Gran Dolina, Sierra de Atapuerca, Bungo, Spain). Journal of Human Evolution 37, 591-622.

Freeman, L. G., 1975. Acheulean sites and stratigraphy in Iberia and the Maghreb. In Butzer, K. W. and Isaac, G.L. (Eds.), After the Australopithecines. Mouton, Paris. pp. 661-743.

Gentry, A., Gentry, A., 1978. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part II. Bulletin of the British Museum of Natural History (Geology) 30, 1-83.

Gifford-Gonzalez, D. P., 1991. Bones are not enough: analogues, knowledge, and interpretive strategies in zooarchaeology. Journal of Anthropological Archaeology 10:215-254.

Gowlett, J.A.J., Harris, J.W.K., Walton, D., Wood, B.A., 1981. Early Archaeological Sites, Hominid Remains and Traces of Fire From Chesowanja, Kenya. Nature 294, 125-129.

Harris , J.W.K , 1978. The Karari industry: Its place in East African prehistory. Ph D dissertation, Berkeley, University of California Press.

Harris , J.W.K , Gowlett, J.A.J., 1980. “Evidence of early stone industries at Chesowanja, Kenya.” Proceedings of the Panafrican Congress of Prehistory and Quarternary Studies, Nairobi 8, 208–212.

Hay, R. 1976. The Geology of Olduvai Gorge. Oxford: Clarendon Press.

Hay, R., 1994. Geology and Dating of Beds III, IV and the Masek Beds. In Leakey, M.D. and Roe, D.A. (Eds.) Olduvai Gorge Excavations in Beds III, IV, and the Masek Beds *1968-1971*. Cambridge University Press, pp. 8-14.

Howell, F. C., Butzer, K. W., Freeman, L. G., Klein, R. G., 1991. Observations on the Acheulean Occupation site of Ambrona (Soria Province, Spain) with particular reference to recent investigations (1980-1983) and the lower occupation. Jahrbuch des Romisch Germanischen Zentralmuseums Mainz 38:33-82.

Isaac, G.L., 1975. Sorting out the muddle in the middle: An anthropologist's post-conference appraisal. In Butzer, K. W. and Isaac, G.L. (Eds.), After the Australopithecines. Mouton, Paris. pp. 875-889.

Jones, P. R., 1981. Experimental implement manufacture and use; a case study from Olduvai Gorge, Tanzania. Phil. Trans. R. Soc. Lond. B 292:189-195.

Jones, P.R. (1994). Results of experimental work in relation to the stone industries of Olduvai Gorge. In Leakey, M.D. and Roe, D.A. (Eds.) Olduvai Gorge Excavations in Beds III, IV, and the Masek Beds *1968-1971*. Cambridge University Press. pp. 254-298.

Kappelman, J., 1996. The evolution of body mass and relative brain size in fossil hominids. Journal of Human Evolution 30, 243–76

Klein, R.G., 1980. The interpretation of mammalian faunas from Stone Age archaeological sites with special reference to sites in the Southern Cape Provice, South Africa. University of Chicago Press, Chicago.

Klein, R. G., 1987. Problems and prospects in understanding how early people exploited animals. In Nitecki, M. H. and Nitecki, D.V. (Eds.), The Evolution of Human Hunting Plenum Press, New York, pp. 11-45.

Korth, W. W., 1979. Taphonomy of microvertebrate fossil assemblages. Annals of the Carnegie Museum 48, 235-285.

Lam, Y.M., Chen, X., Marean, C.W., Frey, C.J., 1998. Bone Density and Long Bone Representation in Archaeological Faunas: Comparing Results from CT and Photon Densitometry. Journal of Archaeological Science 25, 559-570.

Leakey, M.D., 1971. Olduvai Gorge, Volume 3, Excavations in Beds I and II, 1960-1963. Cambridge University Press, Cambridge.

Leakey, M.D., 1975. Cultural patterns in the Olduvai sequence. In Butzer, K. W. and Isaac, G.L. (Eds.), After the Australopithecines. Mouton, Paris. pp. 477-493.

Leakey, M. D., 1994. Chapters 2-7. In Leakey, M.D. and Roe, D.A. (Eds.) Olduvai Gorge Excavations in Beds III, IV, and the Masek Beds *1968-1971*. Cambridge University Press

Lupo, K.D., 1995. Hadza bone assemblages and hyena attrition: An ethnographic example of the influence of cooking and mode of discard on the intensity of scavenger ravaging. Journal of Anthropological Archaeology 14, 288-314.

Lupo, K.D., O'Connell, J.F., 2002. Cut and Tooth Mark Distributions on Large Animal Bones: Ethnoarchaeological Data from the Hadza and Their Implications For Current Ideas About Early Human Carnivory. Journal of Archaeological Science 29, 85-109.

Lyman, R. L., 1994. Vertebrate Taphonomy. Cambridge. Cambridge University Press.

Marean, C.W., 1991. Measuring the post-depositional destruction of bone in archaeological assemblages. Journal of Archaeological Science 18, 677-694.

Marean, C.W., Abe, Y., Frey, C.J., Randall, R.C., 2000. Zooarchaeological and taphonomic analysis of the Die Kelders Cave 1 layers 10 and 11 Middle Stone Age larger mammal fauna. Journal of Human Evolution 38, 197-233.

Marean, C.W., Kim, S.W., 1998. Mousterian large-mammal remains from Kobeh Cave: Behavioral implications for Neanderthals and early modern humans. Current Anthropology 39, S79-S113.

Marean, C. W., Spencer, L., 1991. Impact of carnivore ravaging on zooarchaeological measures of element abundance. American Antiquity 56(4), 645-658.

Marean, C.W., Spencer, L.M., Blumenschine, R.J., Capaldo, S.D., 1992. Captive hyaena bone choice and destruction, the Schlepp effect and Olduvai archaeofaunas. Journal of Archaeological Science 19, 101-121.

Milo, R. G,. 1994. Human-Animal Interactions in Southern African Prehistory: A Microscopic Study of Bone Damage Signatures. Ph. D. Thesis, University of Chicago, Chicago.

Milton, K. (1987). Primate Diets and Gut Morphology: Implications for Hominid Evolution. In Harris, M and Ross, E.B. (eds.) Food and Evolution Toward a Theory of Human Food Habits. Philadelphia, Temple University Press pp. 93-115.

Nicholson, Rebecca A., 1993. A Morphological Investigation of Burnt Animal Bone and an Evaluation of its Utility in Archaeology. Journal of Archaeological Science 20, 411-428.

Oliver, J. S., 1994. Estimates of hominid and carnivore involvement in the FLK *Zinjanthropus* fossil assemblage: some socioecological implications. Journal of Human Evolution 27, 267-294.

Pante, M.C., Blumenschine, R.J., 2010. Fluvial transport of bovid long bones fragmented by the feeding activities of hominins and carnivores. Journal of Archaeological Science, 3, 846-854.

Pante, M.C., Blumenschine, R. J., Capaldo, S. D., Scott, R. S., in review. Validation of bone surface modification models for inferring fossil hominin and carnivore feeding interactions, with reapplication to FLK 22, Olduvai Gorge, Tanzania. Journal of Human Evolution.

Parfitt, S. A., Robert, M. B., 1999. Human modification of faunal remains. In Boxgrove: A Middle Pleistocene Hominid site at Eartham Quarry, Boxgrove, West Sussex. In M. B. Roberts and S. A. Parfitt (Eds.), English Heritage, London, pp. 395-415.

Pettijohn, F. J., Potter, P E., Siever, R., 1972. Sand and Sandstone. Springer-Verlag, New York.
Pickering, Travis Rayne, Dominguez-Rodrigo, M., Egeland, C. P., Brain, C. K., 2004a. New Data and ideas on the foraging behavior of Early Stone Age Hominids at Swartkrans Cave, South Africa. South African Journal of Science 100, 215-219.

Pickering, Travis Rayne, Dominguez-Rodrigo, M., Egeland, C. P., Brain, C. K., 2004b. Beyond Leopards: Tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fossil assemblage. Journal of Human Evolution 46, 595-604.

Pobiner, B.L., Braun, D.R., 2005. Strengthening the inferential link between cutmark frequency data and Oldowan hominid behavior: Results from modern butchery experiments. Journal of Taphonomy 3, 107-119.

Potts, R., and Shipman, P., 1981. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. Nature 291, 577-580.

Potts, R., Behrensmeyer, A. K., Ditchfield, P., 1999. Paleolandscape variation and Early Pleistocene hominid activities: Members 1 and 7, Olorgesailie Formation, Kenya. Journal of Human Evolution 37, 747-788.

Roe, D.A., 1994. A metrical analysis of selected sets of handaxes and cleavers from Olduvai Gorge. In Leakey, M.D. and Roe, D.A. (Eds.) Olduvai Gorge Excavations in Beds III, IV, and the Masek Beds *1968-1971*. Cambridge University Press. pp. 146-234.

Robert, I., Vigne, J., 2002. Bearded Vulture *Gypaetus barbatus* contributions to the constitution of two different bone assemblages: Modern reference data and an archaeological example in Corsica. Acta zoologica cracoviensia 45, 319-329.

Ruff, C. B., Walker A., 1993. "Body Size and Body Shape," In Walker, A., and Leakey, R. (eds.), *The Nariokotome Homo erectus skeleton.* Cambridge, Harvard University Press.

Sanders, W. J., Trapani, J., Mitani, J.J., 2003. Taphonomic aspects of Crowned Hawk-Eagle predation on monkeys. Journal of Human Evolution 44, 87-105.

Schick, K. D., 1984. Processes of Palaeolithic Site Formation: An Experimental Study. Ph. D. Dissertation, University of California, Berkeley.

Schick, K. D., 1986. Stone Age Sites in the Making: Experiments in the Formation and Transformation of Archaeological Occurrences. British Archaeological Reports International Series, No. 319, Oxford.

Selvaggio, M.M., 1994. Evidence from carnivore tooth marks and stone-tool-butchery marks for scavenging by hominids at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. Ph.D. Dissertation, Rutgers University.

Selvaggio, M.M., 1998. Evidence for a Three-Stage Sequence of Hominid and Carnivore Involvement with Long Bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. Journal of Archaeological Science 25, 191-202.

Shipman, P., 1981. Application of scanning electron microscopy to taphonomic problems. Annals of the New York Academy of Sciences. 376, 357-386.

Shipman, P., Bosler, W., Davis, K.L., 1981. Butchering of Giant Geladas at an Acheulean Site. Current Anthropology 22, 257-268.

Shipman, P, Foster, G., Schoeninger, M., 1984. Burnt Bones and Teeth an Experimental Study of Color, Morphology, Crystal Structure and Shrinkage. Journal of Archaeological Science 11, 307-326.

Shipman, P., Rose, J., 1983. Early Hominid Hunting, Butchering and Carcass-Processing Behaviors: Approaches to the Fossil Record. Journal of Anthropological Archaeology 2, 57-98.

Shipman, P., Walker, A., 1989. The costs of becoming of a predator. Journal of Human Evolution 18, 373-392.

Sinclair, A.R.E., Duncan, P., 1972. Indices of condition in tropical ruminants. East African Wildlife Journal 10, 143-149.

Speth, J.D., 1987. Early Hominid Subsistence Strategies in Seasonal Habitats. Journal of Archaeological Science 14, 13-29.

Stahl, A. B., 1984. Hominid Dietary Selection Before Fire. Current Anthropology 25, 151-168.

Stiner, M., Kuhn, S., Weiner, S., Bar-Yosef, O., 1995. Differential Burning, Recrystallization, and Fragmentation of Archaeological Bone. Journal of Archaeological Science 22, 223-237.

Tibshirani, R., 1988. Variance stabilization and the bootstrap. Biometrika 75, 433-444.

Trapani, J., 1998. Hydrodynamic sorting of avian skeletal remains. Journal of Archaeological Science 25, 477-487.

Werdelin, L., Lewis, M.E., 2005. Plio-Pleistocene carnivora of eastern Africa: species richness and turnover patterns. Zoological Journal of the Linnean Society 144, 121-144.

White, T.D., Toth, N., 2007. Carnivora and Carnivory: Assessing Hominid Toothmarks in Zooarchaeology. In: Pickering, T., Schick, K., Toth, N.T. (Eds.), Breathing Life into Fossils: Taphonomic Studies in Honor of CK (Bob) Brain. Stone Age Institute, Gosport, IN, pp 161-179.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. Journal of Human Evolution 21, 27-48.

Villa, P., Soto, E., Santonja, M., Perez-Gonzalez, A., Mora, R., Parcerisas, J., Sese, C., 2005. New Data from Ambrona: Closing the hunting versus scavenging debate. Quaternary International 128, 223-250.

Voorhies, M. (1969). Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County Nebraska. University of Wyoming Contributions to Geology, Special Paper No. 1, Laramie.

Walker, A., Leakey, R., 1993. The Nariokotome *Homo erectus* skeleton. Cambridge, Harvard University Press.

Washburn, S., Lancaster, C. 1968. The evolution of hunting. In Lee, R. B. and DeVore, I. (eds.) Man the Hunter. Chicago: Aldine pp. 293–303.

Wolff, R. G., 1973. Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California (U.S.A). Paleogeography, Paleoclimatology, Paleoecology 13, 91-101.

Wood, B. A., 1992. Origin and evolution of the genus *Homo*. Nature 355, 783–90.

Wrangham, R.W, Holland Jones, J., Laden, G. Pilbeam, D., Conklin-Brittain, N., 1999. The Raw and the Stolen: Cooking and the Ecology of Human Origins. Current Anthropology 40, 567-594.

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2007	Harris, J. W. K., Braun, D. R., Pante, M. C. "Archaeological Archive from Africa: 2.7 myr-300,000 years ago" In *Encyclopedia of Quaternary Studies* Scott A. Elias (Eds.) pp 52-63.
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2010	Pante, M. C., Blumenschine, R. J. Fluvial transport of bovid long bones fragmented by the feeding activities of hominins and carnivores. *Journal of Archaeological Science* 37, 846-854.