

ZOOARCHAEOLOGICAL AND TAPHONOMIC PERSPECTIVES ON HOMINID AND  
CARNIVORE INTERACTIONS AT OLDUVAI GORGE, TANZANIA

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# ABSTRACT

Charles Peter Egeland

## ZOOARCHAEOLOGICAL AND TAPHONOMIC PERSPECTIVES ON HOMINID AND CARNIVORE INTERACTIONS AT OLDUVAI GORGE, TANZANIA

This dissertation examines variability in the foraging strategies of hominids and large carnivores during Bed I and II times (1.9–1.2 million years ago) at Olduvai Gorge, Tanzania. Nine levels from six sites are analyzed and three major issues addressed: (1) the relative roles of hominids and large carnivores in the formation of each faunal assemblage; (2) the identity of the carnivore(s) responsible for carcass accumulation and modification; and (3) the intensity of on-site competition for carcass resources. Competition is utilized as a unifying concept because of its ecological importance and taphonomic visibility. Other than BK in Bed II, little or no evidence for hominid carcass processing is present in the Olduvai faunas examined here. In Bed I, DK likely represents a predation/death arena that was sporadically utilized by hominids for carcass parts while FLKNN 2 and FLKN 5 reflect repeated carcass transport by felids to eating areas. Poor preservation at the Bed II sites of FC West and TK hinders a definitive link to either hominid or large carnivore behavior. A significant portion of the BK assemblage is the result of carcass part transport and processing by hominids. A strong felid taphonomic signature exists in the Bed I faunas, while in the Bed II assemblages hyena involvement with carcasses is much more pronounced. All of the Bed I sites examined here formed in relatively low competition settings. Concomitant with a general shift in site location during Bed II times, FC West, TK and BK all occur in higher competition environments. The co-occurrence of stone tools with fauna that lack butchery damage, especially at the Bed I sites, has important implications for hominid site use. A combination of the faunal and lithic data suggests that hominids were using these sites for activities unrelated to carcass processing. These findings highlight variability in hominid site use at Olduvai Gorge and beyond.

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## CHAPTER 1 INTRODUCTION

The processing of nutrient-dense large mammal tissue by hominids is a characteristic of the Oldowan archaeological record from its inception 2.5–2.6 million years ago (Ma) (de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005; Semaw et al., 2003). Suggestions that this dietary shift eventually fueled encephalization (Aiello and Wheeler, 1995) and the evolution of the human life history (Kaplan et al., 2000; but see Lupo and O’Connell, 2002; O’Connell et al., 2002) underscore the importance of characterizing hominid carcass foraging during the Plio-Pleistocene. However, nearly fifty years of systematic research has failed to provide a consensus opinion over the nature and extent of Plio-Pleistocene hominid carnivory and the socio-economic function of the earliest archaeological sites.

Oldowan, Developed Oldowan and early Acheulean artifacts have been found in association with faunal material at many sites in eastern, southern and northern Africa (Asfaw et al., 1992; Brain, 1993; Chavaillon et al., 1979; Clark, 1987; Clark and Kurashina, 1979; Ditchfield et al., 1999; Domínguez-Rodrigo et al., 2002; Gowlett et al., 1981; Harris et al., 1987; Howell et al., 1987; Isaac, 1997; Kibunjia, 1994; Kimbel et al., 1996; Kuman and Clarke, 2000; Kuman et al., 1997; Plummer et al., 1999; Roche et al., 1999; Sahnouni et al., 2002; Semaw et al., 2003) (Figure 1.1). However, assessing the role of hominids in the accumulation of the bones at these sites is often plagued by poor preservation, small sample sizes and the difficulty of accessing the materials for study. For these reasons the large, well-preserved faunal collections excavated by Mary Leakey (1971) from Olduvai Gorge, Tanzania have figured prominently in discussions of hominid carcass foraging behavior and Plio-Pleistocene site function.

Paramount among the sites from Olduvai Gorge is Level 22 at the FLK locality (FLK 22; the “*Zinjanthropus* Floor”). Located in Bed I and dated to about 1.8 Ma, FLK 22 was initially well-known for the discovery of a nearly complete robust australopithecine skull (OH 5; Leakey, 1959) and now stands as the most intensely studied Plio-Pleistocene faunal assemblage in all of Africa.



Figure 1.1. Location of Olduvai Gorge and other important East African Plio-Pleistocene localities.

Given the extraordinary size and preservation of the FLK 22 assemblage in addition to abundant evidence for hominid involvement with carcasses, it is not surprising that much debate has revolved around this assemblage in particular (e.g., Binford, 1988; Blumenschine, 1995; Bunn, 2001; Bunn and Kroll, 1986, 1988; Capaldo, 1997; Domínguez-Rodrigo, 1997, 1999a; Domínguez-Rodrigo and Barba, 2006; Selvaggio, 1998). Although important zooarchaeological data have been published from FxJj 50 (Bunn et al., 1980, 1997; Domínguez-Rodrigo, 2002) and other occurrences at Koobi Fora,

Kenya (Bunn, 1994, 1997), the ST Site Complex at Peninj, Tanzania (Domínguez-Rodrigo et al., 2002), BK in Bed II of Olduvai Gorge (Monahan, 1996a, b; see also this study) and, most recently, Swartkrans Member 3, South Africa (Pickering et al., 2004c), the impact of these assemblages on models of early hominid carnivory is relatively minor compared to FLK 22 (see, for example, the recent syntheses in Domínguez-Rodrigo [2002]; Domínguez-Rodrigo and Pickering [2003]; Plummer [2004]; Pickering and Domínguez-Rodrigo [2007]).

Interestingly, and despite their generally excellent preservation, low-energy depositional context and traditional prominence in discussions of early hominid behavior (e.g., Binford, 1981; Blumenschine, 1991; Bunn, 1986; Leakey, 1971; Potts, 1988; Potts and Shipman, 1981; Rose and Marshall, 1996; Shipman, 1986a, b), reference to especially the Bed I assemblages from Olduvai (except, of course, FLK 22) as reflections of early hominid diet and subsistence has become increasingly cautious (e.g., Marean et al., 1992; Plummer, 2004). This is due largely to the fact that previous interpretations are based on outdated or underdeveloped taphonomic frameworks that simply cannot address many of the issues raised by recent methodological and theoretical developments. Refined taphonomic techniques can be brought to bear on a number of issues, including: (1) the influence of carnivore ravaging on inferences of skeletal part transport (Capaldo, 1998; Marean et al., 1992); (2) measures of on-site competition for carcass resources (Blumenschine and Marean, 1993; Blumenschine et al., 1994); (3) more secure discrimination of hominid versus carnivore bone breakage (e.g., Bunn, 1989; Capaldo and Blumenschine, 1994; Pickering et al., 2005); (4) identifying the carnivore taxon responsible for carcass modification (Andrews, 1995; Andrews and Armour-Chelu, 1998; Andrews and Fernández-Jalvo, 1997; Domínguez-Rodrigo and Piqueras, 2003; Haynes, 1983; Monahan, 1999; Pickering et al., 2004b; Pobiner and Blumenschine, 2003; Selvaggio and Wilder, 2001); and (5) inferring the timing of hominid and carnivore access to carcasses through the frequency and anatomical location of cutmarks, percussion marks and carnivore tooth marks (Blumenschine, 1988; Blumenschine and Selvaggio, 1991; Bunn, 2001; Capaldo, 1997; Domínguez-Rodrigo, 1997; Domínguez-Rodrigo et al., in press b; Egeland et al., 2004; Selvaggio, 1998).

Against this background, dissertation research seeks to refine our understanding of Plio-Pleistocene hominid diet and subsistence within the broader context of large carnivore guild dynamics. In service of that goal, new zooarchaeological and taphonomic data are presented from nine levels at six Olduvai sites that date to between ca. 1.9–1.2 Ma: DK (Levels 1–3), FLK North North (Level 2) and FLK North (Level 5) from Bed I and FC West, TK and BK from Bed II. In order to place the current analysis in context and to highlight the noteworthy characteristics of the Olduvai assemblages, a brief review of the most influential models of early site formation is presented (for more detailed summaries see Domínguez-Rodrigo [2002]; Plummer [2004]; Potts [1988]).

### **MODELS OF EARLY SITE FORMATION**

Based on her excavations at Olduvai Gorge, Mary Leakey (1971: 258) distinguished four types of archaeological occurrences: (1) living floors; (2) butchering or kill sites; (3) channel sites; and (4) vertically dispersed deposits. Glynn Isaac (1978: 95, 1981b; Isaac and Crader, 1981; Isaac and Harris, 1978: 77-78) developed a similar scheme for Plio-Pleistocene sites, establishing several “types” based on the presence, absence or co-occurrence of bones and stone tools. The sites that generate the most interest for paleoanthropologists are Leakey’s (1971) “living floors” or, following Isaac’s (1978) terminology, “Type C” sites. These sites are characterized by the co-occurrence of bones from several large animals with stone artifacts, often within a vertically discrete horizon. Four particularly influential models have been proposed to explain the formation of such sites in the Plio-Pleistocene.

#### ***Home Base Model***

Leakey’s (1971) interpretation of many Olduvai Bed I and II sites as early hominid campsites was clearly influenced by the prevailing “Man the Hunter” paradigm of the 1960s (Lee and DeVore, 1968). Using a mix of ethnographic, archaeological and ecological data, Isaac (1969, 1971, 1976; Isaac and Isaac, 1975) published a series of papers that expanded on this idea, which culminated in an integrated model centered on “home bases”; i.e., localities to which hominids converged each day to perform both subsistence and social activities (Isaac, 1978a, b). Faunal accumulations were

interpreted as the surplus of scavenged or hunted animals that were transported back to home bases for distribution. Delayed consumption and food-sharing were key aspects of the model, as analogies with contemporary African hunter-gatherers suggested that these behaviors triggered the development of a number of uniquely human traits, including complex language, parental provisioning, sexual division of labor and a tightly-bonded, family-based social organization (an early, non-archaeological view similar to this can be found in Zuckerman [1933]). Although subsequent critiques (e.g., Binford, 1981; see below) and continued work by Isaac and his students at Koobi Fora prompted a reformulation of the home base concept (Isaac, 1981a) and the use of the less emotionally charged term “central place” (Isaac, 1983a, b, 1984), many of the model’s original elements (i.e., early carcass access, long-distance transport and delayed consumption, extensive meat-eating and possibly food-sharing) were still considered important components of early hominid behavior (e.g., Bunn, 1981, 1982, 1986, 2001, 2007a; Bunn and Ezzo, 1993; Bunn and Kroll, 1986).

### ***Routed Foraging Model***

Initially questioning even the functional link between co-occurring fauna and stone tools, Binford (1981, 1984, 1985, 1988) proposed that Plio-Pleistocene sites represented nothing more than abandoned carnivore kills subsequently picked over by hominid scavengers for flesh scraps and marrow. The presence of what were then interpreted as heavy-duty tools at Plio-Pleistocene sites were seen by Binford (1981) as particularly well-suited for scraping dried meat from dessicated carcasses and breaking open bones. Practicing a “feed-as-you-go” strategy, hominids encountered and exploited these kills along their regular foraging routes. Carcass part transport was minimal or non-existent, as stone tools and bones accumulated over time as hominids were attracted to fixed resources at or in close proximity to death sites.

### ***Stone Cache Model***

The “home base” model was predicated on the inference that Plio-Pleistocene sites were safe havens on the landscape where social activities could be carried out. However, Potts (1982, 1984a, 1987, 1988) argued that early sites were in fact focal points on the landscape for potentially intense

competition among large carnivores. The risk produced by such competitive interactions precluded long-term site occupation by hominids and thus encouraged hurried and often incomplete carcass processing. Large accumulations of stone artifacts and bones formed through repeated carcass part transport to “stone caches”; i.e., collections of stone consciously or unconsciously established on the landscape by hominids, potentially in relation to other resources such as shade trees. Potts argued further that it would have been energetically most efficient to establish and utilize several stone caches throughout the foraging range (in contrast to a single home base). This model (slightly refocused as the “resource transport hypothesis” [Potts, 1991, 1993]) interpreted early sites solely in terms of subsistence rather than as foci for social activities. In a slight modification of this model, Schick (1987) pointed out that the density of lithic material at many Plio-Pleistocene sites greatly exceeds what would be required or useful to hominids utilizing them simply as caches. Therefore, she suggested that “concentrations of stone artifacts developed as a *by product* of habitual transport and discard behaviors centered on specific locales, rather than as a deliberate stockpile” (Schick, 1987: 799). Such “passive storage” (Schick, 1987: 799) would result in especially dense accumulations of lithics in areas frequently visited by hominids.

### ***Refuge Model***

The “refuge” model argues that as members of the large carnivore guild hominids occupied a niche based on dry season scavenging of felid kills in riparian woodlands (Blumenschine, 1986a, 1987; see also Foley, 1987: 199-210; Marean, 1989). Given that felids are flesh specialists, hominid foraging efforts would have necessarily focused on within-bone nutrients, although substantial amounts of flesh could occasionally be procured via tree-stored leopard kills (Blumenschine and Cavallo, 1989) or mass drownings (Capaldo and Peters, 1995, 1996). Hominid carcass transport decisions were conditioned by the interplay between competition levels, carcass yields and stone tool needs. High predation risk and low carcass yields would have encouraged short-distance carcass transport to safe places (“refuges”) whose repeated use over time would eventually create large stone and bone clusters (Blumenschine, 1991; Blumenschine et al., 1994). Although central place foraging

was recognized as an ecologically feasible strategy in this framework, the appreciable surplus required to encourage long distance carcass transport and extensive food-sharing was rarely, if ever, available to passively scavenging hominids (Blumenschine, 1991; Blumenschine et al., 1994).

### *Summary*

The debate over these and other models as explanations for Plio-Pleistocene site formation is voluminous and need not be reiterated. However, several key points arise from these discussions that serve to focus further examinations of the Olduvai sites considered here. First, and most importantly, many researchers are in agreement that most “Type C” occurrences do in fact represent the active accumulation of stone tools (by hominids) and carcasses (by hominids and/or carnivores) rather than derived hydraulic jumbles or death sites. For the Olduvai Bed I sites in particular the density and ecological diversity of the fossil material relative to modern landscape scatters (e.g., Behrensmeyer, 1981, 1983; Behrensmeyer and Dechant Boaz, 1980; Behrensmeyer et al., 1979; Blumenschine, 1989; Bunn et al., 1991; Domínguez-Rodrigo, 1993, 1996; Sept, 1994; Tappen, 1995) remains an especially compelling piece of evidence for this contention (Bunn, 1982; Potts, 1982, 1988). Second, regardless of the mode of access (early or late) the presence of butchery marks unequivocally signifies the processing of carcasses by hominids (Bunn, 1981; Potts and Shipman, 1981). Third, the size of animals on which butchery marks appear indicates the acquisition of carcasses significantly larger than those procured by non-human primates (e.g., Boesch and Boesch, 1989; Stanford et al., 1994; Uehara, 1997; Uehara et al., 1992; Watts and Mitani, 2002). Finally, overlap in the use of space by hominids and carnivores is attested by the occurrence of butchery and tooth marks in the same assemblages (Bunn, 1981; Potts and Shipman, 1981), and, in some cases, on the same individual specimens (Blumenschine, 1995; Bunn, 1991; Capaldo, 1997; Monahan, 1996a; Oliver, 1994; Potts, 1982; Shipman, 1983). New insights on these patterns and their implications for hominid and carnivore behavior may be gained through ecologically oriented faunal analysis conducted within a robust taphonomic framework.

## CONCEPTUAL AND ANALYTICAL APPROACH

Potts (1994) has argued that models of early site formation are often treated as competing and mutually exclusive. As other researchers have recognized (e.g., Monahan, 1996a: 94), this approach masks variability in the way hominids utilized, accumulated and modified stones and animal carcasses. Although clearly foreshadowed in earlier work that suggested variability in penecontemporaneous lithic assemblages from the same sedimentary basin reflected “a special phase of culture resulting from adaptation to individual ecological conditions” (Clark, 1959: 223; see also Clark, 1964, 1969; Howell et al., 1962; Kleindienst, 1961), recent landscape studies have borne out this assertion by documenting variable strategies of hominid land use within the same stratigraphic interval (Blumenschine and Masao, 1991; Bunn, 1994; Domínguez-Rodrigo et al., 2002; Potts et al., 1999). Especially significant for this study is Potts’s (1994: 23) call for reanalyses of old sites “to address the variability in...traces of hominid [and carnivore] land use in different spatial and temporal contexts”. Decomposing models into their critical environmental (e.g., resource distribution, competition) and behavioral (e.g., food choice, carcass transport, stone tool discard) elements provides a means of tackling this variability (Potts, 1994).

With its focus on the interaction between behavior and environment and its effects on survival, behavioral ecology provides an ideal conceptual framework for answering Potts’s challenge. Essentially, behavioral ecology strives to link behavioral patterns to the constraints and requirements of the environment in which they are performed. Behavioral variability is easily accommodated in this approach because it “recognizes that the ecological underpinnings of a behavioral strategy are themselves temporally and spatially variable, being defined by an interplay of numerous physical and biotic components of the environment” (Blumenschine et al., 1994: 197).<sup>1</sup> Meshing this approach

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<sup>1</sup> It is important to note that what makes a particular variable “environmental” or “behavioral” differs with the scale and objective of analysis (Foley, 1987: 49). For example, when examining strategies of carcass acquisition competition acts as an environmental variable affecting the availability of resources; however, the effect of habitat type of the intensity of competition transforms competition into a behavioral variable.

with the fossil record is not straightforward and the consequences of such an attempt are discussed in the following section.

### ***Behavioral ecology meets the fossil record***

A behavioral ecological approach to the fossil record must rely on environmental and behavioral variables that leave distinctive archaeological traces. The value of behavioral ecological reconstructions therefore rests on the veracity of behavioral and environmental proxies, which are themselves gleaned from the archaeological and geological record. Given this, behavioral ecological applications to the fossil record must be grounded in solid middle-range research that links observations of modern processes with their material correlates (Blumenschine et al., 1994). Most useful for this study is the host of actualistic studies, both experimental and naturalistic, that link patterns of bone acquisition, accumulation and modification to particular taphonomic actors (see Chapter 3). Attaining ecological richness without sacrificing taphonomic rigor requires that fossil applications of behavioral ecology focus on *zooarchaeologically meaningful* variables that impact hominid and carnivore behavioral strategies. Competition is adopted here as such a unifying concept. As discussed below, competition is particularly valuable because of its ecological importance, zooarchaeological visibility and taphonomic suitability.

### ***The ecology and taphonomy of competition***

Competition is widely recognized as an integral component of ecological communities and how they are structured, maintained and transformed (Cody and Diamond, 1975; Diamond and Case, 1986; Roughgarden, 1983; Tilman, 1982). Although the precise effects of interspecific competition on population densities and community structure are still debated (Chase et al., 2002; Chesson and Huntly, 1997; Gurevitch et al., 2000), field studies leave little doubt for its ubiquity across taxa and trophic levels (Connell, 1983; Grover, 1997; Gurevitch et al., 1992; Schoener, 1983a). Only two conditions are required for interspecific competition to occur (Wallace, 1987: 113-116): niche overlap and resource limitation. The importance of niche overlap suggests that competition should be most intense within a guild, which, according to Root (1967: 335), is “a group of species that exploit the

same class of environmental resources in a similar way” and thus “...overlap significantly in their niche requirements” (see also Simberloff and Dayan, 1991). Therefore, insights into hominid carcass foraging may be gained by considering it within the broader context of a diverse and probably highly competitive Plio-Pleistocene large carnivore guild (cf. Brantingham, 1998a, b; Pobiner and Blumenschine, 2003; Shipman and Walker, 1989; Stiner, 2002b; Turner, 1988, 1992; Van Valkenburgh, 2001).

Research substantiates the view that competition plays an important role in structuring the modern African large carnivore guild, with observations of high potential niche overlap (Caro and Stoner, 2003), frequent intra-guild predation (presumably linked to competitor reduction) (Palomares and Caro, 1999; Van Valkenburgh, 2001) and evidence for superior competitors depressing the population sizes of inferior competitors (lions and hyenas versus wild dogs [Creel and Creel, 1996]). In terms of resource limitation, competition for carcasses and the resources they provide is particularly relevant from a zooarchaeological standpoint. Relative to most plant foods carcasses are rare and exhibit short resource lives (Blumenschine, 1986a, b, 1987). It is important to realize, however, that competition in general and for carcasses in particular is not a stable, continuous phenomenon. In fact, “[t]he degree of competitive interaction between species will vary according to the rate of fluctuations in the environment and the degree of overlap between their requirements” (Foley, 1987: 192). This is especially true in seasonal environments (Foley, 1987; Schoener, 1983b), an observation that laid the groundwork for the refuge model of early site formation (Blumenschine, 1986b, 1987, 1991; Blumenschine et al., 1994). It is expected, therefore, that the affects of competition within the large carnivore guild on largely vegetarian hominids foraging within a seasonal savanna-mosaic environment fluctuated between intense and almost non-existent. Another factor that must be considered is predation risk. The documentation of leopard canine punctures on the SK 54 *Australopithecus robustus* calotte from Member 1 at Swartkrans (Brain, 1970) demonstrates that predation was at least an occasional concern for early hominids just as it is among

modern apes (e.g., Boesch, 1991; D'Amour et al., 2006; Tsukahara, 1993) and humans (e.g., Treves and Naughton-Treves, 1999).

Niche partitioning within guilds is an important way to reduce interspecific competition and thus promote coexistence (Schoener, 1974). Niches are multi-dimensional (Hutchinson, 1957) and can therefore be partitioned along a number of resource axes. Among the modern African large carnivore guild, for example, prey is partitioned by body size, age, and nutritional condition (Bourlière, 1963; Eloff, 1964; Kruuk, 1972; Kruuk and Turner, 1967; Mills and Biggs, 1993; Mitchell et al., 1965; Pienaar, 1969; Radloff and Du Toit, 2004; Schaller, 1972; Tilson, 1979; Van Valkenburgh, 1996; Viljoen, 1993; Wright, 1960). Habitat selectivity indicates that space is also partitioned among large carnivores. Cheetahs, for example, have been shown to select habitats of low prey density in order to reduce competitive interactions with dominant carnivores (Durant, 1998, 2000). Conversely, dominant competitors such as lions will selectively utilize habitats with high prey abundance (Spong, 2002). The way in which carnivores utilize and partition resources is based on the position of species within the guild hierarchy, which is itself determined largely by body size (Van Valkenburgh, 2001; although grouping behavior can reverse this relationship [Eaton, 1979]).

From a zooarchaeological perspective, competition is a particularly useful ecological parameter because: (1) competition varies with habitat type; (2) the intensity and context of competition provides predictions about the availability of particular carcass resources and, to some extent, where on the landscape hominids and carnivores chose to transport, consume and accumulate those resources (Blumenschine, 1986b, 1987, 1991; Blumenschine and Peters, 1998; Blumenschine et al., 1994; Domínguez-Rodrigo, 1994, 2001); and (3) taphonomic work has demonstrated that competition leaves “specific and detectable zooarchaeological signatures” (Blumenschine et al., 1994: 208). Importantly, these observations are grounded in actualistic studies of modern processes.

The intensity of competition is largely determined by carnivore-to-prey ratios and habitat type (Blumenschine et al., 1994). Open habitats tend towards high levels because visibility is good and cues to carcass location (e.g., vultures) are common (Blumenschine 1986b, 1987; Creel and Creel

1996, 1998; Domínguez-Rodrigo 2001). These relatively simple observations generate predictions for a number of factors that condition carcass utilization, including habitat use and carcass transport and processing. As noted above, weaker competitors are expected to forage in low competition habitats in order to avoid interactions with dominant competitors. In terms of carcass transport behavior, Blumenschine et al. (1994) predict that hominids encountering carcasses in low competition settings should simply process and consume them at the site of acquisition while carcasses encountered in high competition settings should be either transported whole (for small carcasses) or field butchered (for larger carcasses). Competition may also affect carcass processing behavior. As levels of competition increase, the number of carcasses available decreases; this is accompanied by a decrease in the amount and range of available carcass resources. Variations in availability will condition how hominids and carnivores may have treated carcass resources when they encountered them. For example, low carcass encounter rates should be accompanied by the utilization of lower-ranking carcass parts, the extraction of multiple carcass tissues (e.g., processing a carcass not only for meat but also for marrow and grease), and/or increased investment in the removal of one particular carcass tissue (e.g., processing a carcass not only for large muscle masses but also for small flesh scraps) (Burger et al., 2005; Egeland and Byerly, 2005).

Inferences of competitive intensity can also provide relatively fine-grained habitat reconstructions. While other paleoecological indicators offer critical information, it is often at scales too broad to infer the microhabitat and level of competition at specific sites. A taphonomic perspective allows these factors to be deduced at the same scale at which hominid and carnivore behavior is taking place (i.e., at a very specific locality). For example, faunal (Gentry and Gentry, 1978a, b; Kappelman, 1984; Kappelman et al., 1997; Leakey, 1971; Plummer and Bishop, 1994; Shipman and Harris, 1988), botanical (Bonnefille, 1984) and isotopic (Cerling and Hay, 1986; Sikes, 1994) evidence suggest a complex mosaic of habitat types within the vicinity of the FLK 22 site. However, the relatively high representation of limb bone epiphyses and compact and axial bones relative to actualistic controls (Capaldo, 1998; Marean and Spencer, 1991; Marean et al., 1992)

indicates that competition was relatively low and therefore suggests a more closed habitat directly on site (Capaldo, 1997; Fernández-Jalvo et al., 1998). Overall, competition can help document and explain variability in hominid and carnivore carcass utilization strategies. To appreciate the competitive dilemmas encountered by hominids and carnivores, we must turn from more theoretical issues to a consideration of the geological and paleontological records to reconstruct Plio-Pleistocene environments and the paleoecology of the large carnivore guild.

### **GOALS AND ORGANIZATION OF THE DISSERTATION**

The data presented in this dissertation are geared towards addressing three key issues. First, to what extent were hominids and large carnivores responsible for the formation of each faunal assemblage? While satisfying the traditional taphonomic goal of discerning what part of a faunal assemblage does not reflect hominid behavior, this exercise is also meant to address the much more interesting question of how carnivore behavior influenced hominid behavior and vice versa. Both are critical for addressing hominid-carnivore interactions. Second, what type(s) of carnivores were responsible for accumulating and modifying carcasses? The variable morphological and behavioral adaptations of carnivores posed different competitive dilemmas for hominids in addition to determining how carcasses were utilized by initial and secondary consumers. Finally, how intense was competition for carcass resources at each site? Synergizing these issues provides an opportunity to establish the effect of spatio-temporal variation in competition on hominid and carnivore foraging strategies and how often and under what circumstances hominids are acquiring carcass resources. Importantly, these issues can be explored using a number of assemblages analyzed with a standardized methodology.

Chapter 2 places the present analysis into a paleoenvironmental and geological context. It begins by providing a multi-scale consideration of African Plio-Pleistocene environments followed by a review of the geology, dating, paleoecology and paleogeography of Olduvai Gorge and a summary of previous work on each of the excavated levels. The chapter concludes with a reconstruction of the African Plio-Pleistocene large carnivore guild.

Chapter 3 describes the zooarchaeological and taphonomic methods employed in this study, including a description of how competition is measured.

Chapters 4 and 5 present zooarchaeological and taphonomic data for the Bed I and II Olduvai faunal assemblages, respectively. It is argued here that hominids played minor (DK Levels 1–3) or almost no (FLK North North [Level 2], FLK North [Level 5]) role in the formation of the Bed I faunal assemblages. The small, poorly preserved Bed II assemblages from FC West and TK are difficult to interpret, although relatively high levels of inferred competition speak to the behavioral capabilities of the hominids using and discarding stone tools at these sites. The analysis of the last Bed II assemblage, BK, presents an interesting picture of site formation. Although previously interpreted as a primarily hominid accumulation, reanalysis suggests a slightly more complicated formational history that includes significant hominid behavior.

In Chapter 6, the Bed I and II faunal data are integrated to identify variability in hominid and carnivore behavior. This variability is then interpreted against the backdrop of large carnivore guild dynamics and paleohabitat reconstructions.

Finally, Chapter 7 discusses the implications of these findings for broader issues of hominid and carnivore site use and the importance of meat in the early hominid diet.

## **CHAPTER 2**

### **PALEOENVIRONMENTAL AND GEOLOGICAL CONTEXT**

Rich behavioral ecological reconstructions require an appreciation of the array of environmental options available to hominids and carnivores. The purpose of this chapter is to summarize Plio-Pleistocene environments at multiple scales in order to isolate key variables affecting hominid and carnivore behavior. This multi-scale perspective involves not only a consideration of the physical environment at continental, regional, basin and site-based levels but also the reconstruction of large carnivore guild dynamics. These data will provide a relevant framework for interpreting the Olduvai faunal assemblages and the behavioral variability they reflect.

#### **PLIO-PLEISTOCENE ENVIRONMENTS**

In the broadest sense, the Plio-Pleistocene of Africa and elsewhere is marked by a gradual cooling and drying trend, a process that has continued throughout the Cenozoic (Denton, 1999; Zachos et al., 2001). Superimposed on this general trend was what deMenocal (2004: 8) summarizes as “a succession of wet-dry cycles with a long-term shift toward drier conditions, punctuated by step-like shifts in characteristic periodicity and amplitude”. These punctuations toward more arid and variable climatic regimes occurred at 3.0–2.6 Ma, 1.8–1.6 Ma and 1.2–0.8 Ma, which coincided with the onset and amplification of high latitude glacial cycles as reflected in records of benthic foraminifera oxygen isotope stratigraphies (Shackelton, 1995) and eolian dust deposition in oceans (deMenocal, 1995, 2004).

These large-scale environmental patterns were accompanied by profound changes in vegetation structure. The rise and expansion of grasslands and savannas in Africa beginning in the Mio-Pliocene and continuing into the Plio-Pleistocene (Cerling, 1992; Cerling et al., 1993, 1997) are especially significant. Importantly, because these C<sub>4</sub> ecosystems (which include tropical grasses and sedges and woody species that do not form continuous cover [Bender, 1971; Cerling, 1992; Smith and Epstein, 1971]) are more tolerant of arid, seasonal environments, their establishment probably signals the commencement of more-or-less modern patterns of seasonality and rainfall (Jacobs et al.,

1999). Cerling (1992: 244) documents two dramatic increases in the abundance of C<sub>4</sub> vegetation in East Africa: one at 1.7 Ma during which C<sub>4</sub> plants comprised between 60–80% of the vegetation and one at 1.2 Ma during which C<sub>4</sub> constituted about 50% of the vegetation. Nevertheless, modern levels of C<sub>4</sub> dominance do not develop in East Africa until the Middle Pleistocene (Cerling, 1992), suggesting that Plio-Pleistocene savannas were generally wetter and more closed than today. Isotopic data from other studies in the Baringo (Kingston et al., 1994) and Turkana (Cerling et al., 1988; Wynn, 2004) basins of Kenya, and at Gona, Ethiopia (Levin et al., 2004), confirm this theme while also documenting subtle variation in the timing and pattern of savanna expansion in other regions of East Africa.

Reconstructions of Plio-Pleistocene lake levels, which are related to precipitation/evaporation cycles, indicate relatively humid periods in East Africa at 2.7–2.5 Ma, 1.9–1.7 Ma and 1.1–0.9 Ma (Deino et al., 2006; Trauth et al., 2005). At first glance, these results seem to conflict with those cited above, which indicate step-wise shifts towards aridification during these same periods. However, this seeming contradiction demonstrates that regional and continental climatic regimes are often decoupled; that is, the regional-scale lake level data, although coinciding with punctuations towards more variable climates, were not strictly tied to broader patterns of aridification at continental scales (cf. Trauth et al., 2005: 2053). This decoupling appears to have been related to tectonic uplift in the East African Rift Valley and concomitant changes in regional-scale topography, rainshadow effects and water availability (e.g., Selpulchre et al., 2006; Trauth et al., 2005).

Patterns of faunal turnover also indicate substantial environmental changes took place during the Plio-Pleistocene. For example, in the well-studied Omo-Turkana Basin, high turnover rates occurred among bovids, equids, suids and primates at 3.4–3.2 Ma, 2.8–2.6 Ma, 2.4–2.2 Ma and especially 2.0–1.8 Ma (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe et al., 2002). These turnover patterns indicate the gradual expansion of grasslands beginning at about 2.5 Ma and peaking after 1.8 Ma. Patterns of change in the Omo-Turkana Basin are also characterized by rapid fluctuations in faunal composition between 2.5 Ma and 1.8 Ma, suggesting increased climatic

variability during this period. Community analyses in the Turkana Basin also show a shift from semi-evergreen rainforest to deciduous woodland and savanna after 2.5 Ma (Fernández and Vrba, 2006). The faunal break documented at Olduvai Gorge at about 1.7 Ma (Gentry and Gentry, 1978b) and broadly contemporaneous faunal turnover between 1.7–1.4 Ma at Konso, Ethiopia (Suwa et al., 2003), both towards open-adapted taxa, are consistent with the Omo-Turkana data. Though less clear given the unique taphonomic problems posed by dolomitic cave systems, data from South Africa also show a general shift toward savanna faunas (Reed, 1997; Vrba, 1995).

Continental- and regional-scale analyses therefore suggest three punctuated, step-wise shifts in aridification in Africa during the Plio-Pleistocene. This long-term change heralded in the expansion of C<sub>4</sub>-dominated savannas, although at slightly different rates in different regions. Faunal evidence supports the inference for savanna expansion, but again patterns of turnover are complex and variability is apparent in different areas. Importantly, “the record does not support unidirectional shifts to permanently drier conditions (deMenocal, 2004: 18), but rather the general trend toward aridification is set against the background of increased levels of environmental variability during the Plio-Pleistocene. That is, relative to earlier periods, Plio-Pleistocene climates displayed both marked differences and rapid transitions between wet and dry periods. Against this broader context, we now turn to basin- and site-specific environmental conditions at Olduvai Gorge.

## **GEOLOGY AND PALEOECOLOGY OF OLDUVAI GORGE**

Olduvai Gorge is situated on the western margin of the East African Rift Valley and rests on the eastern edge of the Serengeti Plain in northern Tanzania (Figure 2.1). The paleontological and archaeological importance of Olduvai Gorge had long been recognized (summarized in Leakey, 1951); however, it was not until after the discovery of OH 5 (Leakey, 1959) that large-scale excavations began throughout the gorge. Under the direction of Mary Leakey (1967, 1971, 1975) a number of localities containing both stone tools and faunal material were uncovered. The large and generally well-preserved faunas from Olduvai figured prominently in the ensuing three decades of debate that revolved around Leakey’s provocative descriptions of early hominid behavior. What

follows is a consideration of the geological, chronological and paleoecological context of the gorge and the each of the excavated levels.

### ***Geology and dating***

Our current understanding of the geology of Olduvai Gorge is due almost solely to the work of Richard Hay (1963, 1967a, b, 1973), which culminated in his seminal monographic treatment (Hay, 1976). The Olduvai Basin itself formed through the uplift of volcanic highlands to the east and south about 2.0 Ma. Eventually, downcutting stream activity over the past 200 thousand years (Ka) formed the modern gorge, which splits into two fingers (the main and side gorges). The

Olduvai Basin is underlain by metamorphic basement rocks, some of which still outcrop today as inselbergs including Naibor Soit and Kelogi, both of which served as important sources of lithic raw material for hominids. Hay (1976) recognizes seven geological formations within the gorge, which are referred to, from oldest to youngest, as Beds I, II, III, IV and the Masek, Ndotu and Naisiusiu Beds. The sediments overlying Beds I and II, which date to between 1.3–1.2 Ma and 40–60 Ka (Hay, 1976, 1990; Leakey and Hay, 1982; Manega, 1993; Skinner et al., 2003), are not considered further here.

Bed I is comprised of lava flows overlain by lake, lake-margin, alluvial fan and alluvial plain deposits. The chronostratigraphy of Bed I is well-known and is based on potassium-argon ( $^{40}\text{K}-^{40}\text{Ar}$ ) and argon-argon ( $^{40}\text{Ar}-^{39}\text{Ar}$ ) dates from a number of lavas and marker tuffs (Figure 2.2) (Blumenshine et al., 2003; Manega, 1993; Walter et al., 1991, 1992). The first Bed I marker tuff,

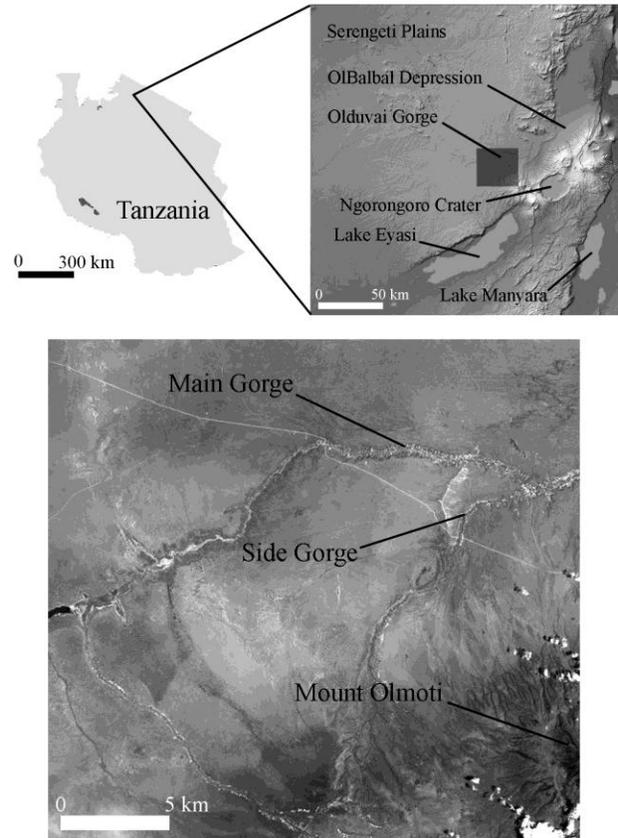


Figure 2.1. Location of Olduvai Gorge and other significant landforms. Satellite images from [http://en.wikipedia.org/wiki/Olduvai\\_Gorge](http://en.wikipedia.org/wiki/Olduvai_Gorge).

Tuff IA, overlays the basal lavas and dates to 1.99 Ma. Capping Tuff IA are the Bed I lavas, which are dated to 1.87 Ma. The Bed I lavas and the sedimentary rocks that underlie them were originally referred to by Hay (1967b) as the Basalt and Lower Members, respectively, of Bed I. Although Hay (1976) later abandoned this classification, it is significant that the sediments below the “Basalt Member” are devoid of stone tools and fossils. Above the Bed I lavas are a series of well-dated marker tuffs. The first of these marker tuffs, Tuff IB, overlies the oldest archaeological occurrences in the gorge and is dated to 1.85 Ma while the last, Tuff IF, marks the boundary between Beds I and II and dates to 1.75 Ma. Therefore, this part of Bed I spans approximately 100 Ka.

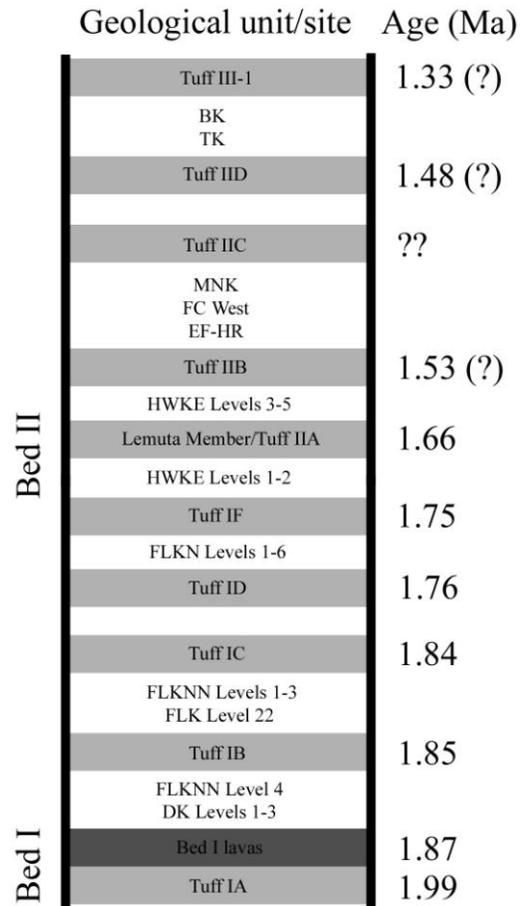


Figure 2.2. Simplified composite stratigraphic sequence for Beds I and II.

Although Bed II is generally characterized by higher-energy fluvio-lacustrine deposits, three separate units can be distinguished in the sequence. Lower Bed II, which contains significant lake, lake-margin and alluvial fan deposits, is quite similar to Bed I in terms of sedimentology and paleogeography (see below). The Lemuta Member is a widespread sequence of eolian tuffs that interfinger with lake-margin sediments. This member represents a period of significant aridification and lake regression. Basin-wide faulting following the deposition of the Lemuta Member is marked by a disconformity that denotes the boundary between the Lemuta Member and the deposits of Middle and Upper Bed II, which are largely of fluvio-lacustrine origin. The chronostratigraphy of Bed II is less straightforward due to the reworked nature of many of the marker tuffs. However, radiometric dates from the bottom (Tuff IF) and top (Tuff III-1) of Bed II suggest an age range of about 1.75–1.33 Ma (Walter et al., 1991, 1992; Manega, 1993).

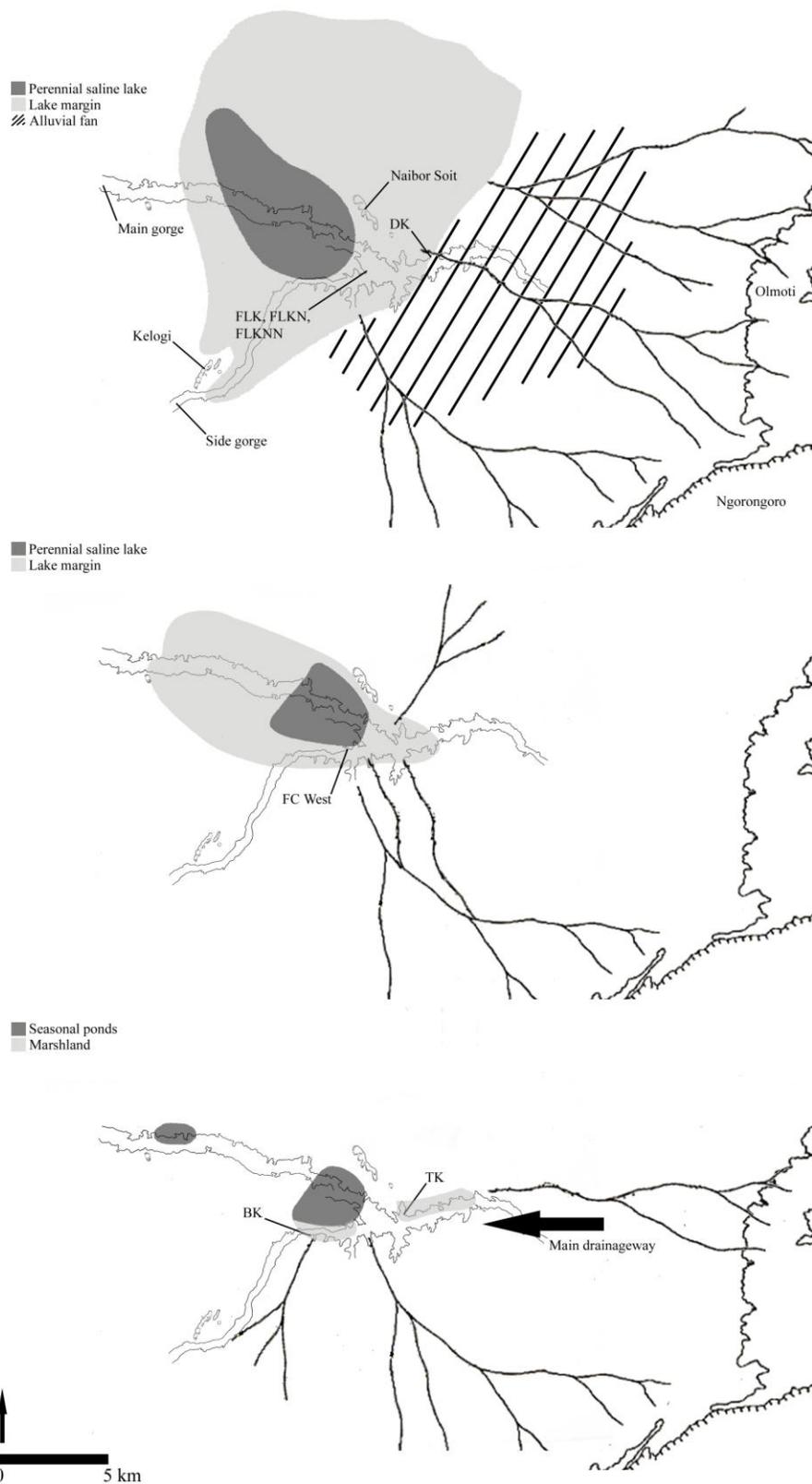


Figure 2.3. Paleogeographic reconstructions of the paleo-Olduvai Basin during Bed I (1.75 Ma; top), middle Bed II (1.50 Ma; middle) and upper Bed II (1.30 Ma; top) times based on Hay (1976). Base map from Hay (1976: Figure 18) and Peters and Blumenschine (1995: Figure 4).

## *Paleoecology*

Paleogeographic reconstructions indicate that during Bed I and lower Bed II times what is now Olduvai Gorge was a basin dominated by a saline and alkaline paleolake of fluctuating size (Hay, 1976; Hay and Kyser, 2001; Peters and Blumenschine, 1995). An alluvial fan and plain were situated on the eastern margin of the basin, a result of intermittent streams draining the volcanic highlands to the south and east of the lake. A majority of the Bed I archaeological occurrences, and all of those considered in this study, occur in Hay's (1976) Eastern Lake Margin lithofacies. This is likely linked to the presence of fresh water along the eastern margin of the basin (Deocampo et al., 2002; Hay, 1976; Peters and Blumenschine, 1995). The lake expanded and contracted several times during middle Bed II. During upper Bed II times (after about 1.3 Ma) the perennial lake disappeared and was replaced by small ponds and marshlands that developed along a large east-west drainage. Overall, archaeological sites are found in a wider variety of settings in Bed II, including both the eastern and western lake margin and near stream channels. Interestingly, and in contrast to Bed I, some middle Bed II sites are also situated well inland of the lake. Figure 2.3 shows the paleogeographic evolution of the Olduvai Basin during Bed I and middle and upper Bed II times in addition to the location of each of the sites.

Like the rest of East Africa, Olduvai Gorge trended towards drier and more open habitats throughout the Pleistocene. Sikes (1994, 1999) documents a shift towards  $C_4$  ecosystems over time at Olduvai, specifically from more closed wooded grasslands (Bed I and lower Bed II) to more open grassy woodlands (middle and upper Bed II) and, eventually, to open grasslands (post-Bed II). Cerling and Hay's (1986) isotopic data suggest a mean annual rainfall of 800 mm and average temperatures of 16°C during Bed I and II times, which is wetter and cooler than the Olduvai Basin is today (mean annual rainfall = 566 mm; average temperature = 22°C). Five major environmental episodes can be distinguished during Bed I and II times. The first episode occurred before the deposition of Tuff ID about 1.76 Ma. Lake levels were high early in this period and fluctuated thereafter (Hay and Kyser, 2001). This was accompanied by the presence of urocyclid slugs

(Verdcourt, 1963) and closed habitat rodents (Fernández-Jalvo et al., 1998; Jaeger, 1976), which indicate that densely vegetated and humid habitats were common (Kappelman, 1986). The bovid data are more equivocal, especially at DK where open habitat alcelaphines and antilopines are quite common; overall, however, closed and mixed habitat bovids are more common below Tuff ID (Gentry and Gentry, 1978a, b; Kappelman, 1984; Kappelman et al., 1997; Plummer and Bishop, 1994; Potts, 1988; Shipman and Harris, 1988). Isotopic data from FLK 22 suggest a riparian or grassy woodland setting during this period (Sikes, 1994). The second environmental episode occurred between the deposition of Tuffs ID and IF (1.76–1.75 Ma). The climate became very arid and, based on pollen evidence, rainfall may have been as low as 350 mm/year (Bonnefille, 1984). The lake level dropped during this period and open habitat rodents and bovids became prevalent. During lower Bed II (1.75–1.70 Ma) a return to moister conditions is indicated as the lake margin appears to have supported relatively closed habitats like riparian and grassy woodlands (Sikes, 1994). The lake expanded again during this interval as well. As discussed above, the Lemuta Member of Bed II represents a hyper-arid period at about 1.7 Ma. Isotopic data indicate a spike in C<sub>4</sub> vegetation at this time in addition to increased temperature and/or decreased rainfall (Cerling and Hay, 1986). The final environmental episode (after 1.7 Ma) was characterized by another spike in C<sub>4</sub> expansion at about 1.5 Ma (Cerling and Hay, 1986) and increasing aridity. The perennial lake also disappeared by about 1.3 Ma.

Bed I and Bed II environments at Olduvai are therefore characterized by long-term aridification. However, at any one time the savanna-mosaic ecosystem of the Plio-Pleistocene Olduvai Basin supported a wide variety of microhabitats including open grassland, marshland and riparian woodland (Peters and Blumenschine, 1995). The next section of this chapter therefore provides the site-specific geology and paleohabitat of each of the excavated levels in addition to summaries of previous work.

## THE STUDY SITES

All of the faunal assemblages studied here are housed in the Department of Paleontology at the National Museums of Kenya in Nairobi and were studied over a period of four months during 2005 and 2006. Each locality within the gorge is named after the individual who first noted its paleontological and/or archaeological significance followed by the Swahili word for gully, which is “korongo” (e.g., DK = Douglas Korongo).

### *Site DK Levels 1–3*

DK is located in lower Bed I and is among the oldest of the archaeological localities within the gorge. It lies above the Bed I lavas and is overlain by Tuff IB, which provides a date for the deposits of 1.85 Ma. Leakey (1971) distinguished three levels within the DK complex, Levels 1–3 from youngest to oldest, each varying in thickness between about one and two and a half feet (30–80 cm). A majority of the Level 3 material lay atop an eroded 9 cm-thick paleosol. The site occurs within Hay’s (1976) Eastern Lake-Margin lithofacies near the intermittent, northwest flowing streams that drained the highlands to the east. The DK deposits consist mainly of claystone and tuffs interspersed with volcanic conglomerates (Hay, 1976). The paleolake was at its greatest extent during the deposition of the DK materials (Hay and Kyser, 2001) and a number of paleoecological indicators, including crocodile remains (Leakey, 1971), urocyclid slugs (Verdcourt, 1963), aquatic and semi-aquatic turtles (Auffenberg, 1981) and papyrus rhizomes and flamingo remains (Hay, 1976) suggest the presence of permanent shallow water and marshland nearby. The presence of reduncine bovids supports this interpretation, although open-adapted alcelaphines and antilopines are prevalent as well (Gentry and Gentry, 1978a, b). More recent taxonomic (Kappelman, 1984; Potts, 1982, 1988; Shipman and Harris, 1988) and ecomorphological (Kappelman et al., 1997; Plummer and Bishop, 1994) studies of the bovids suggest that the DK lake margin environment was mixed but contained a significant grassland component.

DK is perhaps most well-known for the stone circle uncovered at the base of Level 3. Leakey (1971: 24) noted the similarity of this feature to living structure supports among traditional African

societies. The addition of co-occurring stone tools and faunal material to a purported living structure led Leakey to interpret DK Level 3 as the oldest of the Bed I living floors. Binford's (1981) initial analysis of Leakey's (1971) published data classified the DK faunas as carnivore kill and/or den assemblages that were subsequently scavenged by hominids. However, later hands-on taphonomic analyses of the DK Level 2 and 3 assemblages by Potts (1982, 1983, 1984a, b, 1986, 1988; see also Bunn, 1986) attributed the faunas largely to hominid behavior. Drawing extensively upon then current taphonomic data, Potts argued that DK reflects repeated episodes of carcass part transport, perhaps over several years. For Potts (e.g., 1988: 231) the presence of meat-bearing bones and cutmarks at some Olduvai Bed I sites, including DK (Potts and Shipman, 1981; Shipman, 1983, 1986a, b), clearly indicated at least occasional early access to carcasses, although systematic butchery and its inferred corollaries (i.e., food-sharing and other "home base" behaviors) were not necessarily implied. The lithic assemblage at DK is Oldowan in character and comprises 1198 pieces (Leakey, 1971). Lavas make up a greater proportion of lithic raw material at DK than at any other Bed I or II site. There are also a significant number of flakes and flake fragments among the lithic assemblage (Leakey, 1971; Potts, 1988).

#### ***Site FLK North North Level 2***

FLK North North Level 2 (FLKNN 2) is located in middle Bed I between Tuffs IB and IC, stratigraphically just below FLK Level 22 (Leakey, 1971). FLKNN 2 is also found in the Eastern Lake-Margin. The lake appears to have regressed slightly by this time (Hay and Kyser, 2001), placing the site perhaps a kilometer east of the lake shore (Hay, 1976). The sedimentology appears broadly similar to that of DK (clays and a tuff), although with a lack of conglomerates. Several lines of evidence suggest an extremely closed environment at FLKNN, including Level 2. The abundance of reduncines indicates a closed, wet habitat (Bunn, 1982; Gentry and Gentry, 1978a, b; Kappelman, 1984; Potts, 1982, 1988; Shipman and Harris, 1988) and ecomorphological studies also show a significant presence of closed-vegetation species (Plummer and Bishop, 1994). Closed and wet habitat murid rodents are common at FLKNN (Fernández-Jalvo et al., 1998; Jaeger, 1976). Based on

their detailed taphonomic and paleoecological analysis of the microfauna, Fernández-Jalvo et al. (1998: 166) offer the following reconstruction:

The FLKNN levels can be reconstructed as having been thickly wooded, dominated by a single tree canopy as in present-day African closed woodlands. By analogy with such habitats today, there would have also been a thick under-storey of bushes and small trees and abundant ground vegetation consisting of herbs and grasses.

Leakey (1971) reported no stone tools from Level 2 and noted the presence of many complete bones and articulated skeletons. FLKNN 2 was classified as a deposit with vertically dispersed material, unlike the classic Bed I living floors such as DK Level 3, FLK Level 22, and Level 3 at the FLK North North locality where artifacts and faunal material were concentrated in discrete horizons. Both Bunn (1982) and Potts (1982, 1983, 1988) conducted taphonomic analyses of the FLKNN 2 assemblage, and the lack of associated lithic material and a dearth of hominid butchery damage, in addition to substantial evidence of carnivore damage, suggested to these researchers that the site represents a carnivore accumulation. Citing distinctive patterns of bone breakage, they independently surmised that hyenas were likely agents in bone accumulation.

#### ***Site FLK North Level 5***

FLK North Level 5 (FLKN 5) is located in upper Bed I between Tuffs ID and IF. Sediments at FLKN 5 consist mainly of clays with several thin ferruginous bands and tuffs near the base. Faunal and lithic material occurred in a horizon with a maximum thickness of about 40 cm. Lake level decreases during the deposition of the FLKN sequence (Hay and Kyser, 2001) are likely linked to significant aridification during upper Bed I times. The dominance of open-adapted bovids (Gentry and Gentry, 1978a, b; Kappelman, 1984; Plummer and Bishop, 1994; Shipman and Harris, 1988) and rodents (Jaeger, 1976), especially in the upper levels of the FLKN sequence, are consistent with this trend. Land birds also occur at FLKN 5 (Hay, 1976). However, it appears that the relatively high frequencies of open-habitat gerbils in the lower levels of FLKN, including Level 5, are an artifact of predator selection (Fernández-Jalvo et al., 1998). Therefore, FLKN 5 more likely reflects “a rich savanna habitat with woodland vegetation verging on forest” (Fernández-Jalvo et al., 1998: 168).

Although not excavated within a thin paleosol, FLKN 5 was interpreted by Leakey (1971: 61) as a living floor. Apart from Fernández-Jalvo et al.'s (1998) detailed study of the rodents, which suggests that they may have been accumulated by small canids, no systematic taphonomic data have been presented on FLKN 5 since Leakey's (1971) monograph. Therefore, and despite the fact that cutmarks and tooth marks have been identified in the large mammal subassemblage (Potts and Shipman, 1981; Shipman, 1983, 1986a, b), the roles of hominids and carnivores in site formation are poorly understood (cutmarks are purported to exist on micromammal specimens as well [Fernández-Jalvo et al., 1999]). A small Oldowan lithic assemblage of 151 pieces was recovered at FLKN 5 with quartz and lavas the dominant raw materials (Leakey, 1971).

#### ***Site FC West Occupation Floor***

FC West lies between Tuffs IIB and IIC. FC West preserved an exceptionally dense collection of artifacts along with some faunal material, and Leakey (1971) separated the site into two layers: an occupation floor occurring within a thin paleosol, on which this analysis will focus, and a reworked tuff layer overlying the occupation floor. One partially worn hominid molar (OH 19) was uncovered at FC West (Leakey, 1971). Although shrinking in size by this time, the lake had not yet disappeared and the site was located in the southeast lake-margin zone (Hay, 1976). Paleoecological data for FC West are limited; however, hippopotamuses, crocodiles, equids and alcelaphine bovids are the most common taxa in the faunal assemblage (Leakey, 1971). The hippopotamuses and crocodiles indicate the presence of standing water while the equids and alcelaphines suggest open environments.

The FC West Occupation Floor was initially interpreted as a hominid living floor (Leakey, 1971). Binford (1981) interpreted the Occupation Floor as a carnivore kill subsequently picked over by scavengers, including hominids. Although FC West has since been examined (Monahan, 1996b; personal observations), no further systematic zooarchaeological or taphonomic data have been presented. The lithic assemblage from the FC West Occupation Floor consists of 1,184 pieces and is

made predominantly of quartz and quartzite (Leakey, 1971). Several broken bifaces ally the lithic assemblage with the Developed Oldowan B.

#### ***Site TK Upper and Lower Occupation Floors***

The TK sequence is found in upper Bed II between Tuff IID and the bottom of Bed III (Tuff III-1). Leakey (1971) distinguished five levels at TK: a channel fill, an intermediate level, an upper tuff and two occupation floors. Only the two occupation floors, both of which lie on top of weathered clay paleosols, are considered in this study. By the time of TK deposition the perennial lake had disappeared to be replaced by areas with seasonal ponds (Hay, 1976). TK was located on the north side of a large east-west drainage that contained small streams and some marshland (Hay, 1976). Faunal material is scarce at TK, although equids are relatively well-represented (Leakey, 1971; Potts, 1988) and alcelaphines dominate the bovid assemblage (Gentry and Gentry, 1978a, b). Hippopotamuses are also present in both occupation floors. Overall, geological and faunal evidence suggest a marshy area with standing water within an open environmental setting.

Leakey (1971) interpreted TK as a repeatedly utilized hominid camp site with two periods of intensive use represented by the two occupation floors. Like FC West, the TK assemblages have undergone subsequent taphonomic investigation (Monahan, 1996b; personal observations), although no systematic data are available. Large lithic assemblages of 2,153 and 5,180 pieces were uncovered in the Lower and Upper Occupation Floors, respectively. The notable presence of crude bifaces led Leakey (1971) to classify the TK assemblages as Developed Oldowan B. High frequencies of flakes and flake fragments are present at TK, most of which consist of quartz.

#### ***Site BK***

BK is also located between Tuffs IID and III-1 in upper Bed II, although slightly higher in the sequence than TK. Systematic excavations at BK were conducted on numerous occasions between 1952 and 1963. This analysis focuses only on the 1963 material as the selective retention of faunal material is marked for the pre-1963 excavations. Although Leakey (1971: 199) noted the presence of both coarse sands and gravels and fine-grained silts and clays at BK, cross-bedding prevented a

reliable distinction of individual levels within the excavation trenches. Therefore, the material from all seven 1963 trenches (which vary in depth from 4–12 m but with an average depth of about 1.5 m [Leakey, 1971: 199 and Figure 93]) was lumped together. The site was located just south of small seasonal ponds and within a marshy area (Hay, 1976). A small stream also cut through the middle of the site, and most of the material derives from this channel fill. A diverse faunal assemblage reflects the variety of habitats sampled at BK. Crocodiles and hippopotamuses signal the presence of nearby water while a dominance of alcelaphines among the bovids and the presence of *Theropithecus* suggest more open environments, albeit with some local trees. It is also likely that the stream supported a thin band of riparian woodland.

Early excavations at BK unearthed what Louis Leakey (1957) argued was a catastrophic kill by hominids of *Pelorovis oldowayensis*. Others have subsequently suggested that this part of the site may in fact reflect a mass drowning event (e.g., Capaldo and Peters, 1995; Gentry, 1967). Mary Leakey's (1971) later excavations indicated that the site may represent a hominid camp that was later washed into the channel and buried as channel fill. In his detailed taphonomic analysis, Monahan (1996a, b) argued that BK represents a primarily hominid accumulation that was scavenged by carnivores after hominid abandonment. Monahan (1996a, b) argued further that the BK assemblage reflects early carcass acquisition, a focus on meat rather than marrow, the ability to acquire larger carcasses and the utilization of a variety of carcass resources. The lithic assemblage from BK, which comprises 6,801 pieces and displays one of the most diverse toolkits of any of the Bed I and II sites, is also referred by Leakey (1971) to the Developed Oldowan B. Bifaces are present at BK and flakes and flake fragments are also common (Leakey, 1971). Quartz and quartzite are the most common raw materials.

The sites considered in this study represent a variety of microhabitats and should therefore provide an appropriate sample from which to identify and explain variability in hominid and carnivore behavior. However, hominid carcass foraging behavior cannot be understood outside the

context of the large carnivore community in which they foraged. Therefore, this chapter concludes with a reconstruction of the Plio-Pleistocene large carnivore guild in East Africa.

### **THE PLIO-PLEISTOCENE LARGE CARNIVORE GUILD**

The African large (here >20kg) carnivore guild was more diverse during the Plio-Pleistocene than it is today. Besides the ancestors of extant lions, leopards, cheetahs and hyenas, a number of now-extinct carnivores, including the saber-toothed felids *Homotherium* and *Megantereon*, the false sabertooth *Dinofelis*, and the long-legged hunting hyena *Chasmaporthetes* shared the Plio-Pleistocene landscape (Lewis, 1997; Turner, 1990a, b; Werdelin and Lewis, 2005). What follows is a summary of the key adaptations of these extinct carnivores as they relate to feeding behavior, carcass modification ability and habitat preference. Discussions are limited to the Canidae, Felidae and Hyaenidae from East African deposits ranging in age from 2.0–1.0 Ma. Although it is unlikely that these carnivores were sympatric throughout their entire spatial and temporal ranges, the goal is to identify all the possible carnivores that may have affected hominid carcass foraging. It is also noteworthy that Beds I and II at Olduvai Gorge preserve the richest record of fossil carnivores between 2.0–1.0 Ma in East Africa, although important samples also come from northern Kenya (Koobi Fora and West Turkana) and northern (Hadar) and southern (Omo) Ethiopia (Turner et al., 1999; Werdelin and Lewis, 2005).

#### ***Canidae***

The evolution and behavior of the African Canidae is poorly understood relative to other large carnivores. Werdelin and Lewis (2005: 125) suggest that canid fossils are scarce because the open habitats that they likely preferred remain inadequately sampled among fossil localities. There appears to be only one evolving lineage of large Plio-Pleistocene canid, with Pliocene and early Pleistocene *Canis (Lycaon) falconeri* evolving into *C. (L.) lycaonoides*, which is found in Bed II deposits at Olduvai (Martínez-Navarro and Rook, 2003; Werdelin and Lewis, 2005). The scant Olduvai material reveals little about the behavior of this species (Lewis, 1997); however, taphonomic and ecomorphological studies of the slightly more primitive *C. falconeri* from the lower Pleistocene of Spain indicate a hypercarnivorous cursorial predator adapted to open environments (Palmqvist et

al., 1996, 1999). Inferred prey profiles also suggest pack hunting (Palmqvist et al., 1996). The Spanish material provides average adult weight estimates that are similar to modern African wild dogs (30 kg; Palmqvist et al., 1999). The Bed II material from Olduvai derives from a larger, wolf-sized individual (Turner, 1990b), which has prompted some researchers to model the Plio-Pleistocene species as possessing greater bone destructive capabilities relative to modern African wild dogs (Pobiner and Blumenschine, 2003: Figure 2).

### ***Felidae***

Felids are relatively well-represented in Plio-Pleistocene deposits in East Africa. In addition to ancestral cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*) and leopards (*P. pardus*), the latter two of which make their first definite appearance in the fossil record at Bed I Olduvai (Werdelin and Lewis, 2005), much research has been conducted on the saber-toothed felids (subfamily Machairodontinae). Four genera of sabertooths are typically recognized, *Megantereon*, *Dinofelis*, *Homotherium*, and *Metailurus* (Turner, 1990a, b; Werdelin and Lewis, 2005). The presence of *Metailurus* in East Africa is tenuous and is therefore not considered further here. Paleontologists and taphonomists have focused in particular on the role of sabertooths as carcass providers to scavengers, including hominids (e.g., Arribas and Palmqvist, 1999; Blumenschine, 1987; Marean, 1989; Pobiner and Blumenschine, 2003; Turner, 1988, 1992).

*Megantereon* was a medium-sized felid, weighing on average between 95–100 kg (Martínez-Navarro and Palmqvist, 1995; Van Valkenburg, 2001), although wide variation in weight estimates for individual specimens suggests either a high degree of sexual dimorphism (Turner, 1987) or several different species (Martínez-Navarro and Palmqvist, 1995). Ecomorphological analyses indicate *Megantereon* possessed heavily muscled forelimbs and a body plan similar to modern jaguars (Lewis, 1997). Overall, this suggests a non-cursorial ambush predator that preferred to hunt in closed vegetation such as riparian woodland (Marean, 1989; Palmqvist et al., 1996; Turner and Antón, 1998). Given its body plan, it has been argued that *Megantereon* cached carcasses in trees much as modern leopards do (Van Valkenburgh, 2001). However, its long, thin canines would have been

especially susceptible to breakage during activities involving long distance transport or vertical dragging (Lewis, 1997). Based simply on its inferred body size, *Megantereon* probably focused on medium-size prey (84–296 kg), although its robust forelimbs suggest it may have been capable of taking larger prey (Marean, 1989). *Dinofelis* remains display a similar morphology to *Megantereon*, despite having been larger in live weight (150 kg) (Lewis, 1997), again suggesting a more closed habitat ambush predator, in this case capable of taking medium and large-sized prey. Tree caching of prey has also been suggested for *Dinofelis* (Van Valkenburgh, 2001), although its large body size suggests that this behavior was not as common as among modern leopards and jaguars. The most recent analyses recognize at least three different species (*D. aronoki*, *D. piveteaui* and one unnamed) of *Dinofelis* in East Africa between 2.0–1.0 Ma (Werdelin and Lewis, 2001, 2005). *Homotherium* was similar in size to the male lion (170 kg; Van Valkenburgh, 2001) and its longer limbs and shorter claws suggest that it was cursorial and thus preferred to hunt in open habitats (Antón et al., 2005; Lewis, 1996, 1997; Turner and Antón, 1998). Its inferred ability to hunt large, social animals such as mammoths (Marean and Ehrhardt, 1995; Palmqvist et al., 1996) and its slight build relative to lions and tigers (Turner and Antón, 1997, 1998) suggest that *Homotherium* was a social predator (Antón et al., 2005). There is also evidence for denning behavior among North American *Homotherium* species (Marean and Ehrhardt, 1995; Rawn-Schatzinger, 1992).

### ***Hyaenidae***

The Plio-Pleistocene of East Africa was home to close relatives or direct ancestors of all three extant hyena species. Interestingly, there are no fossils dated between 2.0–1.0 Ma that can be definitively linked to the living brown hyena (*Parahyaena brunnea*). However, the presence of the genus at about 3.5 Ma and the appearance of the modern species just after 1.0 Ma (Werdelin, 2003; Werdelin and Lewis, 2005) strongly suggest its membership in the carnivore guild between 2.0–1.0 Ma. The striped hyena (*Hyaena hyaena*) is known from 1.9 Ma, and recent revisions recognize at least three species of the genus *Crocuta* between 2.0–1.0Ma (Lewis and Werdelin, 2000; Werdelin and Lewis, 2005). The earliest known species, *C. dietrichi*, which persisted until about 1.7 Ma,

possessed a dentition less well-adapted for bone-crushing than subsequent species of the genus. Cursoriality and the ability to carry large food items were also presumably reduced relative to the modern spotted hyena (Lewis and Werdelin, 2000). *C. ultra* makes its last appearance during Bed II times at Olduvai. Larger than the modern spotted hyena, its dentition indicates greater bone-crushing ability and, because of this, Lewis and Werdelin (2000: 35) suggest that it may have been a more dedicated scavenger. The third species, dated to about 1.0 Ma, remains unnamed and little is known of its adaptations. The long-legged hunting hyena *Chasmaporthetes nitidula* was also present during this time period in East Africa. The less derived enamel structure (Ferretti, 1999) and gracile, cat-like dental morphology (e.g., Pickering et al., 2004a: 292) of this relatively small (21 kg; Van Valkenburgh, 2001) hyenid indicates more flesh-slicing ability than other hyenids and its long limbs strongly suggest a cursorial, open habitat hunter (Berta, 1981; Turner, 1990a).

### ***Summary***

Table 2.1 and Figure 2.4 summarize, respectively, the key adaptations and relative carcass destruction capabilities of the extant and extinct large carnivores. Several inferences emanate from these data that are important for understanding hominid and carnivore behavior. First, the combination of higher carnivore population densities, which is likely in the absence of modern human culling (Van Valkenburgh, 2001: 114-115), and increased diversity suggests that competition was generally more intense during the Plio-Pleistocene than it is in modern African ecosystems. The existence of an additional large, social predator (*Homotherium*) is particularly noteworthy given the dominant role of such species (e.g., lions and spotted hyenas) in the modern guild. Second, the last appearance of *Megantereon* and *Homotherium* in East Africa at about 1.5 Ma (Werdelin and Lewis, 2005: Figure 2) indicates that middle and upper Bed II hominids may have encountered a less diverse large carnivore guild than their Bed I and lower Bed II counterparts. Third, the Olduvai hominids would not have interacted with the formidable giant hyena *Pachycrocuta*, which becomes extinct in East Africa at about 2.5 Ma (Werdelin, 1999; Werdelin and Lewis, 2005). Therefore, the large carnivore guild in East Africa probably lacked a species that could destroy the carcasses of



large-sized animals and thus remove them as edible resources. Finally, if the relative quantity of fossil finds is any indication of actual abundances (an assumption that requires rigorous taphonomic testing), sabertooths were probably conspicuous members of the large carnivore guild, outnumbering even the fossil relatives of modern cats during Bed I times (Werdelin and Lewis, 2005: 130). Several researchers have suggested that these cats were inefficient at defleshing carcasses and that their abandoned kills would provide scavengers large amounts of meat (e.g., Blumenschine, 1986a, 1987; Ewer, 1954, 1967; Marean, 1989; Turner, 1988, 1992). More recent analyses have suggested that this is unlikely, at least for *Homotherium*, which appears to have been efficient at both disarticulation and defleshing (Marean and Ehrhardt, 1995).

Given the relationship of competition intensity to habitat type, it is worthwhile to conclude with a discussion of habitat preferences among carnivores. It is tempting, for example, to associate the diversity and abundance of especially ambush predators with greater carcass availability in closed habitats (e.g., Blumenschine, 1986a, 1987; Marean, 1989). In addition to the fact that modern carnivores are notoriously non-habitat specific, Van Valkenburgh (2001: 111-112) points out that habitat preferences of extinct species are inferred indirectly through locomotor adaptations and thus hunting style (e.g., climbing versus cursorial and cursor versus ambush); that is, a carnivore interpreted as an ambush predator is not necessarily tied to closed habitats, all they require is cover of some sort. This is not to say that habitat associations for Plio-Pleistocene carnivores are meaningless: carnivores certainly hunt more successfully in particular habitats. Moreover, habitat partitioning was probably stricter among the diverse and competitive Plio-Pleistocene large carnivore guild. Nevertheless, when they were not competitively excluded from particular habitats carnivores likely ranged wherever prey were located (Van Valkenburgh, 2001).

Table 2.1. Summary of key adaptations of Plio-Pleistocene and extant large carnivores.

Taxon	Body size (kg)	Preferred prey	Habitat	Hunting method	Carcass transport
<b>Canidae</b>					
<i>Canis lycaonoides</i> *	30	Size Class 2 and 3	Open	Cursorial, group	No
<b>Felidae</b>					
<i>Panthera leo</i>	170	Size Class 3	Open	Ambush, group	No
<i>Panthera pardus</i>	45	Size Class 1 and 2	Mixed	Ambush, solitary	Yes
<i>Acinonyx jubatus</i>	60	Size Class 1 and 2	Open	Cursorial, solitary	No
<i>Megantereon sp.</i> *	100	Size Class 3	Closed	Ambush, solitary	Yes
<i>Dinofelis sp.</i> *	150	Size Class 3	Closed	Ambush, solitary	Yes
<i>Homotherium sp.</i> *	170	Size Class 3 and 4	Closed	Cursorial, group	Yes
<b>Hyenidae</b>					
<i>Parahyaena brunnea</i>	39	Varies	Open	Scavenging, solitary	Yes
<i>Hyaena hyaena</i>	32	Varies	Open	Scavenging, solitary	Yes
<i>Crocuta dietrichi</i> *	60	Varies	Open	Confrontational scavenging, group?	No
<i>Crocuta ultra</i> *	70	Varies	Open	Confrontational scavenging, group?	No
<i>Chasmaporthetes nitidula</i> *	21	Size Class 1	Open	Cursorial, group?	No

Body mass data from Bailey (1993), Lewis (1997), Mills (1990) and Van Valkenburgh (2001); see text for behavioral references. Note: Table provides modal behavior; asterisk (\*) denotes extinct taxon.

### CHAPTER 3

## ZOOARCHAEOLOGICAL AND TAPHONOMIC METHODS

Archaeological taphonomy has made great strides over the past twenty-five years towards understanding the contribution of various agents to site formation. This chapter details various analytical procedures aimed at providing refined behavioral interpretations of the Olduvai faunas. The methods outlined here are all guided by actualism, which involves “observing present-day events and their effects in order to give meaning to the prehistoric record” (Gifford, 1981: 367; see also Lyman, 1994: 46-69; Pobiner and Braun, 2005b; Simpson, 1970). Because it provides unambiguous linkages between traces (e.g., a mark on a bone), causal agencies (e.g., a stone tool slicing a bone), effectors (e.g., a sharp-edged flake) and actors (e.g., a hominid wielding a stone tool) (terminology follows Gifford-Gonzalez, 1991), actualism and its uniformitarian assumptions provide *the* critical referential framework for understanding past processes.

Marean (1995) usefully distinguishes between naturalistic and experimental actualism. Experimental studies directly control the variables influencing the observed traces, as in studies that purposely vary tool raw material to examine differences in cutmark morphology between metal and stone knives (Greenfield, 1999). Naturalistic research observes actors and the resultant traces but does not intentionally manipulate the variables. Capaldo (1998) and Selvaggio (1994a, b) conducted such studies by observing carnivores modifying carcasses in the Serengeti ecosystem and reporting on the resulting patterns of tooth-marking and bone survival. Actualism runs counter to a so-called “comparative approach” (e.g., Klein and Cruz-Uribe, 1984), which involves comparisons of fossil assemblages where the link between trace and actor is inferred. For example, Cruz-Uribe (1991) establishes distinguishing characteristics of hyena accumulations based on comparative analyses of *purported* Pleistocene brown hyena dens. Comparative approaches are useful and necessary for tracking spatio-temporal variability in assemblage composition and are in fact employed extensively in this study. However, the comparative approach must be grounded in actualism to provide reliable interpretations of that variability (Marean, 1995).

This study also takes what Potts (1988: 143-146) refers to as a “contextual approach” to site formation. A contextual approach relies on sequential inferences that depend on multiple lines of evidence and rest on the veracity of lower-level inferences. Egeland et al. (2004: 345) propose a hierarchical model that is amenable to this approach where assemblage formation is decomposed into three components: (1) carcass acquisition, which entails gaining access to a carcass regardless of the mode of that access and the nutritional condition of the carcass; (2) carcass accumulation, which involves the transport and deposition of a carcass or carcass part to a particular locale; and (3) carcass modification, where differential destruction of bones or bone portions and/or the infliction of surface modifications occurs. The recognition that assemblage formation consists of distinct, albeit interdependent, stages stresses that reconstructions of one parameter do not necessarily extend to others. For example, the presence of cutmarks and tooth marks in an assemblage, although securely linking hominids and carnivores to the modification of carcasses, does not necessarily speak to the agent of accumulation or the mode of carcass access (cf. Potts, 1988: 143). The modification component of site formation can be inferred with the most confidence, while the accumulation and acquisition phases are more remote and must be based on secure linkages gained at the modification level. The following sections outline the methods employed in this study, including zooarchaeological measures of abundance, bone surface modifications, fracture patterns, other physical attributes, mortality analysis and, finally, zooarchaeological measures of competition.

### **ZOOARCHAEOLOGICAL MEASURES OF ABUNDANCE**

This study utilizes four zooarchaeological measures of abundance: number of identified specimens (NISP), minimum number of elements (MNE), minimum animal units (MAU) and minimum number of individuals (MNI) (see Lyman [1994] for an excellent summary). More traditional paleontological approaches to zooarchaeological analysis typically summarize these measures by species (e.g., Klein and Cruz-Uribe, 1984). The work of Gentry and Gentry (1978a, b) for bovids, Harris and White (1979) and L. Bishop (personal communication) for suids and Potts

(1988 and references therein) for primates, carnivores and other ungulates guides species identifications.

Although species data are provided in this study, paleontological approaches limit analysis to only the most

Table 3.1. Body Size Classes.

Size Class	Body size (lbs)	Representative taxa
1	<50	Thompson's gazelle
2	50–250	Impala, warthog
3a	250–500	Hartebeest, Topi
3b	500–750	Wildebeest, Zebra
4	750–2000	Eland, Cape buffalo
5	2000–6000	Rhinoceros, Giraffe
6	>6000	Elephant

taxonomically diagnostic material and thus eliminate from consideration most of the (taphonomically informative) fragmentary specimens (Bunn, 1982: 22-24, 1986: 684; Bunn and Kroll, 1987: 96-97). Therefore, the bulk of this analysis is based on a maximally inclusive level of identification by body Size Class (Brain, 1974, 1981; Bunn, 1982) (Table 3.1). This permits the inclusion of a large amount of taxonomically indeterminate material that was partly ignored in previous analyses of especially DK and FLKN 5. In most analyses, data are grouped into small (Size Class 1 and 2), medium (Size Class 3a and 3b) and large (Size Class 4 and larger) carcasses. Size Class analyses are limited to the ungulate subassemblages.

### *Number of identified specimens*

NISP is the number of identified specimens per species, Size Class, skeletal element or element portion. A very small proportion of each assemblage was identifiable to species; however, most of the fragments belong to ungulates and a vast majority of these derive from bovids. The equid material is currently on loan from the National Museums of Kenya and was therefore not available for study. Identification to Size Class was determined by overall specimen size and comparisons to skeletons of known Size Class available in the Department of Osteology at the National Museums of Kenya. For those specimens not identifiable to skeletal part less precise attributions such as unidentified cranial fragment or unidentified vertebral fragment were entered into the database. Because of their diagnostic morphologies it was often possible to categorize unidentified limb bone (defined here as ungulate humeri, femora, radii, tibiae and metapodials; see Pickering et al., 2003: 1469) pieces as upper (humerus or femur), intermediate (radius or tibia) or metapodial fragments

(Barba and Domínguez-Rodrigo, 2005). Domínguez-Rodrigo (1997, 1999b) demonstrates that these are useful analytical groups for understanding hominid and carnivore utilization of carcasses (see below). Although the NISP is applied here in a more traditional context to measure taxonomic abundance, it is more often used to calculate taphonomic variables such as surface mark frequencies and fragmentation intensity (see below).

### ***Minimum number of elements***

The MNE is the “highest justifiable estimate of the minimum number of original skeletal elements required to account for all of the fragmentary specimens in an assemblage” (Bunn, 1986: 677). Although there is considerable debate over the best way to provide accurate MNE estimates, it is clear that all specimens, regardless of their completeness, must be examined and included. The selective exclusion of more fragmentary material has an especially profound effect on limb bone abundances. Building largely on Bunn’s pioneering work (1982, 1986; Bunn and Kroll, 1986, 1988; see also Morlan, 1994; Todd and Rapson, 1988; Watson, 1979) many studies stress the importance of including more-difficult-to-identify shaft fragments into limb bone MNE estimates (e.g., Bartram and Marean, 1999; Marean and Spencer, 1991; Marean, 1998). The rationale for this is simple: limb bone epiphyses are made up of low-density cancellous bone that is more susceptible to density-mediated destructive processes like carnivore ravaging (Brain, 1967, 1969; Capaldo, 1998; Marean and Spencer, 1991; Marean et al., 1992). Limb bone shafts, on the other hand, are considerably denser (Lam et al., 1998, 1999; Lyman, 1984, 1994) and therefore survive such processes at higher rates (Pickering et al., 2003). When limb bone shaft specimens are not included into MNE estimates, a “Type II” profile (Marean et al., 2004: 70) often emerges where head and foot parts falsely dominate the assemblage. Such spurious profiles are interpreted by some to reflect real patterns of hominid behavior (e.g., Klein, 1976; Stiner, 1994, 2002a).

Published MNE estimates cannot be adequately assessed unless researchers make explicit the methodology utilized in making those estimates (Marean et al., 2004). All MNE estimates in this study took into account overlapping landmarks in addition to the side, age and overall size of a

specimen (Bunn and Kroll., 1988; Hesse and Wapnish, 1985; Potts, 1988). A manual overlap approach was used to estimate skeletal element abundances, in which all specimens (including limb bone shafts) identified to a particular skeletal part were placed together on the table and visually inspected for potential overlap. Following Marean and Spencer (1991) limb bone MNEs were calculated for five separate bone portions: proximal epiphysis, proximal shaft, midshaft, distal shaft and distal epiphysis (Figure 3.1), with the highest taken as the total MNE for each limb bone. This is meant to measure the influence of limb shaft inclusion on MNE estimates and to gauge the intensity of epiphyseal destruction and thus

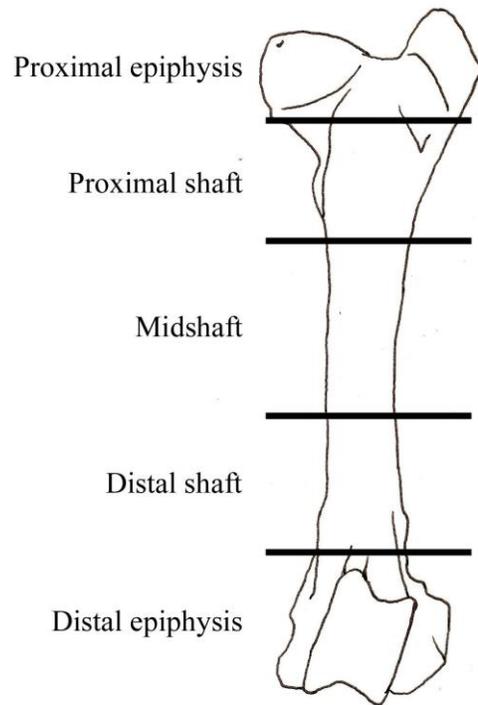


Figure 3.1. Cranial view of a femur showing limb bone portions.

carnivore ravaging. Refitting of limb shafts both within and between (in the case of DK) levels was also attempted in order to (1) potentially conjoin unidentifiable specimens into more identifiable sets (Bunn, 1986; Marean and Kim, 1998), (2) to test the vertical and horizontal integrity of the assemblages (Bunn, 1982; Kroll and Isaac, 1984) and (3) to analytically reduce the number of fragments with dry breakage.

### ***Minimum animal units***

The MAU (Binford, 1984: 50-51) is a measure developed by Binford (1978; Binford and Bertram, 1977) to specifically identify differential survivorship and transport of skeletal parts. The MAU is calculated by dividing the MNE for a particular element by the number of times that element occurs in a living animal. The MNE of paired elements such as the humerus, for example, is divided by two; for ribs, the MNE is divided by 26. MAU values are standardized (%MAU) by dividing each MAU value by the highest MAU value in the assemblage. MAU does not take into account the side or age of each element.

### ***Minimum number of individuals***

The MNI is the minimum number of individuals represented by each skeletal element. In determining MNIs the size, morphology and age of each skeletal element was taken into account. In most cases the highest MNI was attained from dental remains where subtle differences in eruption and wear could be considered. Dental MNIs were estimated by first laying out complete tooth rows (either in maxillae or mandibles) and then locating among the isolated teeth possible matches based on wear patterns. Because a vast majority of the dental remains consist of isolated teeth many of the individuals are made up only of isolated teeth. These dental individuals form the basis for mortality analysis (see below).

### ***Interpreting skeletal element frequencies***

The analysis of skeletal element frequencies has two major goals in this study. The first is to determine the extent to which element representation differs from a complete skeleton given the number of individuals present at each site. The second is to explain the documented patterning. The MNE forms the basis for the construction of skeletal element profiles and MAU and %MAU allow deviations from expected frequencies to be identified. Traditionally, differential transport is invoked to explain element representation (e.g., Brantingham, 1998b; Blumenschine, 1991; Bunn, 1982, 1983b, 1986; Perkins and Daly, 1968; Potts, 1983, 1988; Stiner, 1991a, b; Thomas and Mayer, 1983; Wheat, 1972; White, 1952, 1953a, b, 1954, 1955). Identifying differential transport is significant because studies of modern foragers and carnivores show that it can be mediated by a number of interesting situational variables including competition, presence of dependent offspring, time of day, size of carrying party, transport distance, carcass size, economic utility and even willingness to share (Bartram, 1993; Blumenschine, 1986a, b; Bunn et al., 1988; Domínguez-Rodrigo, 1994; Kruuk, 1972; Mech, 1970; O'Connell et al., 1988, 1990; Schaller, 1972).

However, bones are susceptible to a number of taphonomic processes that affect their survivorship after initial discard. Destruction due to subaerial weathering (Behrensmeier, 1978), sediment compaction (Klein and Cruz-Urbe, 1984: 69-75; Marean, 1991) and especially carnivore

ravaging (Brain, 1967, 1969, 1981; Capaldo, 1998; Marean et al., 1992; Pickering et al., 2003; Richardson, 1980) can skew the original pattern of skeletal representation almost beyond recognition. The effects of attrition are estimated by regression and Spearman's rank-order correlations between %MAU values and bulk mineral density (BMD) data for wildebeest (*Connochaetes taurinus*) from Lam et al. (1999: 351). Internal shaped-corrected data (for those elements with medullary cavities) are used when applicable. Because Lam et al. (1999) report little intertaxonomic variation in BMD between species of similar overall morphology, the wildebeest data are considered suitable analogues for all small, medium and large ungulates.

Grayson (1989) and Lyman (1984, 1985, 1993) also point out that high utility elements and element portions (i.e., those associated with the greatest amount of meat, marrow and/or grease) tend to be the least dense, which further complicates inferences of butchery and transport in relation to economic utility. One potential solution is to focus transport analyses on so-called "high survival" elements whose original abundances can be reliably estimated even in the wake of attrition (Cleghorn and Marean, 2004; Marean and Cleghorn, 2003; Marean et al., 2000: 221). The high survival set includes the cranium, mandible and the limb bones (when midshafts are included in MNE estimates), while the "low survival" set is made up of less-dense and grease-laden axial elements and small compact bones (which, although relatively dense, are often consumed completely by carnivores [Capaldo, 1998; Marean et al., 1992; Pickering 2001a, b]). As with attrition, regression and Spearman's rank-order correlations are run to track the effect of economic utility on patterns of skeletal part representation. In this case, %MAU values are plotted against several measure of utility, including a meat utility index (MUI; Metcalfe and Jones, 1988), a marrow utility index (MI; Blumenschine and Madrigal, 1993) and a combined food utility index (FUI; Metcalfe and Jones, 1988) that measures the amount of meat, marrow and grease associated with each skeletal element. Regression and correlation are run separately for high survival and low survival elements. Although several types of transport strategy are recognized in the archaeological literature (Binford, 1978; Faith and Gordon, 2007; Thomas and Mayer, 1983), only two are of real concern for understanding carcass

utilization by carnivores and early hominids. The first is an “unbiased” strategy where elements are transported in direct proportion to their utility (however measured) and the second is an “unconstrained” strategy in which all elements are transported regardless of their economic utility (i.e., complete carcass transport).

The Metcalfe and Jones (1988) data are derived from Binford’s (1978) original data on caribou while the marrow indices (Blumenschine and Madrigal, 1993) are based on African bovids. Although data on meat utility are available for African bovids, the division of carcass units is rather coarse (i.e., “neck” = all cervical vertebrae; “ribcage” = thoracic vertebrae + ribs [Blumenschine and Caro, 1986: 276]). The caribou data are considered more useful because values are provided for more precise carcass units. Despite differences in absolute values between the caribou and African bovid meat utility data, the rank of skeletal elements are identical and the magnitude of differences between them very similar.

In addition to bivariate scatterplots this study employs a quantitative measure of evenness to interpret skeletal element abundances. Faith and Gordon (2007) suggest that the use of the Shannon evenness index can be used in unison with the rather subjective visual interpretations of scatterplots. Evenness, which varies between 0.0 (lowest evenness) and 1.0 (perfectly even), is calculated using the following formula:

$$-(\sum p_i * \ln p_i) / \ln S$$

Where  $p_i$  is the proportional representation of a particular skeletal element and  $S$  is the number of element types. Proportional representation is measured using MAU. Their experimental data indicate that at sample sizes of 50 and 100 elements, an unconstrained (complete carcass) transport strategy results in evenness values between 0.961–0.996, while values below this suggest incomplete carcass transport of some sort (Faith and Gordon, 2007: 876). Faith and Gordon (2007) also demonstrate the sensitivity of inferred transport strategies to sample size. For the purposes of this study it is noteworthy that sample sizes of 50 can reliably distinguish between transport strategies using evenness data. It must be stressed that these values only inform on the *evenness* of element abundance

and not necessarily on the *pattern* of representation. For example, an assemblage dominated by low utility crania and one in which high utility femora predominate could produce similarly low evenness values. In other words, different depositional histories and/or behavioral strategies can result in comparable evenness values. Unraveling these issues requires examination of both evenness values and the element profiles from which they are calculated.

### **BONE SURFACE MODIFICATIONS**

Bone surface modifications, particularly carnivore tooth marks and cutmarks and percussion marks, are critical taphonomic data because they provide one of the few unambiguous indicators of carnivore and hominid involvement with bone assemblages. Given the potential of various abiotic processes such as sediment abrasion to mimic especially hominid-imparted bone surface damage (e.g., Andrews and Cook, 1985; Behrensmeier et al., 1986, 1989; Fiorillo, 1989; Oliver, 1989; Potts and Shipman, 1981; Shipman and Rose, 1983), this analysis utilized a “configurational approach” to surface mark identification. Mark morphology, anatomical placement and the sedimentary context from which the specimen derives were all considered important factors for secure identifications (e.g., Binford, 1981; Binford and Stone, 1986; Bunn, 1981, 1991; Bunn and Kroll, 1986; Blumenschine, 1995; Domínguez-Rodrigo et al., 2005; Fisher, 1995; Pickering and Wallis, 1997; Pickering et al., 2000, 2004c, in press a; White, 1992). In this study all mark identifications were conducted with the aid of 10X magnification and a strong oblique light source (Blumenschine et al., 1996; Bunn, 1981).

Blumenschine et al. (1996) report that experts accurately identify experimentally produced surface marks at rates of 99%, while novices with less than three hours training with experimental controls achieve identification rates of 86%. These data show that surface marks possess diagnostic morphologies and can reliably inform on prehistoric behaviors. However, in fossil assemblages of unknown derivation confident inferential associations of surface marks with particular actors is much less straightforward. At Swartkrans, for example, bone surfaces are affected by manganese formation, soil leaching and water action. This, coupled with the complex sedimentary matrix from which the fauna derives, led Pickering et al. (2004b, in press a) to reject as cutmarked several specimens that

probably did result from stone tool butchery. Moreover, Pickering et al. (2004c, in press a) required the corroborating identifications of three experts to consider a specimen as preserving a particular surface mark. Many hours of experience with the Olduvai faunas substantiates this caution in that although most of the marked specimens are easily identified, a significant number are less so. Fortunately, M. Domínguez-Rodrigo was in Nairobi conducting parallel faunal analyses of other Olduvai sites during periods of this study. Therefore, he was available for consultation during the examination of at least the Bed I assemblages and confirmed all purported hominid damage and a number of problematic specimens with suspected carnivore damage from DK, FLKNN 2 and FLKN 5. The next two sections summarize diagnostic morphological features of hominid and carnivore bone surface damage.

### *Hominid damage*

In the absence of more sophisticated hunting and cooking technology, Plio-Pleistocene hominid-imparted surface marks include cutmarks and hammerstone percussion marks. Stone tool cutmarks appear as fine, V-shaped linear striations that often possess parallel to sub-parallel microstriations on the wall of the main groove (“shoulder effects”) (Bunn, 1981; Potts and Shipman, 1981; Shipman

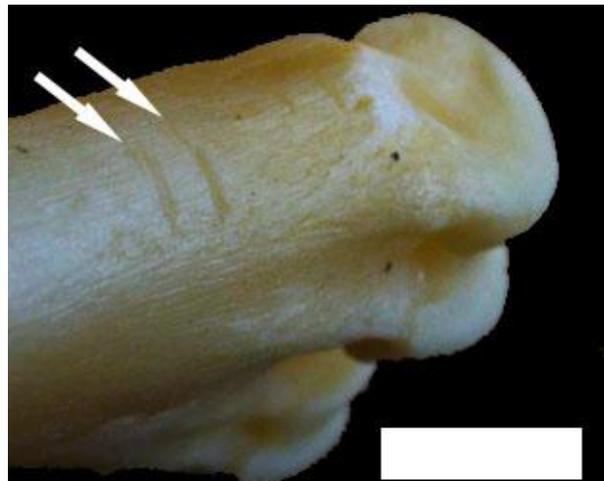


Figure 3.2. Stone tool cutmarks (arrows) on a modern sheep metacarpal. Scale bar = 1 cm.

and Rose, 1983) (Figure 3.2). Some cutmarks also preserve barbs, which are small hooks that occur at the heads and/or tails of cutmarks and result from “small, inadvertent motions of the hand either in initiating or in terminating a stroke” (Shipman and Rose, 1983: 66). Sediment abrasion is also known to create fine, linear striations on bone (Behrensmeyer et al., 1986, 1989; Fiorillo, 1989; Oliver, 1989) and, in fact, is quite common at DK in particular (see Chapter 4). However, sediment abrasion in the Olduvai faunas is readily distinguished from cutmarks for two reasons. First, the fine-grained

sedimentary matrix at most sites creates very superficial striae that contrast markedly with the deep grooves interpreted as cutmarks. This is less straightforward at other Plio-Pleistocene sites such as Swartkrans, where the cave fill, composed of karstic coluvium with large angular clasts, holds greater potential to create cutmark mimics (Pickering et al., 2004c, in press a). Second, sediment abrasion results in randomly oriented striae rather than the parallel to sub-parallel orientation of cutmarks.

Hammerstone percussion marks result from the use of unmodified cobbles (hammerstones) to breach the medullary cavities of long bones, often rested on stone anvils, for fat-rich marrow. Classic percussion marks “occur as pits, grooves or isolated patches of microstriations” (Blumenshine, 1995: 29). Microstriations are found within and/or emanate from the percussion pit (Blumenshine and Selvaggio, 1988, 1991; Turner, 1983; White, 1992). In addition to classic percussion marks (pits with associated microstriae) this analysis also recognizes “striae fields”, which “are composed of extremely shallow, subparallel scratches that usually cover relatively expansive lengths of cortical surface, between 5 and >50 mm” (Pickering and Egeland, 2006: 462, Figure 2; see also Turner, 1983; White, 1992). The distinction is potentially significant, as Pickering and Egeland (2006) find that 78% of striae fields are located on the anvil-resting surface of the bone.

### ***Carnivore damage***

Identification of carnivore damage is guided by the morphological descriptions of Binford (1981: 44-49), Blumenshine (1995: 29), Blumenshine and Marean (1993: 279-280), Blumenshine et al. (1996: 496), Fisher (1995), Haynes (1980) and Shipman (1983). Four categories of carnivore damage are recognized: furrowing, punctures, pits and scores (Binford, 1981: 44). Furrowing is caused by sustained chewing of soft epiphyseal regions and is frequently manifest as partial or total epiphyseal destruction (Figure 3.3). Crenulated



Figure 3.3. Furrowing caused by a leopard on a modern deer femur. Scale bar = 1 cm.

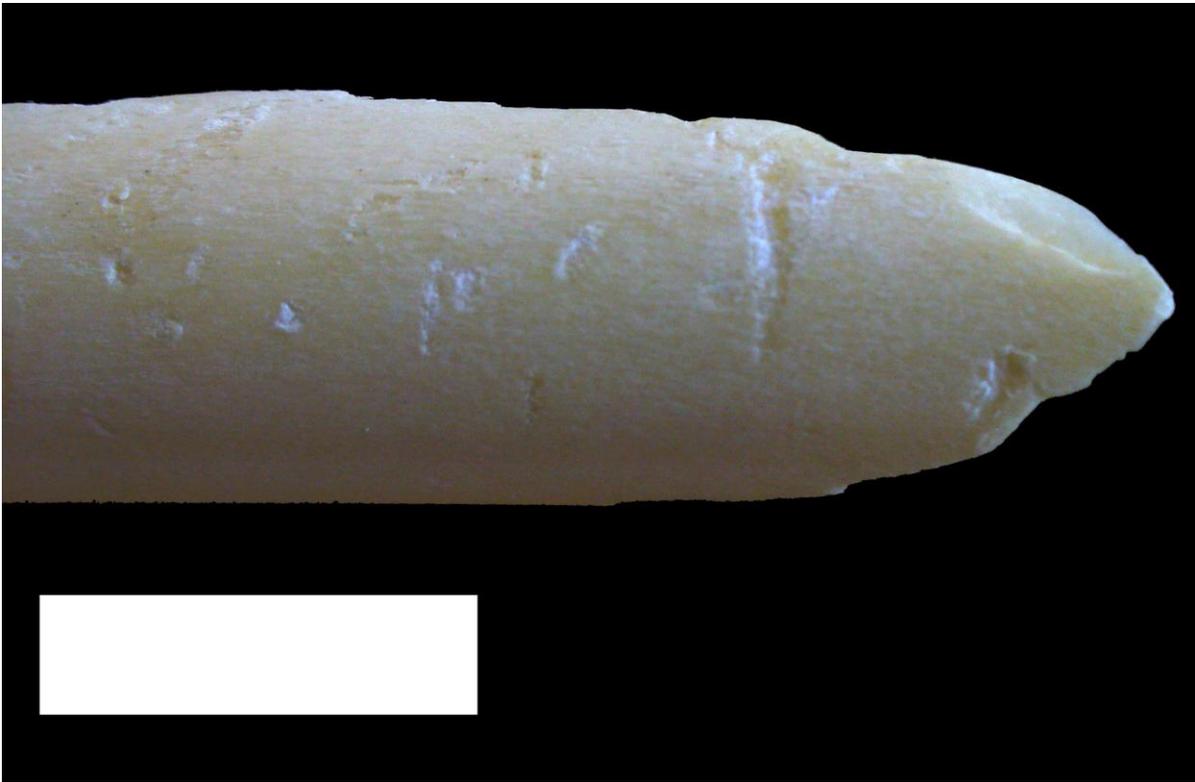


Figure 3.4. Pitting and scoring caused by a mountain lion on an ungulate limb bone shaft. Scale bar = 1 cm.

edges (following Pickering and Wallis, 1997: 1118) are the final product of epiphyseal destruction and are therefore included in this category. Tooth punctures result from the bone collapsing under the tooth and are characterized by distinct holes in the cortical surface. Tooth pits are roughly circular in plan view while tooth scores are elongate with U-shaped cross-sections (Figure 3.4). Both pits and scores commonly show internal crushing as a result of tooth-on-bone contact.

Pickering (1999: 14) found in his analysis of the Sterkfontein fauna that furrowing and crenulation were often difficult to unambiguously attribute to carnivores in the absence of more definitive marks such as punctures, pits and scores. This observation applies equally well to the Olduvai faunas examined here and therefore only specimens preserving unambiguous punctures, pits and/or scores are considered “tooth-marked”. Although this no doubt underestimates the frequency of carnivore-damaged specimens, the fact that furrowing/crenulation results in partial or total epiphyseal

destruction means that the calculation of skeletal part abundances by bone portion partly compensates for this by estimating the severity of epiphyseal loss due to carnivore ravaging (see above).

### ***Digested bone***

Bones that have been regurgitated after some time in the stomach or that have passed completely through the gastrointestinal tract of a carnivore often show characteristic thinning and rounding (Lyman, 1994: 204-205, 210-211). Each specimen is coded for presence/absence of digestion damage.

### ***Rolling damage***

Fluvial transport within a sedimentary load results in abrasion and ultimately rounding of fragment edges (Andrews, 1990: 18-19; Shipman, 1981). Each specimen is coded for presence/absence of rounding.

### ***Quantification and analysis of bone surface modifications***

This analysis employed three methods to quantify and analyze bone surface modifications (for useful summaries see Abe et al. [2002] and Lyman [1992, 1994: 303-306]). The first simply calculates the proportion of specimens in any one category that preserve surface marks (“NISP-based counts”). Bartram (1993: 209-211; see also Abe et al., 2002; Rapson, 1990) correctly points out that NISP-count data are sensitive to differential fragmentation and therefore suggests surface marks be counted by MNE (“MNE-based counts”). Therefore, both NISP-based and MNE-based counts are presented. The second method counts individual marks on a specimen. For cutmarks, each discernable striation was counted (following Egeland, 2003) while for percussion marks each pit and its accompanying microstriae were counted individually and striae fields >5 mm apart are considered distinct (following Pickering and Egeland, 2006). Each discernable tooth pit and tooth score were counted separately. Those specimens with especially intense damage where individual marks cannot be discriminated were entered into the database as preserving “multiple” marks. The final method involves drawing the location of surface marks on digital templates. This procedure was confined to those limb bone specimens that could be accurately oriented and is meant to provide detailed

information on the anatomical location of surface marks. Each specimen was oriented on an Adobe® Photoshop file with cranial, caudal, medial and lateral views of each limb bone (Figure 3.5). Photoshop allows the user to create “layers”, each of which represents the location of surface

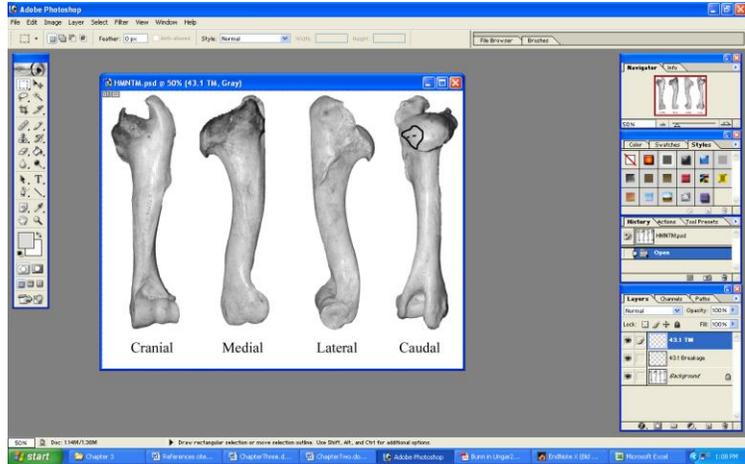


Figure 3.5. Photoshop screen shot showing anatomical location of tooth marks.

marks for a particular specimen. The advantage of this approach is that the user can choose which layers are visible and thus which combination of specimens (e.g., those from large carcasses only) is presented for interpretation.

All surface mark frequencies are presented by skeletal element (e.g., mandible, thoracic) or skeletal region (e.g., vertebrae, upper limb bones). For limb bones in particular surface marks are also tallied by bone segment and bone section. Bone segment definitions follow Blumenshine (1988: 467) where (1) epiphyseal specimens bear “all or a portion of the proximal or distal articular surface”; (2) near-epiphyseal specimens lack “any articular surfaces, but preserving cancellous tissue on the medullary surface that is indicative of proximity to an epiphysis”; and (3) midshaft specimens lack “articular surfaces and cancellous bone”. Although Blumenshine’s (1988) system is extremely successful at determining the order of carnivore access to carcasses (see below) its implementation has one potential shortcoming; namely its insensitivity to the actual location of a particular surface mark. For example, because most epiphyseal specimens as defined by Blumenshine (1988) include an attached portion of shaft, it is impossible to tell if a cutmarked epiphyseal fragment actually bears cutmarks on the articular surface or if, in fact, the cutmarks occur on the attached shaft. Therefore, high frequencies of cutmarked epiphyseal fragments may give the false impression that cutmarks cluster near the joints when most actually occur on midshaft sections. As both Bunn (2001: 209-210)

and Domínguez-Rodrigo (1997: 674) recognize, bone section analysis can help circumvent this problem. This study follows Bunn (2001) and Domínguez-Rodrigo (1997) by dividing limb bones into three major anatomical sections: (1) proximal and distal epiphysis; (2) proximal and distal shaft; and (3) midshaft (these are broadly equivalent to the limb bone MNE portions defined above). The major difference is that an epiphyseal specimen in Blumenschine's system may include one or more sections in the Bunn/Domínguez-Rodrigo system. Therefore, surface mark analysis by bone section tracks the actual location of marks, which is important in both determining the order of hominid access to carcasses and identifying the type of carnivore responsible for carcass modification (see below). As the following section will demonstrate, bone surface modifications can be interpreted in light of a growing body of actualistic work to answer questions regarding hominid and carnivore carcass utilization.

*Actualistic samples and the timing of hominid and carnivore access to carcasses*

A number of actualistic control samples now exist that provide data on the frequency and anatomical location of surface marks. The goal of these studies is to aid reconstructions of hominid butchery practices and to assess the timing of hominid and carnivore access to carcasses. Because of the relatively high survivability of limb bones, actualistic studies that focus on these elements are particularly useful. Blumenschine's (1988) pioneering work has fostered several studies that provide surface mark data on limb bone specimens. Two general scenarios are modeled by these studies. The first involves carcasses that are processed completely and exclusively by hominids or carnivores ("hominid-only" and "carnivore-only"). When carnivores (mainly hyenas) have sole access to complete limb bones they break them open to access marrow and grease, which results in tooth mark frequencies on midshaft segments of between 50–80% (Blumenschine, 1988, 1995; Capaldo, 1995, 1997). Experimental and ethnoarchaeological work indicates that hominid butchery results in cutmark and percussion mark frequencies that range between 15–40% (depending on the size of the carcass and the intensity with which carcasses are butchered [Blumenschine and Selvaggio, 1988, 1991; Bunn, 1982; Domínguez-Rodrigo, 1997, 1999b; Domínguez-Rodrigo and Barba, 2005; Lupo and

O’Connell, 2002; Pickering and Egeland, 2006; Pobiner and Braun, 2005a]). The second scenario deals with the sequential utilization of carcasses in so-called “dual-” or “multi-patterned” models (Blumenschine and Marean, 1993; Capaldo, 1995). The basic premise of dual-patterned studies is that a carcass processed by previous consumers “offers a carnivore [or hominid] a shortened menu of parts and a reduced nutrient yield compared to that available on a whole carcass” (Blumenschine and Marean, 1993: 275). In “hominid-to-carnivore” assemblages where hammerstone breakage and marrow extraction is followed by carnivore ravaging, midshaft segments are tooth-marked at rates of only 5–15% (Blumenschine, 1988, 1995; Blumenschine and Marean, 1993; Capaldo, 1995, 1997). This is because hammerstone-broken midshafts no longer encase the nutrient-rich marrow cavity and thus give scavenging carnivores little or no reason to tooth-mark them. Therefore, tooth mark frequencies on midshafts allow a clear differentiation between primary and secondary access by bone-crushing carnivores to carcasses. Domínguez-Rodrigo et al. (in press b) have recently shown that tooth mark frequencies similar to “hominid-to-carnivore” experiments can also be produced when felids rather than hyenas are the primary agent of carcass modification. This is because felids lack the bone-crushing ability of hyenas and therefore impart many fewer tooth marks on midshaft sections even when they have initial and sole access to carcasses. It is therefore important to consider the type of carnivore responsible for modifying carcasses when tooth mark frequencies are interpreted.

In terms of hominid access to carcasses, several authors argue that cutmarks on midshaft sections indicate the butchery of fully fleshed limbs and, by extension, early access to carcasses (Bunn, 2001; Bunn and Kroll, 1986; Domínguez-Rodrigo 1997, 1999b, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering and Domínguez-Rodrigo, 2007; Pickering et al., 2004c). This argument is strengthened by Domínguez-Rodrigo’s (1999a) observations of abandoned lion kills in East Africa. These data show that flesh scraps are never or rarely present on the midshaft sections of upper and intermediate limb bones, respectively. If hominids were relegated to passively scavenging picked-over carnivore kills (cf. Binford, 1981) there would be no reason to impart cutmarks on those bone sections (i.e., midshafts) that are defleshed completely by carnivores. Cutmarks on other

elements that are consumed early in the carnivore consumption sequence like pelves and ribs (Blumenschine, 1986a) are also indicative of early hominid access to carcasses.

### ***Comparisons between fossil and actualistic assemblages***

Researchers conducting actualistic research correctly stress the importance of comparability between modern datasets and fossil assemblages (Blumenschine, 1995: 28, 33-39; Capaldo, 1997: 556-557; 1998: 312-314; Marean, 1991; Selvaggio, 1994b: 194). The most important processes not operant in the above-mentioned actualistic controls that affect fossil assemblages are cortical surface degradation and diagenetic breakage. Although the Olduvai faunas are generally well-preserved, those cortical surfaces that do show degradation are most often affected by water action (e.g., rolling), curation (e.g., glue or ink) or subaerial weathering. To assess the relative fidelity with which surfaces are expected to preserve prehistoric surface modifications, a subjective score of “poor”, “moderate” or “good” was assigned to each specimen (cf. Pickering, 1999: 13; Pickering et al., 2000: 581-582; Pickering et al., in press a). In addition, breakage type was recorded for each specimen (see below). All comparisons with actualistic samples therefore included only those fossil specimens with good surface preservation and green breakage (i.e., breakage that presumably occurred during nutrient extraction). Finally, because the bone segment actualistic controls do not consider limb bone specimens <2 cm in maximum dimension, these specimens were also eliminated in comparisons, even if they preserve prehistoric surface modifications.

### ***Tooth pit dimensions and identifying carnivore types***

There is a growing body of research aimed at identifying species-specific patterns of bone modification among carnivores (Andrews, 1995; Andrews and Armour-Chelu, 1998; Andrews and Fernández-Jalvo, 1997; Domínguez-Rodrigo and Piqueras 2003; Haynes 1983; Pickering et al., 2004b; Piqueras 2002; Pobiner and Blumenschine 2003; Selvaggio 1994b; Selvaggio and Wilder 2001). In particular, Domínguez-Rodrigo and Piqueras (2003) found that the dimensions (length and breadth maxima) of tooth pits created by cheetahs, leopards, lions, spotted hyenas, large dogs and jackals on the dense cortical bone of limb bone diaphyses reliably separate carnivores into two

groups: those with less robust dentitions (i.e., cheetahs, leopards, and jackals) and those with more robust dentitions (i.e., large dogs, lions, and spotted hyenas). The length and breadth maxima of each identified tooth pit were measured to the nearest 0.01 mm with digital calipers on polyvinylsiloxane molds (see Pickering et al., 2004b: 598). The mean of two measurements is taken as the final datum for each pit. Although a more precise discrimination (i.e., by species) based on tooth pits is desirable, data on carcass size, levels of bone destruction and the anatomical placement of carnivore tooth marks can aid in more precisely identifying the carnivore or carnivores involved in the formation of the Olduvai assemblages. This information is potentially important because, as alluded to in Chapter 1, carnivores present a variety of adaptive and competitive dilemmas for each other and for hominids.

### **FRACTURE PATTERNS**

Most faunal assemblages contain many more bone specimens that are fragmented than preserve surface modifications. Given this and the dependency of surface mark frequencies on cortical preservation, patterns of bone fragmentation provide important ancillary information on the taphonomic history of a faunal assemblage.

#### ***Breakage type***

The first and most important step in fracture analysis is to distinguish breakage that occurred during the “nutritive” phase (i.e., between the death of an animal and when all nutritious tissues become inedible [Blumenschine, 1986b; Capaldo, 1995: 7, 1997: 557]) from breakage that occurred during the subaerial and diagenetic phases, referred to collectively as “non-nutritive” breakage (Marean et al., 2000: 207). Nutritive phase breakage, which is termed “green” or “fresh” breakage in this study, results from nutrient extraction by biological agents, namely carnivores and hominids, and is characterized by smooth fracture release surfaces and a predominance of oblique fracture outlines. Non-nutritive breakage, on the other hand, is the outcome of processes unrelated to nutrient extraction like trampling and sediment compaction. Such breakage is recognizable by stepped fracture outlines and ragged release surfaces (Johnson, 1985; Marean et al., 2000; Morlan, 1984; Villa and Mathieu, 1991). These are referred to here as “dry” or “diagenetic” breakage. Green and dry breakage are

distinguished from “recent” breakage, which occurs after the fossil is removed from the sedimentary matrix during excavation. Recent breaks were easily diagnosed by the bleach white coloration and chalky appearance of their fracture edges.

### *Patterns of bone breakage*

Whereas many carnivores, especially hyenas, are morphologically adapted to break open bones with their teeth (Sutcliffe, 1970), early hominids were forced to utilize hammerstones to breach the medullary cavities of limb bones. Given this difference in

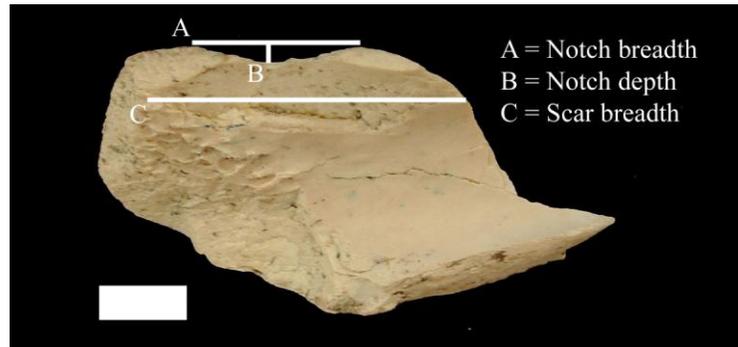


Figure 3.6. Medullary view of a complete notch showing the measurements taken in this analysis. Scale bar = 1 cm.

breakage method, it is not surprising that the mechanics of hominid- and carnivore-induced bone fracture differ, as “carnivores employ static loading, increasing pressure with opposing teeth until bone fracture is attained, while hammerstone-on-anvil breakage employs dynamic loading, which is a sudden, high-impulse impact to the bone” (Capaldo and Blumenschine, 1994: 725; see also Johnson, 1985). Building upon much previous work, studies of breakage notches and fracture planes provide important quantitative data on distinguishing dynamic (i.e., hammerstone percussion) from static (i.e., carnivore chewing) breakage. Notches appear as arcuate indentations along the otherwise rectilinear fracture outline of limb bones and are associated with negative flake scars on the medullary surface (Binford, 1981: 66, 157; Bunn, 1981: 575, 1982: 44, 1989; Brain, 1981: 141; Potts, 1988: 113-116). Capaldo and Blumenschine (1994) show quantitatively that hominid- and carnivore-created notches differ predictably in their shape; carnivore notches tend to be semi-circular in plan view while hominid notches are much broader and shallower. They provide three linear measurements (notch breadth, notch depth and scar breadth) and two derived ratios (notch breadth : notch depth and scar breadth : notch depth) that allow notch shape to be quantified (Figure 3.6). Using digital calipers,

these linear dimensions were measured to the nearest 0.01 mm on all complete notches in the Olduvai assemblages. It is also known that the platform angle of bone flakes, which are fragments of limb bone shaft that possess a platform and bulb of percussion at the impact point (Fisher, 1995), are more obtuse in hammerstone-created assemblages (Capaldo and Blumenschine, 1994). Platform angles were measured with a goniometer to the nearest degree either on the flake itself or on the negative flake scar of the notch. Finally, each notch was assigned to one of ten types (modified from Blumenschine and Capaldo, 1994: 744-745):

1. “Complete” notches have two inflection points on the cortical surface and a non-overlapping negative flake scar.
2. “Opposing Complete” notches are two, complete notches that appear on opposite sides of a fragment and result from two opposing loading points.
3. “Incomplete Type A” notches are missing one of the inflection points.
4. “Incomplete Type B” notches have a collapsed loading point that removes or reduces that negative flake scar on the medullary surface.
5. “Incomplete Type C” notches show negative flake scars that overlap with an adjacent (Incomplete Type C) notch.
6. “Incipient” notches show a partially detached flake.
7. “Bifacial” notches show double scars that emanate from the cortical and medullary surfaces.
8. “Micronotches” are very small indentations on the cortical surface that do not extend onto the medullary surface.
9. “Incomplete Type D” notches originate from the thickness of the bone and may or may not penetrate onto the medullary surface.
10. “Inverse” notches emanate from the medullary surface and produce a negative flake scar on the cortical surface.

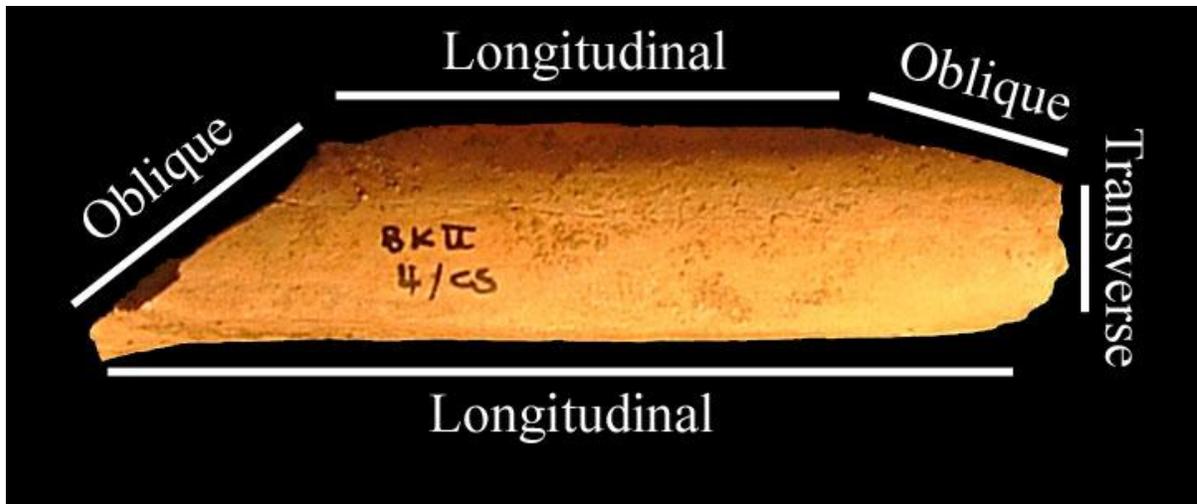


Figure 3.7. Green-broken limb bone shaft fragment from BK illustrating the three types of breakage plane.

The first seven types are termed “normal notches” and the last three types “pseudonotches” by Capaldo and Blumenschine (1994: 744-745). Data collected in the summer of 2005 by the author and M. Domínguez-Rodrigo on a spotted hyena den assemblage from the Maasai Mara Reserve in Kenya (currently housed in the Department of Osteology at the National Museums of Kenya and originally reported in Peterhans [1990]) show that carnivore assemblages are dominated by Opposing Complete, Incomplete Type C and micronotches. Opposing Complete notches result when opposite loading points are created by the opposing forces of the upper and lower dentition, while Incomplete Type C notches arise when adjacent tooth cusps create multiple, closely spaced impact points. Capaldo and Blumenschine (1994) demonstrate that Incipient notches characterize hammerstone-generated assemblages (see Chapters 4 and 5 for examples of notch types).

Alcántara García et al. (in press) have recently demonstrated that limb bone fracture angles (i.e., that “angle formed by the fracture surface and the bone cortical surface” [Villa and Mathieu, 1991: 34]) can also help distinguish hominid- from carnivore-induced breakage at the assemblage level. The dynamic impact produced by a hominid-wielded hammerstone tends to create obtuse and acute angles, while the static loading of carnivore teeth tends toward right-angle breaks. Following Alcántara García et al. (in press) and Pickering et al. (2005), each longitudinal, transverse and oblique (with reference to the specimen long axis) fracture plane (as shown in Figure 3.7) >4 cm in length

was measured at its midpoint to the nearest degree using a goniometer. Alcántara García et al. (in press) found that fracture angles on metapodials do not consistently distinguish dynamic from static loading and therefore only angles from non-metapodial fragments are provided in this study.

### *Shaft circumference*

It is well documented that limb bone breakage by both hominids and carnivores results in numerous shaft fragments and their associated articular ends, the latter of which are mostly consumed by ravaging carnivores (Blumenschine, 1988; Binford and Bertram, 1977; Binford et al., 1988; Bunn, 1989, 1991; Capaldo, 1995, 1998; Marean and Spencer, 1991; Pickering et al., 2003; Todd and Rapson, 1988). Bunn (1982: 230, 1983a: 145, 147) created a useful system for documenting the degree of limb bone fragmentation, which is based on the percentage of original diaphyseal circumference preserved. In a slight modification of Bunn's (1982, 1983a) system, shaft specimens and epiphyseal specimens with attached portions of shaft were coded for cross-sectional completeness in increments of 25%: <25%, <50% but >25%; <75% but >50%; <100% but >75% and 100% of the original circumference (referred to as "cylinders" when epiphyses are absent [Binford, 1981: 71]). In fragmented assemblages Bunn's (1982, 1983a) "Type 1" fragments (<50%) dominate relative to "Type 2" (>50%) and "Type 3" (100%) fragments. However, in hyena dens "Type 3" fragments are better represented relative to hammerstone-generated assemblages (Bunn, 1982, 1983a). Therefore, the distribution of circumference types can help distinguish hominid from carnivore fragmentation.

Marean et al. (2004: 83-85) have recently argued that circumference type distribution can also provide a simple measure of bias in a faunal assemblage. Particularly in excavations conducted prior to the mid-1970s skeletal material that was diagnostic to species was selectively retained at the expense of more fragmented material that was less identifiable. Marean et al. (2004) show that in experimental assemblages where all fragments are retained and analyzed, fragments preserving <50% of the original circumference are always the most abundant. Therefore, completely collected fossil assemblages should also be dominated by such fragments.

### ***Fragmentation ratios***

The NISP:MNE (e.g., Richardson, 1980: 111; see also Lyman, 1994: 336-338) and NISP:MNI (e.g., Bunn, 1983b: 145) ratios are used as simple measures of fragmentation. A correction procedure is required because dry and recent breakage will artificially inflate these ratios. Therefore, the number of dry- and recently-broken fragments is divided by two (because at least two separate fragments are produced when a single specimen is broken) and the resulting number added to the count of green-broken fragments. The resulting NISP is utilized in the calculation of fragmentation ratios.

## **OTHER PHYSICAL ATTRIBUTES**

### ***Specimen dimensions***

The maximum length and width of all specimens was measured to the nearest 0.01 mm with digital calipers. Specimen length distributions for the fossil samples are compared to actualistic samples (e.g., Blumenschine, 1995; Pickering and Egeland, 2006). A paucity of very small fragments may be indicative of water action and/or the lack of systematic screening during excavation, both of which introduce some level of bias.

### ***Subaerial weathering***

Each specimen was assigned a subaerial weathering stage based on the pattern and extent of surface cracking and exfoliation (Behrensmeyer, 1978). The goal of weathering analysis is to provide an estimate of the time since animal death and thus accumulation time (e.g., Potts, 1986, 1988). However, weathering begins only after soft tissue is removed, which does not necessarily occur immediately after death. Therefore, weathering is more accurately regarded as measuring the exposure time of a defleshed bone (Bunn and Kroll, 1987). The problem is that different weathering stages can co-occur on the same carcass and even on the same bone (Behrensmeyer, 1978; Todd, 1983, 1987). Lyman and Fox (1989) argue that variables such as taxon and skeletal element must be controlled for in order to ensure that a weathering profile is in fact measuring the accumulation time rather than the maximum exposure time of a particular carcass and/or skeletal element. Therefore,

weathering analysis in this study is limited to limb bone shafts and small compact bones. Confining analyses to similarly small fragments will decrease the effects of differential burial times.

### **MORTALITY ANALYSIS**

The construction of mortality profiles is deeply embedded in zooarchaeological analysis and can address a number of questions concerning population dynamics, site seasonality and the hunting and carcass processing strategies of hominid and non-hominid predators (Lyman, 1994: 118-126). Two basic, idealized mortality profiles are recognized by zooarchaeologists: “catastrophic” and “attritional” (Klein, 1982; Levine, 1983; Lyman, 1987). Catastrophic profiles show an abundance of young individuals with older ages progressively less abundant. Such a profile emerges when a population is wiped out in a single event (e.g., floods, jumps, droughts). Because catastrophic events should sample the age structure of a live herd, these are also referred to as “living” mortality profiles (e.g., Stiner, 1990). Attritional profiles are characterized by high relative frequencies of very young and very old individuals and result from normal population turnover where the weakest members of the herd die at higher rates. Variations on these general types have been proposed to account for the foraging strategies of human and non-human predators (Levin, 1983; Stiner, 1990, 1994).

Traditionally, histograms of life-stages have been the most popular method of mortality analysis because they provide a fine resolution of age classes (e.g., Frison and Reher, 1970; Klein, 1982; Todd et al., 1996; Voorhies, 1969). Following Stiner (1990, 1994) some researchers have recently turned to analyzing mortality profiles with triangular or ternary diagrams, which plot the proportional representation of three age classes: juvenile, adult and old-aged (e.g., Carlos Díez et al., 1999; Kahlke and Gaudzinski, 2005; Marean, 1997; Speth and Tchernov, 1998). Each corner of the triangular diagram represents 100% representation of young, adult or old individuals, respectively. Several zones, including the catastrophic and attritional profiles, exist between these extremes (Figure 3.8).

Because of small samples, systematic mortality analysis is only possible for a fraction of the Olduvai faunas. Those that can be analyzed are more amenable to ternary analysis for two reasons.

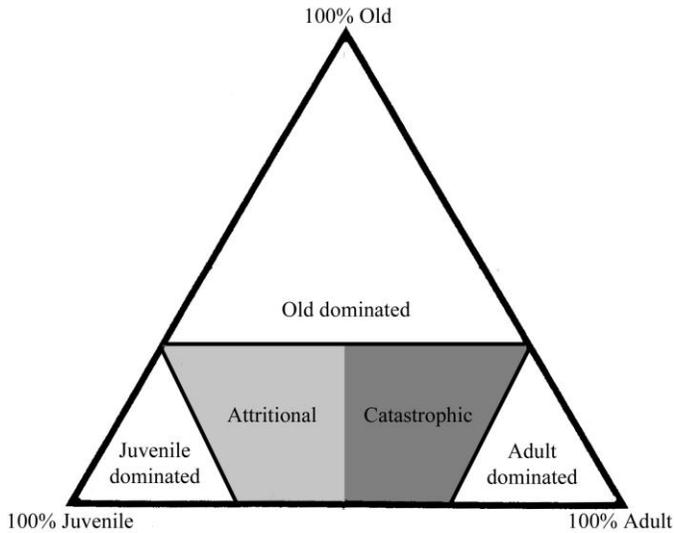


Figure 3.8. Triangular diagram showing three age axes and general profile types. Adapted from Stiner (1990: Figure 6).

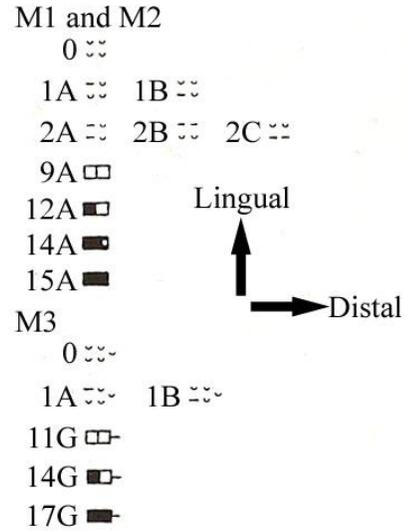


Figure 3.9. Dental wear stages and associated codes. Adapted from Payne (1987: Figure 1).

First, the Olduvai sites contain a maximum of only 29 individuals from any one bovid tribe (at BK) and 18 from a single species (at FLKN 5), which fall below the recommended sample size of 30 or 40 individuals for reliable histogram analysis (Klein and Cruz-Uribe, 1984: 59, 213; Lyman, 1987; Shipman, 1981: 157). On the other hand, a minimum of 12 individuals is considered an adequate sample for ternary analysis (Stiner, 1998: 315). Second, because ternary graphs collapse age groups into three classes they can compare data from a number of species with different life histories and accommodate studies that utilize a variety of ageing methods (e.g., archaeological versus wildlife biology data). However, as Steele and Weaver (2002: 19; see also Steele, 2005) point out, the ability of ternary diagrams to remain robust with smaller sample sizes does not eliminate the possibility of spurious patterning. Therefore, this study utilizes a “modified triangular graph” (Steele and Weaver, 2002) that allows both a satisfyingly simple visual interpretation and a statistical comparison of mortality profiles. This Apple™ Macintosh macro (provided courtesy of T.E. Steele) calculates 95% confidence intervals and plots them as a circle around each data point. This allows a more statistically realistic interpretation of the data. The majority of the assemblages were not conducive to such

systematic treatment because of small sample sizes. Therefore, much of the mortality data were subjected to less rigorous interpretation.

Regardless of the method utilized, mortality analysis requires that the boundaries between age classes are well defined and replicable. Relative ages in this study are based on tooth wear stages modified from Payne (1973, 1987). Although originally developed for sheep and goats, this method is widely applicable (e.g., cattle: Davis and Payne [1993]; pronghorn: Lubinski [2001]; bison: Todd et al. [1996]) and divides tooth wear into well-defined stages based on the pattern of exposed dentine (Figure 3.9). Each code comprises a number and a letter suffix. Unworn teeth are coded as “0” and a number is added to the code each time a cusp comes into wear and/or the exposed dentine of one cusp connects with the dentine of another cusp. For example, “a first molar with one cusp in wear...is coded as 1, one with two cusps in wear as 2, and so on; similarly, a first molar with all four cusps in wear and two dentine unions is coded 6, one with all four cusps in wear and three dentine unions is coded 7, and one in ‘full wear’, with all four cusps in wear and five dentine unions, is coded as 9” (Payne, 1987: 612). Variations within each numeric category are given a letter suffix (e.g., 4A, 4B, etc.). Only the deciduous fourth premolar (DP4) and the permanent molars (M1–M3) for each dental individual (as defined in the “MNI” subsection above) are assigned wear codes. In this study, age classes are defined as follows. Juveniles have the DP4 present and/or an M1 or M2 not in full wear (wear stage < 9A). Adults have either: (1) both the M1 and M2 in full wear (wear stage 9A and higher); (2) M1 or M2 and M3 in full wear (wear stage 11A and higher for M3s); or (3) M3 not in full wear (wear stage < 11A). Old-aged individuals are identified by the presence of either an M1 or M2 with both infundibula worn away (wear stage 15A and higher). These conventions are meant to match closely with the comparative data of Schaller (1972: 439-442, 447-449; see also Fuller and Kat, 1990: 338; Mitchell et al., 1965: 307), who provides the most comprehensive and replicable set of prey data for modern African carnivores. The youngest age class (i.e., neonates and other very young individuals) were not included in comparisons between the fossil assemblages and the modern comparative data for two reasons. First, because of their low overall density such individuals are not

encountered in the Olduvai assemblages and thus are certainly unrepresented (see below). Second, such young animals are “harvested” (i.e., simply picked up off the ground when encountered) rather than hunted, which says little about the hunting prowess of a particular predator (Bunn, 2007b). The relative representation of each age class is based on the maximum possible MNI and therefore may use a combination of mandibular and maxillary teeth. Mortality analyses focus only on the bovid subassemblages.

Marean (1997: 213-214) makes the useful distinction between “archaeological” profiles (i.e., those that are estimated from archaeofaunas) and “death” profiles, which, because they represent the actual age distributions of predatory episodes, is what zooarchaeologists ultimately seek to reconstruct. As Marean (1995, 1997; see also Klein and Cruz-Uribe, 1984: 57) notes, it is important to realize that the differential destruction of juvenile dentitions and preferential transport patterns can complicate mortality analysis by obscuring the original death profile. Actualistic research demonstrates convincingly that juvenile dentitions survive carnivore ravaging at very low rates relative to adult dentitions (Munson, 2000; Munson and Garniewicz, 2003). The addition of unfused bones to estimates of juvenile representation, which was conducted in this study, can help mitigate this potential bias (Marean, 1995, 1997). Differential transport can also bias the archaeological profile. In particular, because juveniles of any species are smaller than their adult counterparts, the assumption is that they will tend to be transported as complete carcasses. Therefore, juvenile crania (and their associated teeth) may appear in higher frequencies relative to their actual abundance in the death profile. Both of these factors are taken into account in interpretations of the Olduvai mortality data.

### **MEASURING COMPETITION**

As outlined in Chapter 1, competition plays an important role in structuring the large carnivore guild and is adopted here as a unifying concept for understanding hominid and carnivore carcass procurement and utilization strategies. Both Binford (1981) and Domínguez-Rodrigo (1994) demonstrate that interspecific competition can determine the nature and extent of carcass part

transport by carnivores. More importantly, several studies show that competition directly impacts carcass persistence and the completeness of skeletal parts (Blumenschine, 1986a, b, 1989; Blumenschine et al., 1994; Domínguez-Rodrigo, 1996, 1999b, 2001; Faith and Behrensmeyer, 2006; Haynes, 1982; Selva et al., 2003).

Complete limb bones represent untapped within-bone resources such as marrow and grease. Potts (1982, 1984a: 343-344; 1988: 353-255) has argued that a high frequency of complete limb bones at many Bed I Olduvai sites reflect hurried and incomplete carcass processing by hominids and thus high levels of on-site competition. However, in high competition settings incompletely processed carcasses would be quickly consumed by other carnivores subsequent to their abandonment by hominids. Therefore, many complete limb bones should reflect just the opposite; that is, low levels of on-site competition (cf. Capaldo, 1997: 589-590). Both Blumenschine (1989) and Domínguez-Rodrigo (1996) encountered higher frequencies of complete limb bones in low competition settings such as riparian woodlands. Faith and Behrensmeyer (2006) document a decline in the frequency of complete limb bones at Amboseli National Park (Kenya) from the 1970s to the 2000s, which they linked to the gradual increase of carnivore populations (and thus competition) during that time interval.

It is well-known that carnivores, especially hyenas, preferentially consume and thus delete less-dense, grease-laden axial bones and limb bone epiphysis (Brain, 1967, 1969, 1981; Capaldo, 1998; Marean et al., 1992; Pickering et al., 2003; Richardson, 1980). Therefore, the extent to which these bones or bone portions are deleted should reflect differing levels of competition. Blumenschine (1989), Domínguez-Rodrigo (1996) and Haynes (1982) have shown that these bones and bone portions survive at higher rates in areas of low competition. The representation of axial bones and limb bone epiphyses has also fallen dramatically with increased competition at Amboseli over the past 30 years (Faith and Behrensmeyer, 2006). Finally, levels of epiphyseal destruction are known to increase as the number of carnivores feeding on a carcass increases (Selvaggio, 1994a, b).

Based on these observations, a number of indices can be used to measure competition. For example, based on actualistic samples modified by hyenas, Blumenschine and Marean (1993: 286-287) suggest that low epiphysis-to-shaft (= near-epiphyseal + midshaft) fragment ratios accompanied by high tooth mark frequencies characterize low competition settings. This is because consumption (and thus tooth-marking) and epiphyseal destruction occur on-site. On the other hand, when competitors, including conspecifics, are present, hyenas remove skeletal parts elsewhere for undisturbed consumption (Kruuk, 1972: 125; Marean et al., 1992: 112). Although epiphyseal loss often remains high in settings of elevated competition, on-site tooth-marking decreases because carcass consumption takes place off-site. Domínguez-Rodrigo and Organista (in press) propose that the intensity of ravaging can be measured using three ratios (as measured by MNE): (1) the ratio of ribs and vertebrae to limb bones; (2) the ratio of femora to tibiae; and (3) the ratio of proximal humeri + distal radii to distal humeri + proximal radii. Each of these ratios presents as the numerator bones or bone portions that are less dense and therefore extremely susceptible to carnivore ravaging, while the denominator represents more dense bones or bone portions. No ravaging is characterized by ratios that are more or less equal the relative proportion of skeletal parts in a complete skeleton, while more intense ravaging shows decreasing ratios until complete carcass destruction occurs. Finally, Faith and Behrensmeyer (2006: 1727) argue that high correlations between density and skeletal part abundances signal lower competition because carnivores under little or no competitive pressure will chose to consume only the most greasy (and lowest density) bones and bone portions. Under conditions of intense competition carnivores will consume both low (high grease yield) *and* high (low grease yield) density bones and bone portions, resulting in low or insignificant correlations.

## CHAPTER 4 BED I ZOOARCHAEOLOGY AND TAPHONOMY

This chapter summarizes pertinent zooarchaeological and taphonomic data for the Bed I faunas. More detailed data, particularly for skeletal part frequencies, are located in the Appendices.

### GENERAL ASSEMBLAGE COMPOSITION

Table 4.1. Number of identified specimens (NISP) by taxon for the Bed I sites.

Taxon	DK 1		DK 2		DK 3		FLKNN 2		FLKN 5	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Bovidae	133	83.1	824	77.6	516	78.1	175	49.3	909	76.2
Suidae	20	12.5	116	10.9	53	8.0	160	45.1	81	6.8
Equidae	0	0.0	18	1.7	23	3.5	18	5.1	1	0.1
Proboscidean	0	0.0	20	1.9	20	3.0	0	0.0	0	0.0
Hippopotamidae	2	1.3	13	1.2	21	3.2	0	0.0	0	0.0
Giraffidae	0	0.0	8	0.8	4	0.6	0	0.0	0	0.0
Rhinocerotidae	1	0.6	4	0.4	10	1.5	0	0.0	0	0.0
Primates	0	0.0	50	4.7	5	0.8	0	0.0	0	0.0
Carnivora	4	2.5	9	0.8	9	1.4	2	0.6	202	16.9

Note: Primate NISPs from Potts (1988: Table A.1); equid counts include 17 specimens from DK 2, 22 from DK 3 and 18 from FLKNN 2 (Potts, 1988: Tables A.1 and C.1).

For DK, a total of 1,249 specimens was examined from Level 3, 1,686 from Level 2 and 217 from Level 1. As at many of the classic “Type C” sites, DK preserves a diverse fauna, including bovids, suids, equids, giraffids, proboscideans, rhinoceroses, hippopotamuses, carnivores and primates (Table 4.1). Both FLKNN 2 and FLKN 5, which comprise 426 and 1,580 total specimens, respectively, have less diverse faunas. Although bovids dominate the taxonomic composition of all three Bed I sites, suids are prevalent at FLKNN 2 and carnivores are common at FLKN 5. Between 14 and 41 large mammal individuals are represented at the Bed I sites (Table 4.2). A vast majority of the carcasses at both DK and FLKNN 2 derive from medium-sized (Size Class 3) animals while the extinct Size Class 1 bovid *Antidorcas recki* makes up almost 53% of the MNI at FLKN 5. Bovids are represented by all parts of the skeleton at the Bed I sites (Table 4.3). With the possible exception of the FLKNN 2 suids, this pattern contrasts with the more sporadic representation of the other ungulate groups, which likely reflects a different taphonomic history for the bovid subassemblages.

Table 4.2. Minimum number of large mammal individuals (MNI) represented at the Bed I sites.

Taxon	DK 1	DK 2	DK 3	FLKNN 2	FLKN 5
<b>Bovidae</b>					
<i>Parmularius altidens</i>	–	2	1	–	5
<i>Kobus sigmoidalis</i>	–	–	–	8	–
<i>Antidorcas recki</i>	–	–	–	–	18
<i>Beatragus sp.</i>	–	–	–	–	1
Size 3a Alcelaphini	2	4	11	1	–
Size 3b Alcelaphini	1	4	3	1	3
Size 1 Antilopini	1	5	4	–	–
Size 1 Neotragini	–	–	–	–	1
Size 3 Tragelaphini	3	–	4	2	–
Size 3b Tragelaphini	–	5	–	–	2
Size 3 Reduncini	–	4	3	–	–
Size 3 Hippotragini	–	2	1	2	1
Size 4 Bovini	–	1	2	–	–
<b>Proboscidean</b>					
Proboscidean indet.	–	2	–	–	–
<i>Deinotherium sp.</i>	1	–	1	–	–
Rhinocerotidae indet.	1	1	2	–	–
<b>Equidae</b>					
<i>Equus oldowayensis</i> *	–	2	2	1	–
<i>Equus burchelli</i> *	–	1	–	–	–
<b>Suidae</b>					
<i>Metridiochoerus modestus</i>	–	1	1	–	–
<i>Kolpochoerus limnetes</i>	–	2	2	3	2
<b>Hippopotamidae</b>					
<i>Hippopotamus gorgops</i>	1	1	2	–	–
<b>Giraffidae</b>					
<i>Libytherium sp.</i>	–	1	–	–	–
<i>Giraffa sp.</i>	–	1	1	–	–
<b>Carnivora</b>					
<i>Pseudocivetta ingens</i>	–	1	–	–	–
<i>Panthera pardus</i>	–	1	–	–	–
<i>Crocuta crocuta</i>	–	–	1	–	–
<i>Canis mesomelas</i>	1	–	–	–	–
<i>Galerella debilis</i> *	–	–	–	1	–
<i>Prototocyon recki</i>	–	–	–	–	1
Total	11	41	41	19	34

Note: Presence of taxa marked with an asterisk (\*) from Potts (1988: Tables A.2, A.11, C.2).

Table 4.3. Number of identified specimens (NISP) by ungulate group and skeletal element for the Bed I sites.

Element	Bovidae	Suidae	Proboscidean	Hippopotamidae	Giraffidae	Rhinocerotidae
<b>DK 1</b>						
Cranium	4	1	–	–	–	–
Teeth	45	16	–	2	–	1
Mandible	4	–	–	–	–	–
Vertebrae	7	–	–	–	–	–
Ribs	7	–	–	–	–	–
Innominate	–	–	–	–	–	–
Scapula	1	–	–	–	–	–
Humerus	–	–	–	–	–	–
Radio-ulna	5	1	–	–	–	–
Carpals/Tarsals	17	–	–	–	–	–
Metacarpal	6	–	–	–	–	–
Femur	2	–	–	–	–	–
Tibia	9	–	–	–	–	–
Metatarsal	4	–	–	–	–	–
Patella	–	–	–	–	–	–
Phalanges	12	2	–	–	–	–
Sesamoids	8	–	–	–	–	–
Metapodial	2	–	–	–	–	–
Limb bone shaft	–	–	–	–	–	–
<b>DK 2</b>						
Cranium	26	5	–	–	–	–
Teeth	202	85	4	9	1	2
Mandible	36	6	–	–	1	–
Vertebrae	26	2	–	–	–	–
Ribs	13	3	14	–	–	–
Innominate	15	–	–	–	1	2
Scapula	15	–	–	–	–	–
Humerus	31	1	–	–	–	–
Radio-ulna	66	4	–	1	–	–
Carpals/Tarsals	67	3	1	2	–	–
Metacarpal	50	–	–	–	–	–
Femur	40	1	–	–	–	–
Tibia	69	–	–	1	3	–
Metatarsal	50	1	–	–	–	–
Patella	4	–	–	–	–	–
Phalanges	65	5	–	–	2	–
Sesamoids	28	–	1	–	–	–
Metapodial	20	–	–	–	–	–
Limb bone shaft	1	–	–	–	–	–

Table 4.3. cont.

Element	Bovidae	Suidae	Proboscidean	Hippopotamidae	Giraffidae	Rhinocerotidae
<b>DK 3</b>						
Cranium	13	4	–	–	–	–
Teeth	105	32	9	15	2	7
Mandible	24	2	–	–	–	1
Vertebrae	12	4	–	3	–	–
Ribs	17	1	7	–	–	–
Innominate	8	–	–	–	–	–
Scapula	5	–	–	–	–	–
Humerus	27	2	–	–	–	–
Radio-ulna	35	1	–	–	–	1
Carpals/Tarsals	47	1	2	–	–	–
Metacarpal	27	–	–	–	2	–
Femur	30	–	–	–	–	–
Tibia	54	3	–	–	–	–
Metatarsal	46	1	–	–	–	1
Patella	–	–	–	–	–	–
Phalanges	26	2	–	1	–	–
Sesamoids	12	–	1	1	–	–
Metapodial	23	–	–	1	–	–
Limb bone shaft	5	–	1	–	–	–
<b>FLKNN 2</b>						
Cranium	12	2	–	–	–	–
Teeth	18	48	–	–	–	–
Mandible	12	7	–	–	–	–
Vertebrae	7	1	–	–	–	–
Ribs	3	4	–	–	–	–
Innominate	2	3	–	–	–	–
Scapula	10	2	–	–	–	–
Humerus	15	2	–	–	–	–
Radio-ulna	21	2	–	–	–	–
Carpals/Tarsals	4	5	–	–	–	–
Metacarpal	15	8	–	–	–	–
Femur	10	3	–	–	–	–
Tibia	16	3	–	–	–	–
Metatarsal	17	5	–	–	–	–
Patella	1	–	–	–	–	–
Phalanges	7	37	–	–	–	–
Sesamoids	3	13	–	–	–	–
Metapodial	2	2	–	–	–	–
Limb bone shaft	–	–	–	–	–	–

Table 4.3. cont.

Element	Bovidae	Suidae	Proboscidean	Hippopotamidae	Giraffidae	Rhinocerotidae
<b>FLKN 5</b>						
Cranium	40	2	—	—	—	—
Teeth	165	49	—	—	—	—
Mandible	22	5	—	—	—	—
Vertebrae	19	2	—	—	—	—
Ribs	10	3	—	—	—	—
Innominate	23	—	—	—	—	—
Scapula	15	3	—	—	—	—
Humerus	21	2	—	—	—	—
Radio-ulna	51	2	—	—	—	—
Carpals/Tarsals	127	—	—	—	—	—
Metacarpal	42	—	—	—	—	—
Femur	32	—	—	—	—	—
Tibia	57	—	—	—	—	—
Metatarsal	61	—	—	—	—	—
Patella	5	—	—	—	—	—
Phalanges	145	13	—	—	—	—
Sesamoids	54	—	—	—	—	—
Metapodial	18	—	—	—	—	—
Limb bone shaft	2	—	—	—	—	—

### SITE INTEGRITY

Fragments from all size ranges are represented in the Bed I assemblages. However, relative to actualistic control samples all three sites show a deficiency in specimens <4 cm (Figure 4.1). Among the DK assemblages Levels 1 and 2 are the most biased in terms of specimen size. Compared to the actualistic controls FLKNN 2 shows the opposite pattern of specimen size distribution. However, this is likely due not to a systematic bias against small fragments but to low levels of fragmentation (see below). FLKN 5 shows the closest correspondence with the actualistic samples. It is worth noting that these data are slightly misleading as comparisons with the actualistic assemblage are necessarily limited to limb bone fragments. All three sites contain many small (<4 cm) non-limb bone fragments.

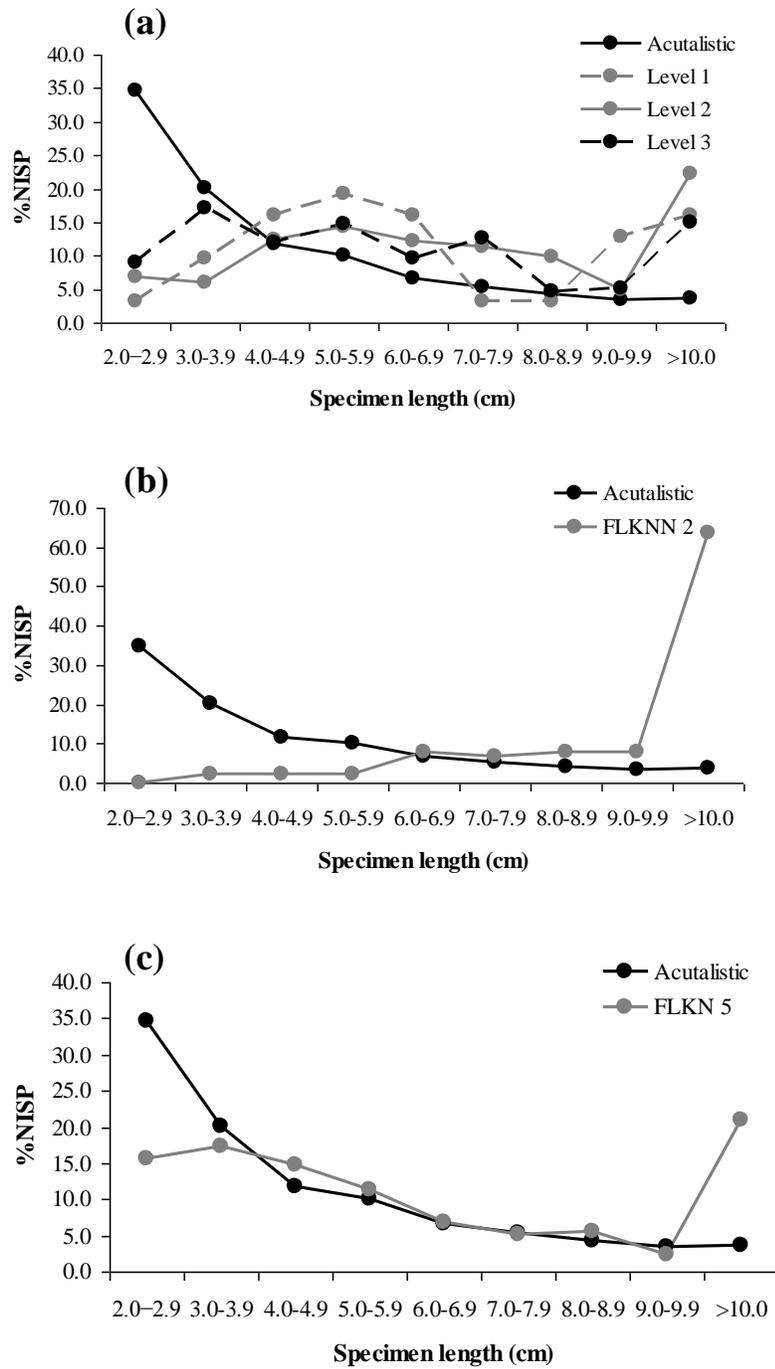


Figure 4.1. Distribution of limb bone fragment sizes for (a) DK (b) FLKNN 2 and (c) FLKNN 5 compared to an actualistic sample from Pickering and Egeland (2006).

At DK, only one specimen from Level 1 (0.5% of total NISP), ten from Level 2 (0.6%) and eight from Level 3 (0.6%) display the polishing damage indicative of long distance water transport. Similarly, only one (0.2%) specimen from FLKNN 2 and three (0.2%) from FLKN 5 show such damage. Therefore, although it is likely that low-energy water activity removed some small fragments from the sites, the fine-grained sedimentary matrix and lack of extensive rolling damage to bones eliminate water action as a significant agent of bone accumulation (see also Potts, 1988: 57-69). FLKN 5 appears to have undergone the least amount of post-depositional disturbance and DK Level 1 the most.

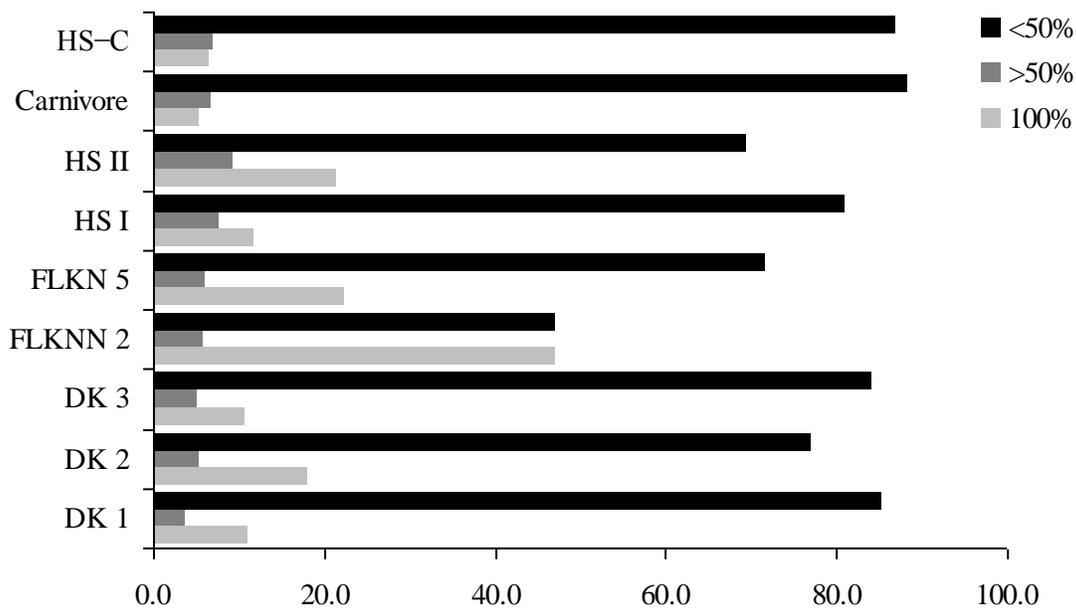


Figure 4.2. Percentage of Bunn's (1982, 1983a) circumference types from the Bed I sites and several actualistic samples. Note: fossil data include only green-broken specimens; Abbreviations: HS-C = hammerstone-to-carnivore; Carnivore = carnivore only; HS = hammerstone-only; HS-C, HS I, and Carnivore data from Marean et al., (2004); HS II data from Pickering and Egeland (2006).

The distribution of Bunn's (1982, 1983a) circumference types shows a predominance of Type 1 fragments at DK and FLKN 5 (Figure 4.2). Although Type 3 fragments occur at a high frequency in the FLKNN 2 assemblage, this is again likely due to low fragmentation levels. The overall incidence of circumference types suggests complete retention of limb bone shaft fragments. Nevertheless, it is still possible that some of the smaller fragments were not discovered because of incomplete or

unsystematic screening of sediments. Only a few boxes of screened material (i.e., with bags of dozens of small [ $<4$  cm] bone fragments without catalogue numbers) could be located among the DK and FLKN 5 material. Such material is common among other site collections that were known to have been screened systematically (e.g., FLK 22). Although screening was undoubtedly carried out at FLKNN 2, most of these small fragments were discovered in and labeled as “undifferentiated Level 2/3” material (Potts, 1988: 362; personal observations) and could therefore not be included in the analysis. The loss of the smallest bone fragments probably does not significantly affect most of the analyses presented below. Refitting efforts were largely unsuccessful. For DK, no refits were found for Level 1 while Levels 2 and 3 had seventeen and two, respectively. No inter-level refitting occurred, which seems to confirm the stratigraphic integrity of each of the levels. The FLKNN 2 assemblage had ten refits, most of which were comprised of green-broken fragments. A total of twenty-six refits was found in the FLKN 5 assemblage, although many occurred between dry- and recently broken specimens.

### ***Exposure and accumulation times***

All five subaerial weathering stages are represented at the Bed I sites, a finding that mirrors Potts’s (1982, 1986, 1988) previous weathering analysis of DK. When only limb bone shafts and small compact bones are considered, a predominance of stages 0 through 2 is evident (Table 4.4). In estimating exposure and accumulation times, it is important to remember that exposure time will be less than (or equal to) time-since-death (which weathering stages were originally meant to measure). In relative terms, the weathering data suggest a relatively short exposure time for DK 1, followed closely by FLKNN 2. Longer exposure times are evident for DK 2 and 3 and FLKN 5.

The weathering data can be used to make some tentative inferences about the exposure and accumulation time of the Bed I faunas. At DK the depth of the Level 1 and 2 deposits would seem to indicate a prolonged accumulation relative to Level 3, which consists of a thin paleosol. However, higher weathering stages are expected on the DK 3 paleosol, the formation of which indicates that the

Table 4.4. Maximum weathering stage data for the Bed I sites.

Stage	DK 1		DK 2		DK 3		FLKNN 2		FLKN 5	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
0	18	54.5	170	49.1	148	50.2	19	39.6	206	57.4
1	9	27.3	92	26.6	69	23.4	22	45.8	106	29.5
2	6	18.2	68	19.7	49	16.6	5	10.4	26	7.2
3	0	0.0	15	4.3	23	7.8	2	4.2	19	5.3
4	0	0.0	0	0.0	1	0.3	0	0.0	2	0.6
5	0	0.0	1	0.3	5	1.7	0	0.0	0	0.0

Note: Only limb bone shaft fragments and compact bones included.

surface was stable for several years, if not a decade or more (see also Potts, 1986). In contrast, the lower frequencies of weathered bone in Level 1 suggest rapid sedimentation and burial times. The same pattern is found at FLKNN 2. On the other hand, the thick deposit of FLKN 5 is associated with some higher weathering stages, which likely reflects slower sedimentation rates and thus longer exposure times.

### SKELETAL ELEMENT ABUNDANCES

Tables 4.5 and 4.6 provide element abundances as measured by NISP and MNE, respectively, for three size groupings (small, medium, large). Large carcasses are sporadically represented in the Bed I assemblages and therefore only the small and medium carcass samples are considered further here. Figure 4.3 displays graphically limb bone MNEs by portion (DK 1 not pictured). In a vast majority of cases shaft portions, and midshafts in particular, provide the highest MNE estimates. The low overall representation of limb bone epiphyses is mirrored by the relative paucity of greasy and less-dense axial bones (Figure 4.4). These patterns are strongly suggestive of some level of density-mediated attrition, an inference that is supported by a positive relationship between skeletal part representation and density. The linear regression and Spearman's rank-order correlation show that this relationship is highly significant for most of the assemblages (Table 4.7). What appears as a weaker relationship between skeletal representation and density for DK 1 may be slightly misleading. As Table 4.3 shows, isolated teeth are particularly well-represented relative to other skeletal parts in the DK 1 assemblage. Therefore, the regression and Spearman's coefficients may not be sensitive to

the fact that DK 1 may have undergone severe attrition that left behind only the densest remains (i.e., isolated teeth). Among the other assemblages, skeletal part representation at DK 2 appears most strongly affected by attrition while DK 3 and FLKNN 2 are the least affected. Except for FLKNN 2, medium carcass skeletal representation is more strongly correlated with density than small carcass representation. Given that most of the bone breakage at the Bed I sites occurred during nutrient extraction (see below), carnivore ravaging is a possible candidate for the creation of the observed skeletal part patterning. The Bed I skeletal profiles compare favorably to actualistic data from Capaldo (1998), Pickering (2001a, b) and Snyder (1988), which show that carnivore ravaging results in a paucity of axial bones (Figure 4.5). Although compact bones are also poorly represented both in some of the Bed I assemblages and in Capaldo's (1998) sample of ravaged African ungulates, FLKN 5 in particular shows higher compact bone representation that matches better with Pickering's (2001a, b) data on ravaged baboon carcasses and Snyder's (1988) wolf-ravaged deer sample. Preferential transport of axial bones to an off-site location can also account for their scarcity in the Bed I assemblages, but it is difficult to test this with certainty.

The FUI and MUI are not significantly correlated with element representation at any site, even when high survival elements are considered separately. However, regression values show that the marrow index is significantly correlated with element representation in two cases, among the small carcasses from DK 1 and the medium carcasses from DK 2, and approaches statistical significance among medium carcasses at DK 3 (Table 4.8).

When evenness values (calculated only for high survival elements; Table 4.9) are coupled with the data from Figure 4.4, three types of skeletal part profile emerge among the Bed I sites: (1) assemblages with very low evenness indices ( $<0.900$ ); (2) assemblages with intermediate evenness values ( $\sim 0.950$ ) that are dominated by crania; and (3) assemblages with very high evenness ( $>0.997$ ) and a prevalence of both crania and limb bones. The first type of profile, represented by DK 1 and the small carcass sample from FLKNN 2, is almost certainly a sampling artifact. The second profile type is found among the medium carcasses at DK 3, the small carcasses at FLKN 5 and, more equivocally,

Table 4.5. Number of identified specimens (NISP) by skeletal element and carcass size for the Bed I sites.

Element	DK 1			DK 2			DK 3			FLKNN 2		FLKN 5		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Small	Medium	Large
Cranium	5	15	2	23	58	6	9	38	7	2	19	90	30	1
Mandible	4	16	0	36	88	9	17	54	12	2	17	57	27	2
Vertebrae	5	8	1	14	50	7	8	24	6	4	13	16	27	1
Innominate	1	0	1	6	25	4	2	12	2	–	2	25	7	–
Ribs	4	11	1	20	32	67	16	31	26	3	39	23	22	9
Scapula	0	4	1	6	21	6	2	15	4	3	8	14	12	1
Humerus	0	1	0	6	44	0	5	33	1	2	14	16	28	–
Radius	2	3	0	10	43	2	4	26	1	1	12	26	21	–
Ulna	0	1	0	3	16	6	1	10	2	–	8	10	13	–
Carpals	3	5	0	9	17	1	2	11	1	1	2	33	19	–
Metacarpal	0	6	0	14	37	0	8	20	2	–	15	24	17	–
Femur	0	4	0	14	44	1	8	35	4	4	11	23	30	–
Patella	0	0	0	4	1	0	0	0	0	–	1	6	2	–
Tibia	3	7	0	17	73	5	11	48	7	3	19	36	57	1
Tarsals	1	8	0	16	24	4	12	21	3	–	1	49	28	–
Metatarsal	0	4	0	10	41	0	11	35	0	4	14	38	22	1
Phalanges	6	6	0	30	35	2	17	8	2	1	6	127	21	–
Sesamoids	1	5	2	9	20	4	4	9	2	–	3	35	20	–
<b>Total</b>	<b>35</b>	<b>104</b>	<b>8</b>	<b>247</b>	<b>669</b>	<b>124</b>	<b>137</b>	<b>430</b>	<b>82</b>	<b>30</b>	<b>204</b>	<b>648</b>	<b>403</b>	<b>16</b>

Table 4.6. Minimum number of element (MNE) estimates by carcass size for the Bed I sites.

Element	DK 1			DK 2			DK 3			FLKNN 2		FLKN 5		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Small	Medium	Large
Cranium	3	7	1	7	15	2	3	19	3	2	6	19	7	1
Mandible	2	7	0	9	24	3	5	13	3	2	6	16	7	2
Vertebrae	4	7	1	12	38	6	6	17	5	1	10	14	18	1
Innominate	1	0	1	6	15	2	2	7	2	0	1	17	4	–
Ribs	2	6	1	7	7	11	3	8	9	2	13	5	8	2
Scapula	0	2	1	3	13	2	1	6	2	3	8	13	3	1
Humerus	0	1	0	4	25	0	5	18	1	2	13	13	14	–
Radius	1	2	0	8	21	2	2	13	1	1	12	19	10	–
Ulna	0	1	0	3	10	2	1	5	2	0	6	9	9	–
Carpals	3	5	0	9	17	1	2	11	1	1	2	33	17	–
Metacarpal	0	3	0	11	20	0	6	9	1	0	13	17	13	–
Femur	0	2	0	8	23	1	6	17	2	3	5	10	12	–
Patella	0	0	0	4	1	0	0	0	0	0	1	6	2	–
Tibia	3	5	0	10	30	3	6	22	5	3	9	23	17	1
Tarsals	1	8	0	16	23	1	12	21	2	0	1	47	28	–
Metatarsal	0	4	0	6	23	0	7	16	0	4	8	20	16	1
Phalanges	6	6	0	28	31	2	17	7	2	1	6	119	18	–
Sesamoids	1	5	2	9	20	4	4	9	2	0	3	35	20	–
Total	27	71	7	160	356	43	88	218	43	25	123	435	223	9

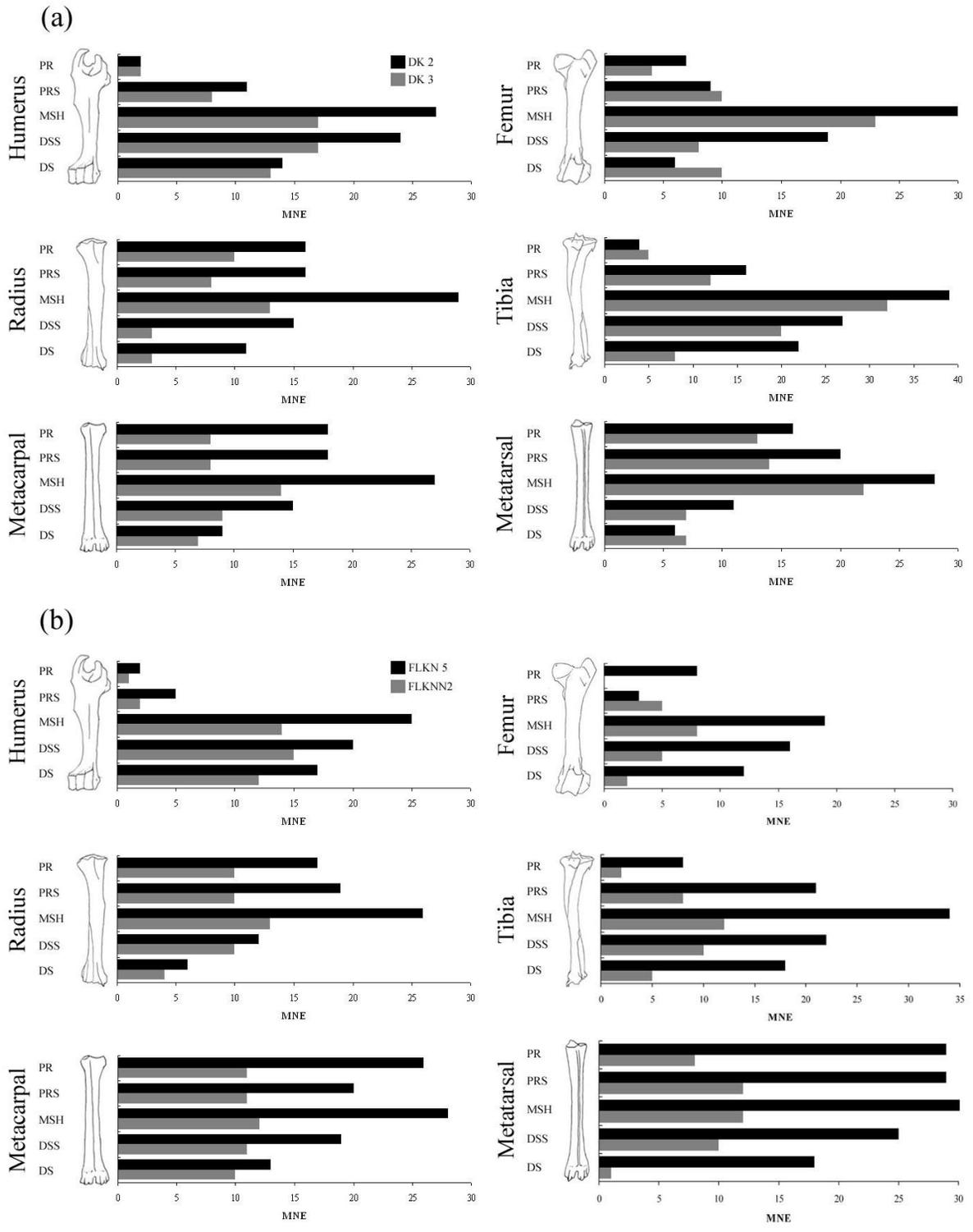
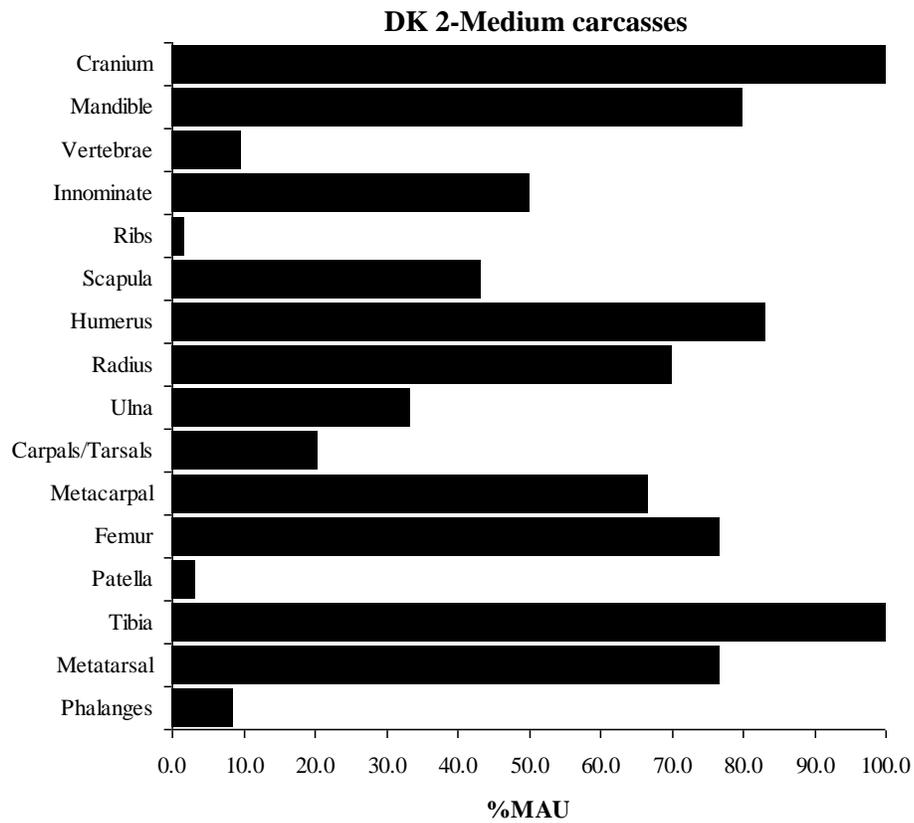
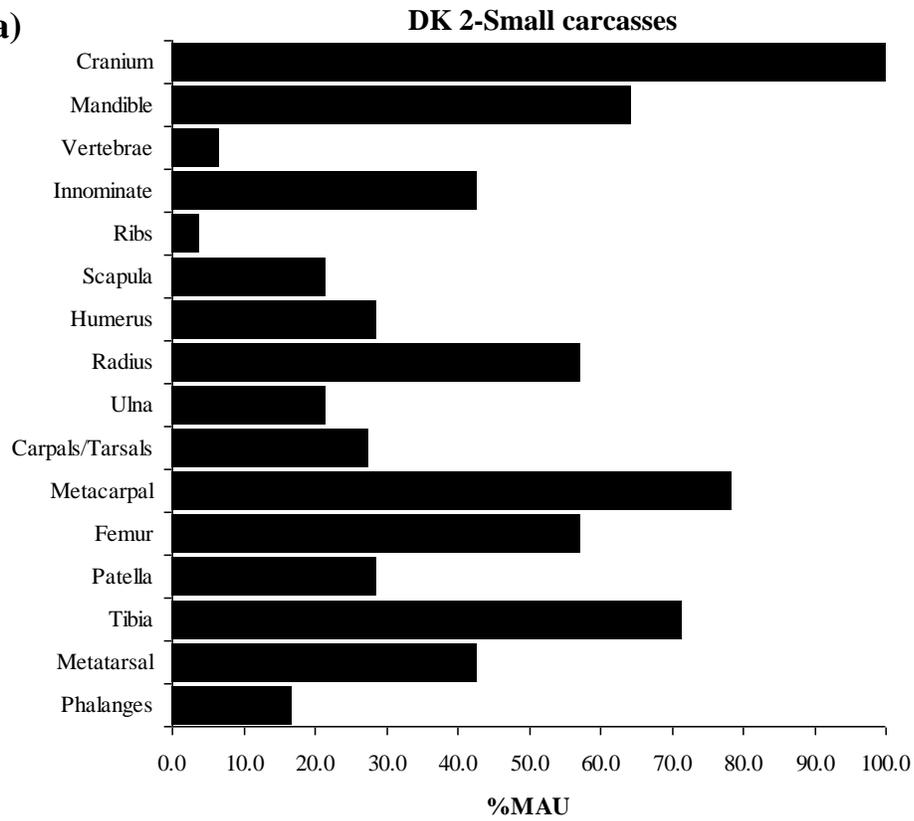
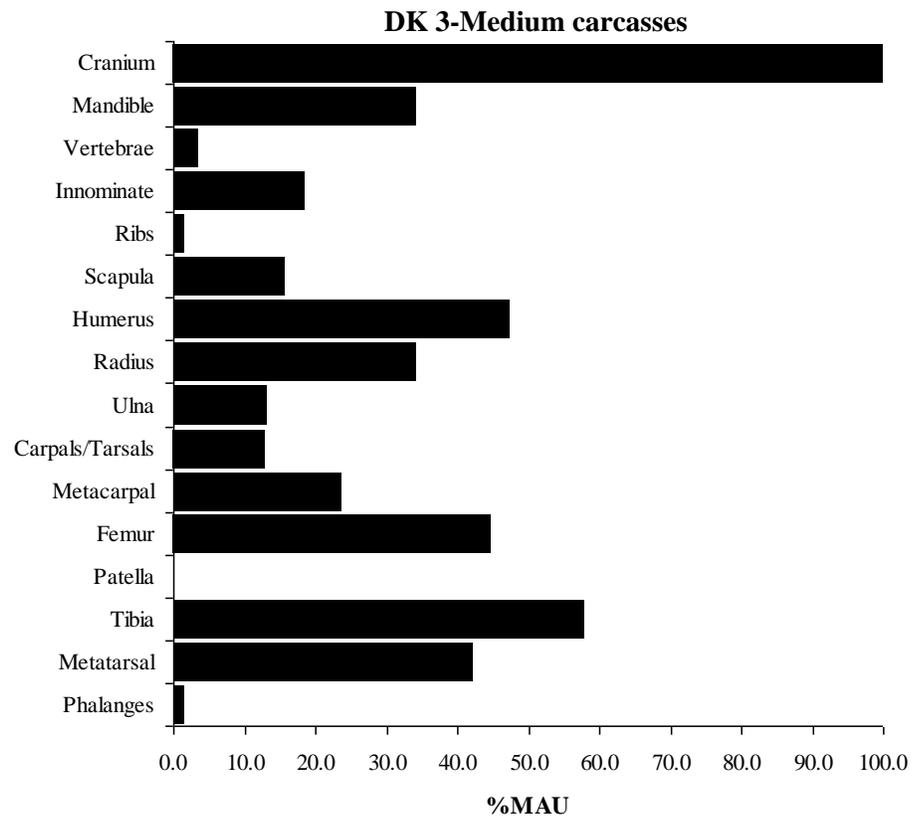
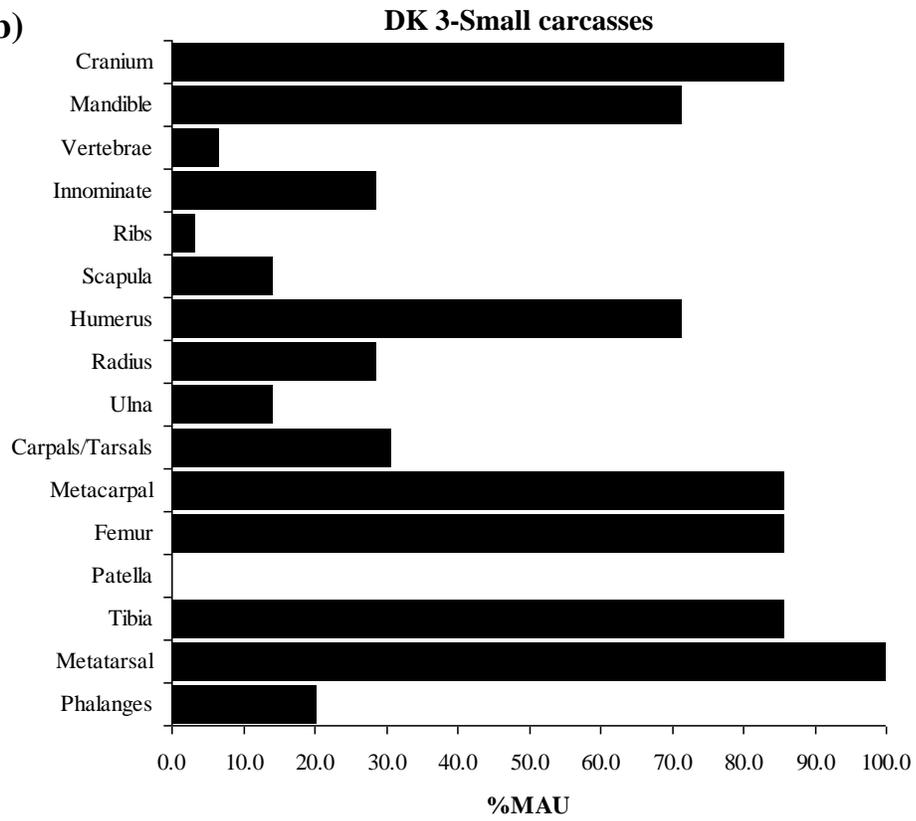


Figure 4.3. Limb bone MNEs (all Size Classes combined) by portion for (a) DK and (b) FLKN 5 and FLKNN 2. Codes: PR = proximal, PRS = proximal shaft, MSH = midshaft, DSS = distal shaft, DS = distal.

(a)

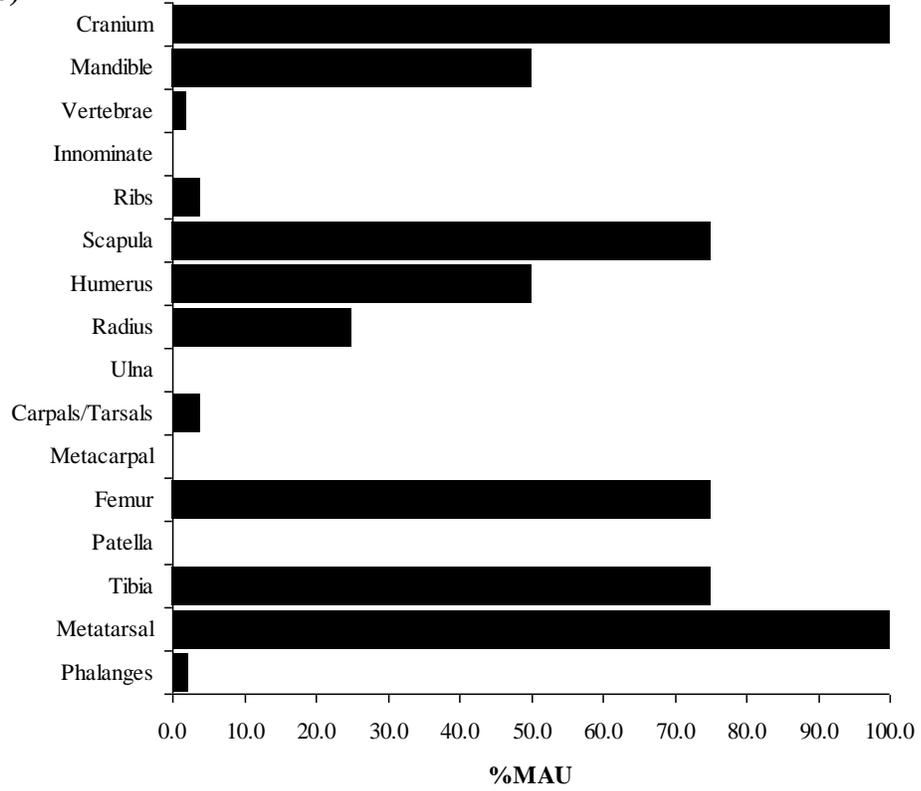


(b)

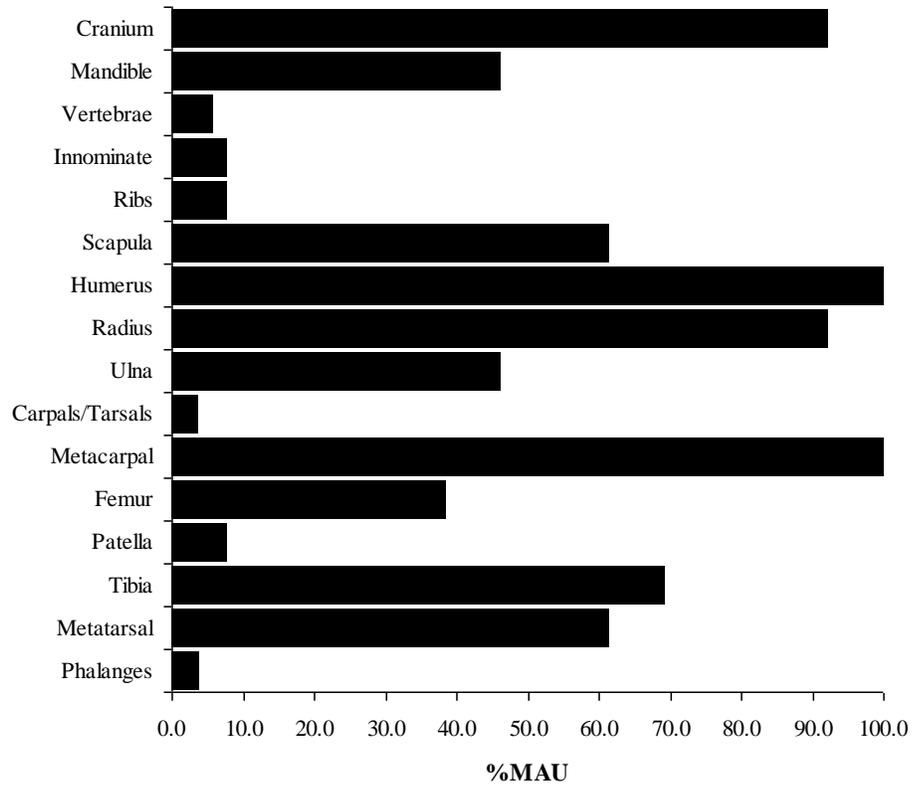


(c)

**FLKNN 2-Small carcasses**

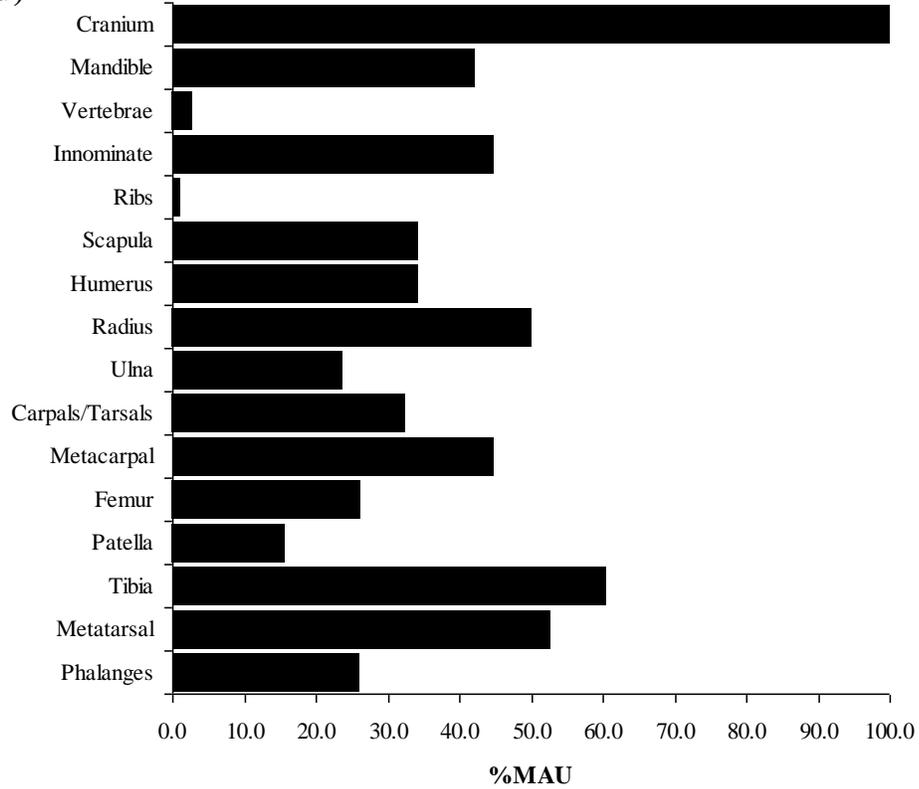


**FLKNN 2-Medium carcasses**

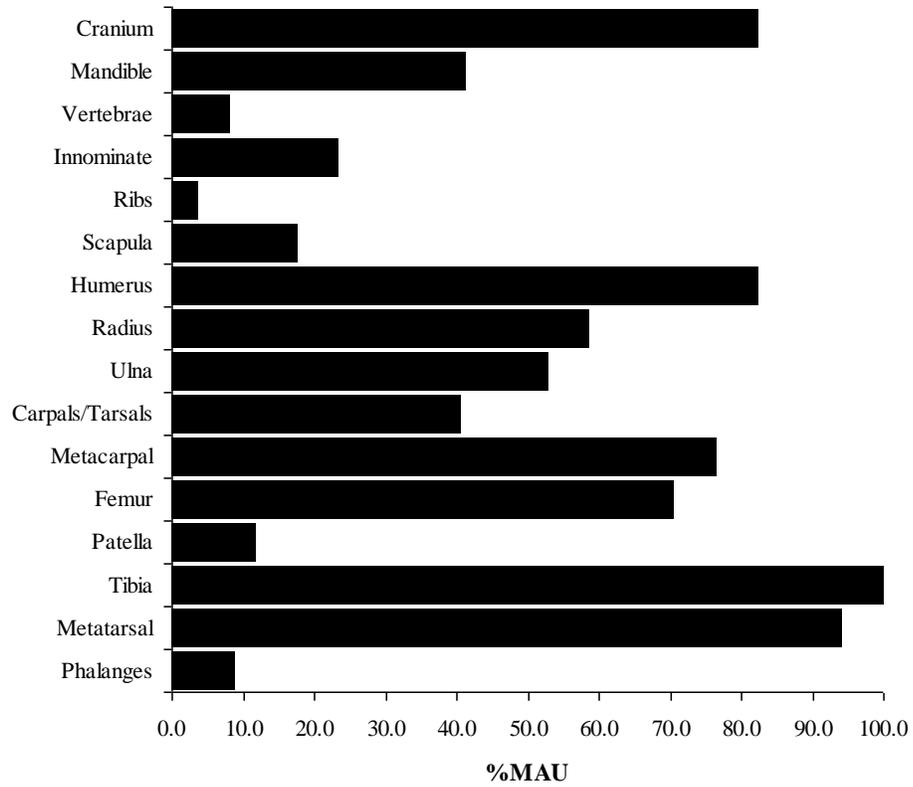


(d)

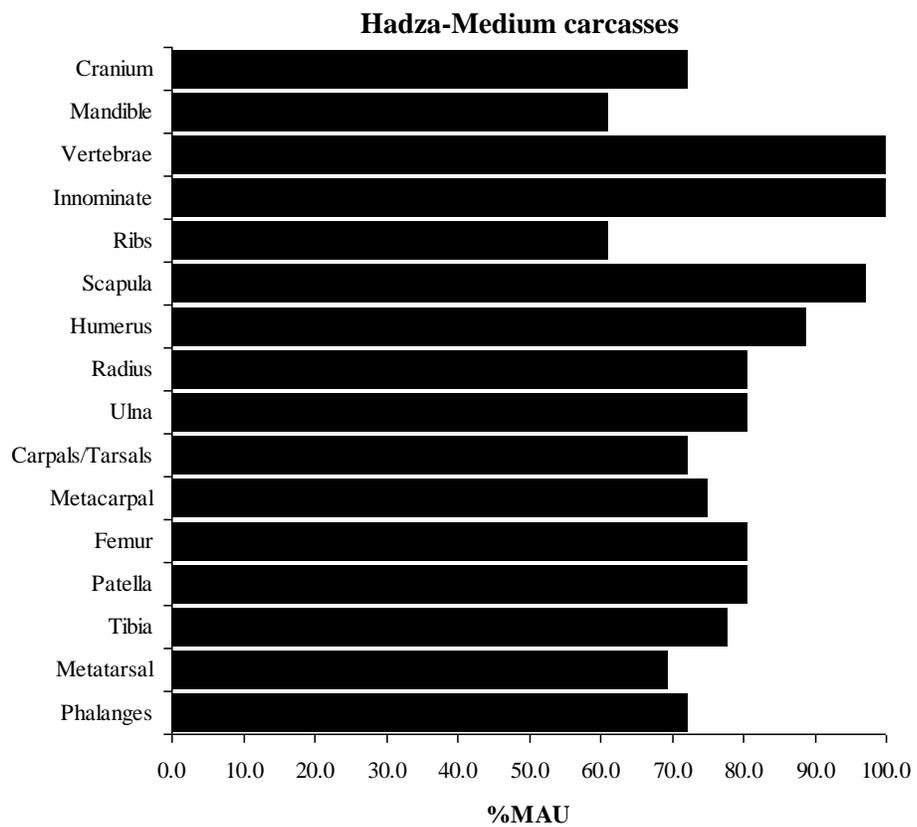
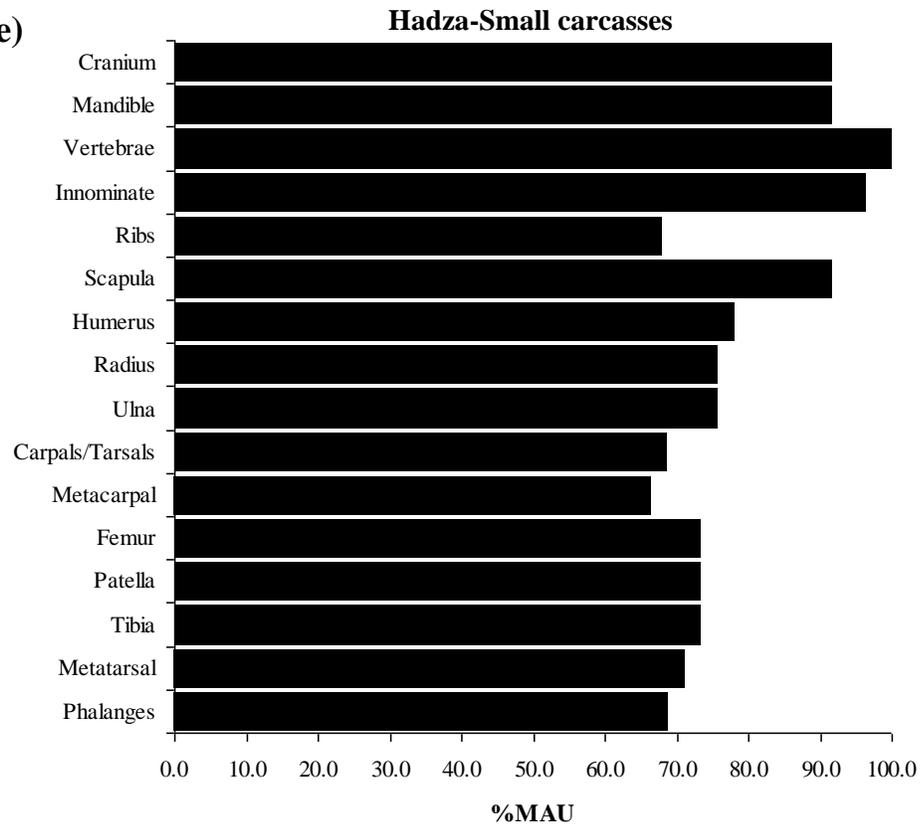
**FLKN 5-Small carcasses**



**FLKN 5-Medium carcasses**



(e)



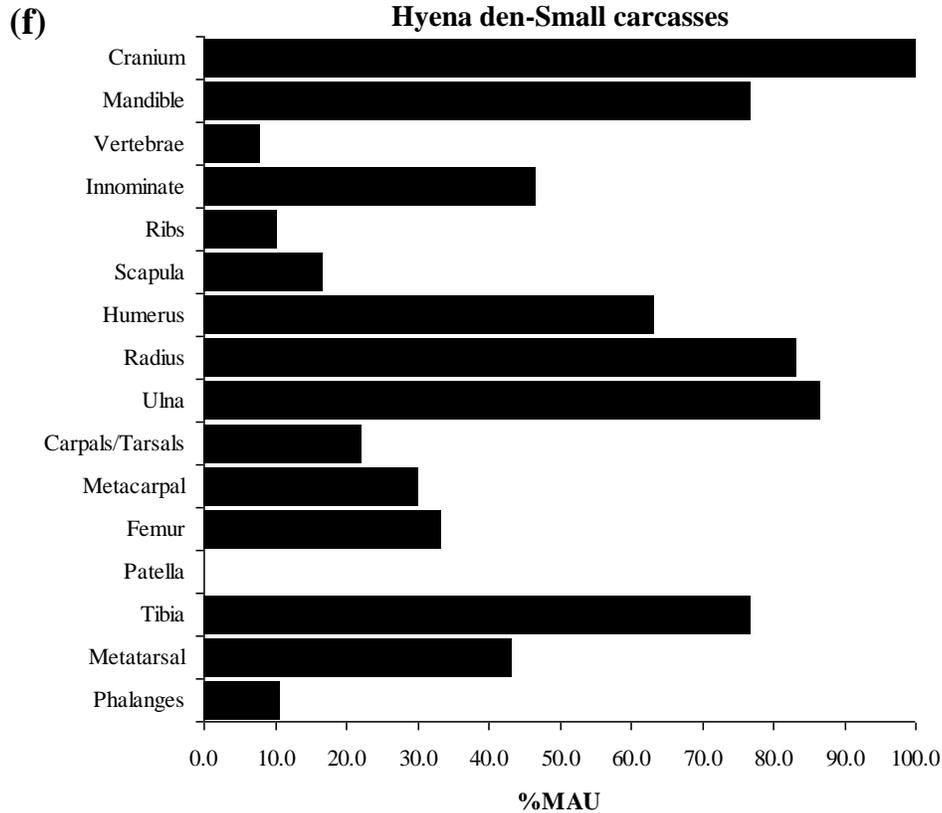


Figure 4.4. %MAU values by skeletal element for (a) DK 2, (b) DK 3, (c) FLKNN 2, (d) FLKN 5, (e) Hadza transported assemblages (Monahan, 1998) and (f) a modern spotted hyena den (Lam, 1992).

the small carcasses from DK 2. The intermediate evenness values for these assemblages are due to the dominance of crania. Such an uneven profile is unexpected especially at FLKN 5 because the Size Class 1 carcasses that dominate the assemblage would have imposed limited transport constraints for the bone-accumulating agent. In fact, such small animals are often transported whole by leopards (Bailey, 1993; Brain, 1981; Cavallo and Blumenschine, 1989) and modern foragers transport both small and medium carcasses more-or-less completely (Bunn et al., 1988; O'Connell et al., 1988, 1990; Figure 4.4 and Table 4.9). Therefore, even the medium-sized carcasses at DK 3, many of which are only Size Class 3a animals, presumably would not have posed significant transport problems.

Nevertheless, the large sample sizes upon which the evenness values are based suggest that high cranial representation relative to all other elements, including limb bones, is a real pattern for these subassemblages. Assuming that low axial representation is mainly the result of on-site carnivore

Table 4.7. Regression and Spearman's statistics for the relationship between %MAU and density.

	DK 1		DK 2		DK 3		FLKNN 2		FLKN 5	
	<u>Small</u>	<u>Medium</u>								
R <sup>2</sup>	<b>0.17</b>	<b>0.29</b>	<b>0.37</b>	<b>0.60</b>	<b>0.28</b>	<b>0.46</b>	<b>0.38</b>	<b>0.36</b>	<b>0.35</b>	<b>0.50</b>
F	<b>8.42</b>	<b>16.40</b>	<b>24.32</b>	<b>61.30</b>	<b>15.00</b>	<b>35.15</b>	<b>25.39</b>	<b>22.77</b>	<b>21.86</b>	<b>41.63</b>
P	<b>&lt;0.05</b>									
r <sub>s</sub>	0.19	<b>0.52</b>	<b>0.58</b>	<b>0.74</b>	<b>0.44</b>	<b>0.69</b>	<b>0.65</b>	<b>0.55</b>	<b>0.56</b>	<b>0.70</b>
P	0.22	<b>&lt;0.05</b>								

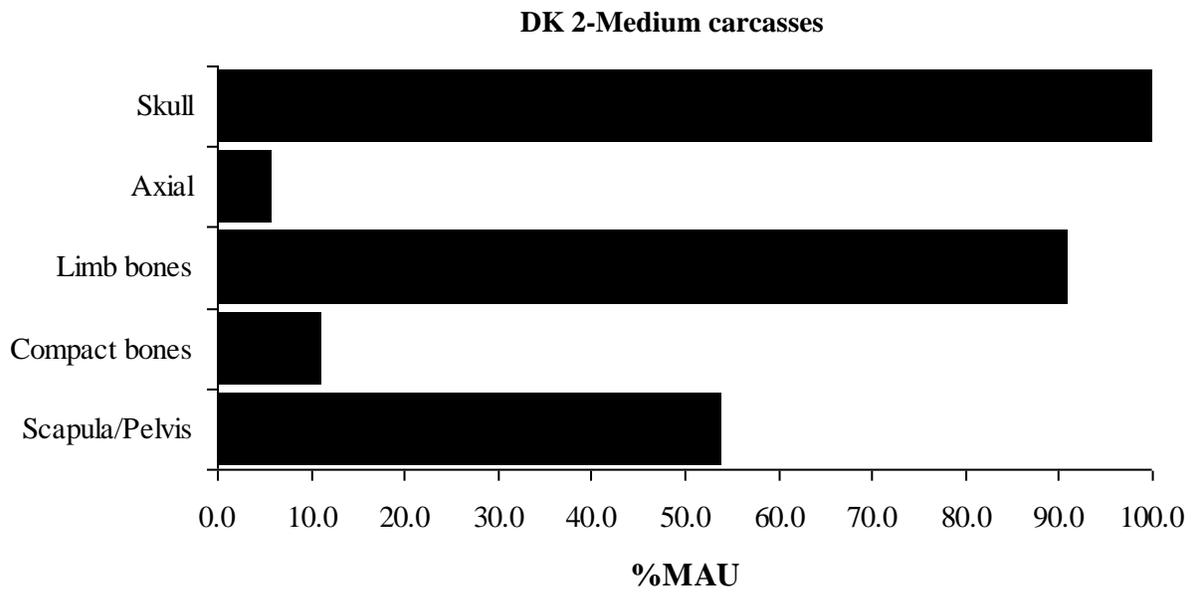
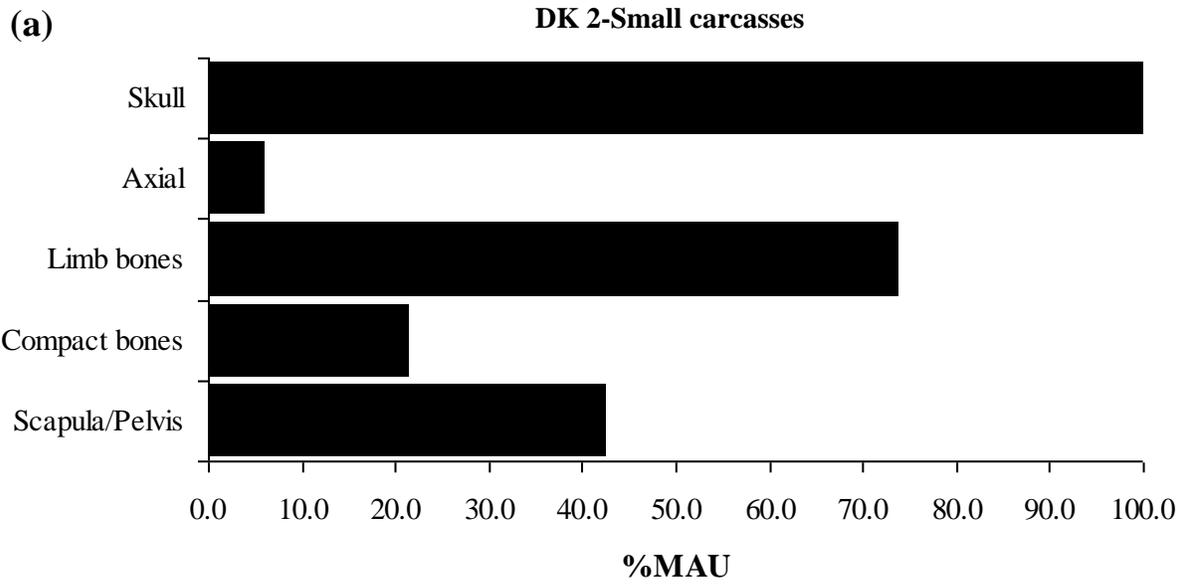
Note: Significant values expressed in bold.

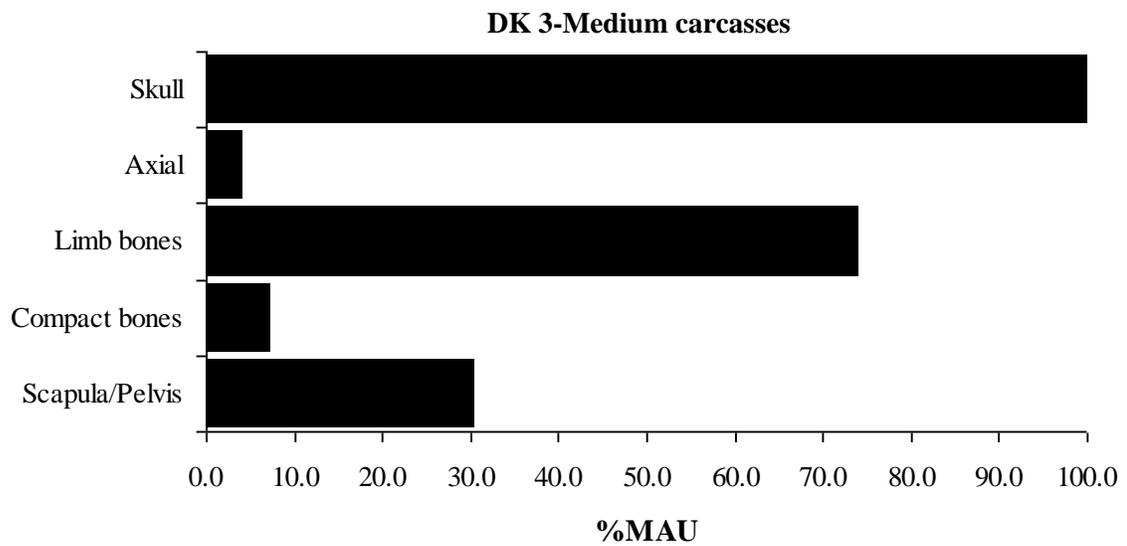
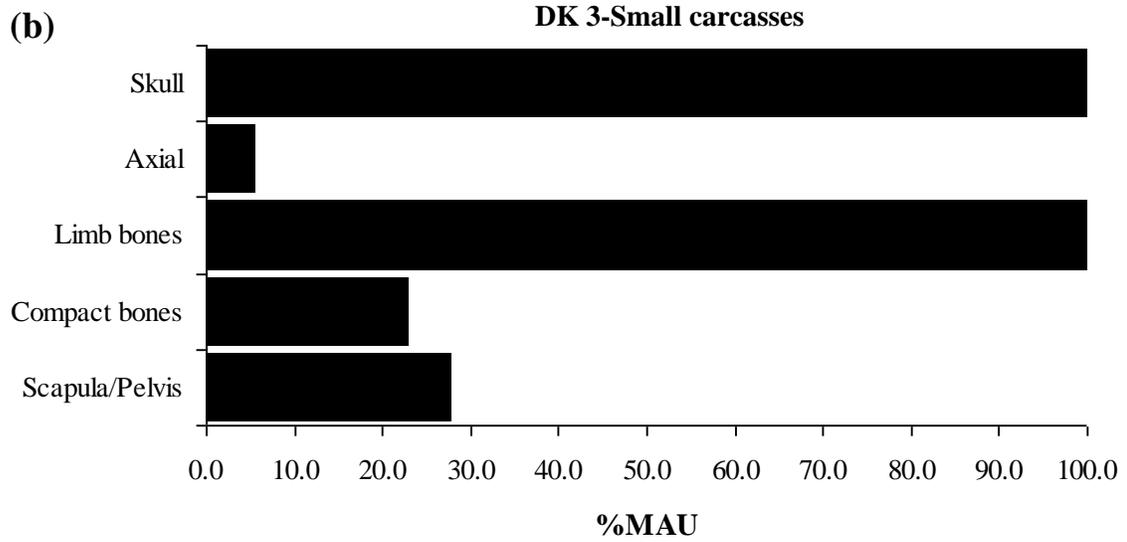
Table 4.8. Regression and Spearman's statistics for the relationship between %MAU and %MI.

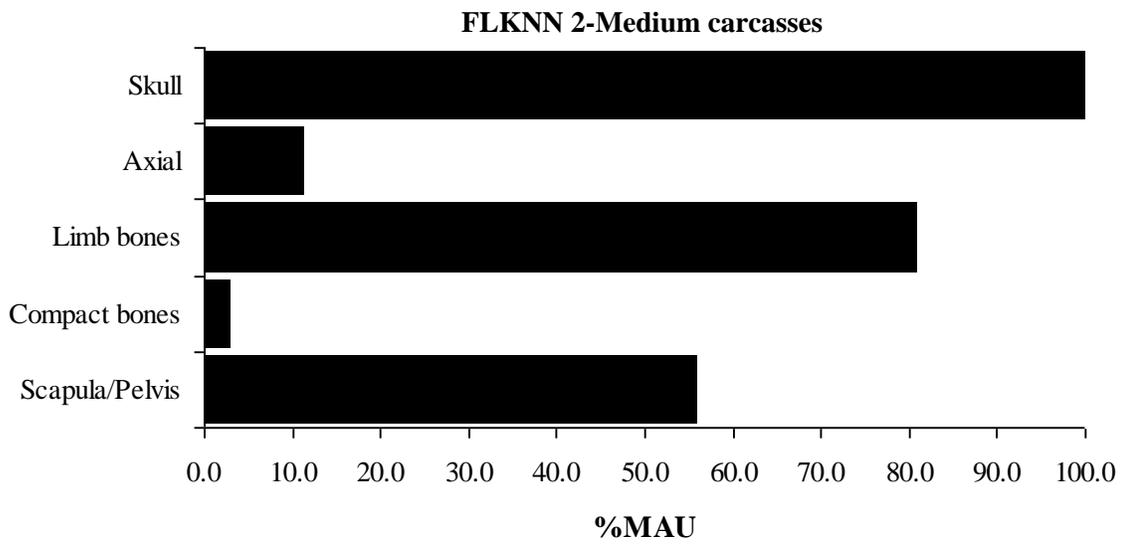
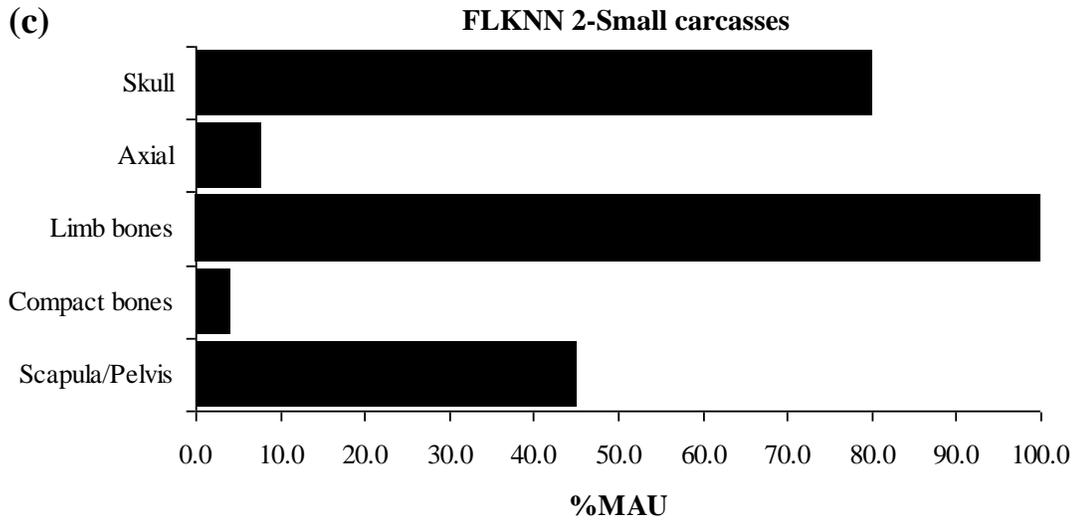
	DK 1		DK 2		DK 3		FLKNN 2		FLKN 5	
	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>
R <sup>2</sup>	<b>0.75</b>	0.23	0.09	<b>0.73</b>	0.01	0.62	0.38	0.41	0.29	0.39
F	<b>11.91</b>	1.20	0.42	<b>10.67</b>	0.02	6.56	0.68	0.83	0.38	0.74
P	<b>&lt;0.05</b>	0.334	0.554	<b>&lt;0.05</b>	0.89	0.06	0.46	0.41	0.57	0.44
r <sub>s</sub>	0.67	0.12	0.06	0.64	-0.21	0.71	0.35	0.49	0.14	0.09
P	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05

Note: Significant values expressed in bold.

ravaging, at least three processes can account for this patterning among the medium carcasses at DK 3 and the small carcasses at FLKN 5. First, it is possible that limb bones were selectively transported off-site for consumption elsewhere. Although a negative correlation between element abundances and economic utility is not seen in either assemblage, this would not necessarily be expected if limbs were removed as complete units. Second, carcasses may not have been complete when they entered the site. Again, a lack of correlation (positive in this case) between element abundances and economic utility is not necessary if complete limbs were transported to the site. However, the abundance of crania cannot be easily reconciled with preferential transport unless the transporting agent had access to incomplete and/or nutrient-depleted carcasses. Some evidence for this is found in the fact that the evenness values for the small carcasses from FLKN 5 and the medium carcasses from DK 3 are comparable to a spotted hyena den reported on by Lam (1992), which, incidentally, also shows a

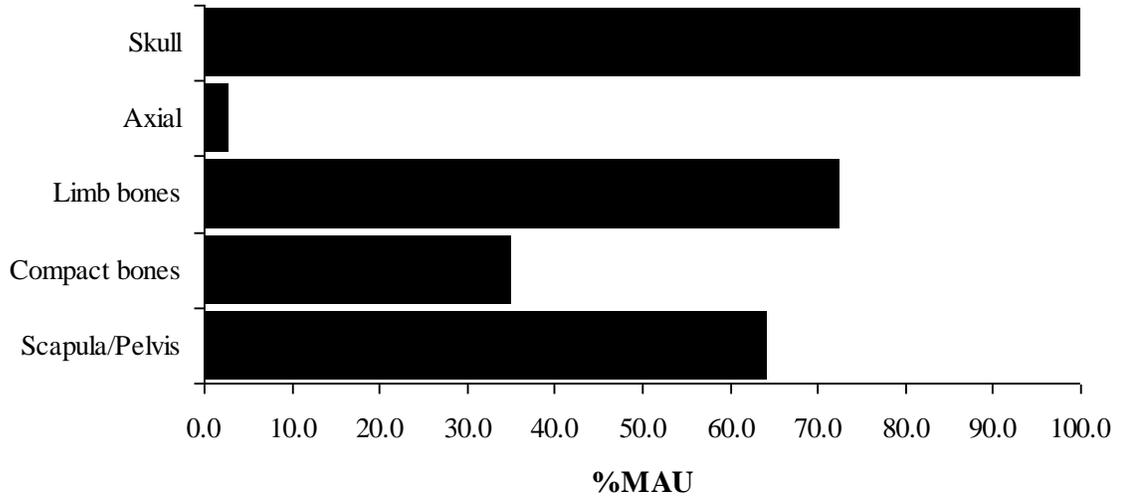




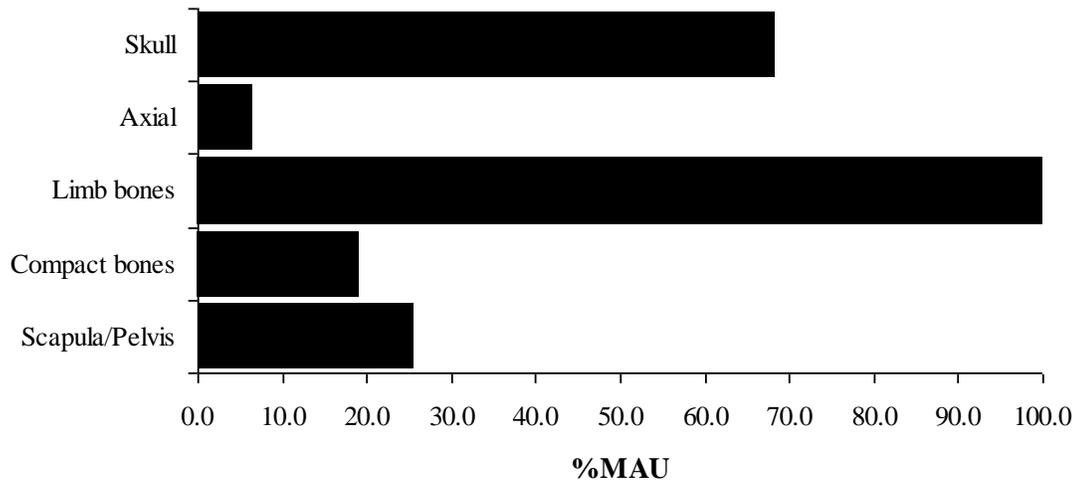


**(d)**

**FLKN 5-Small carcasses**

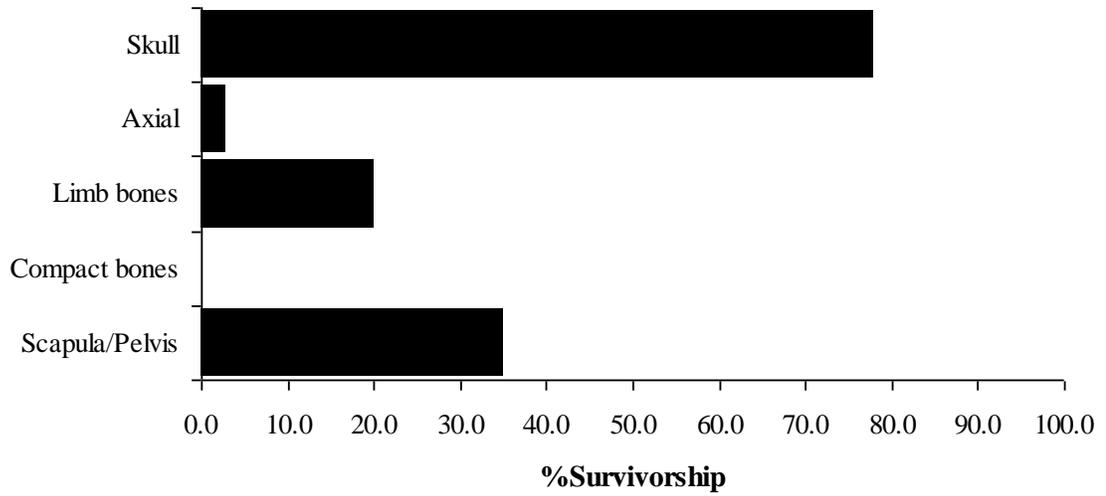


**FLKN 5-Medium carcasses**

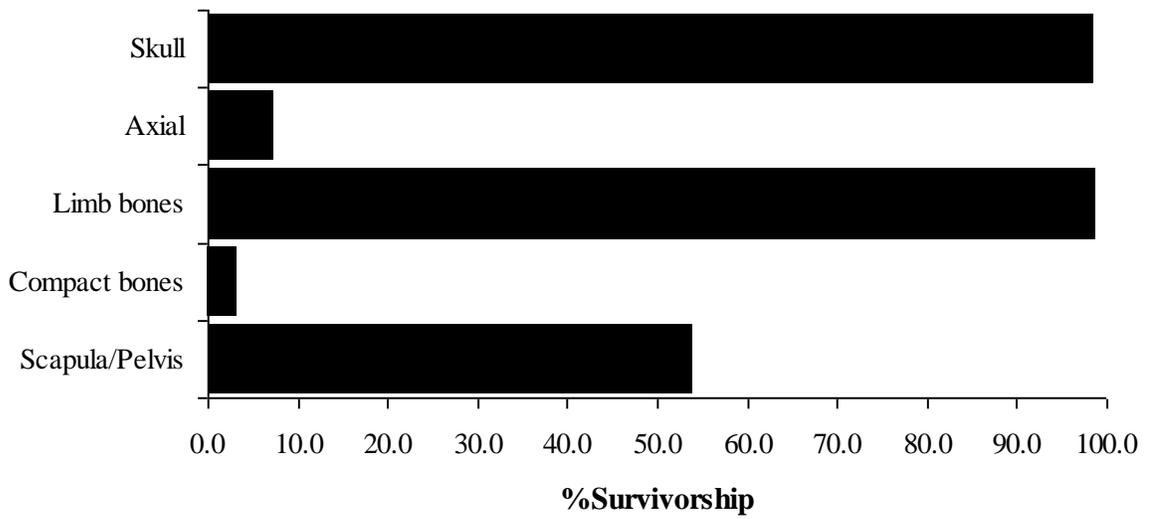


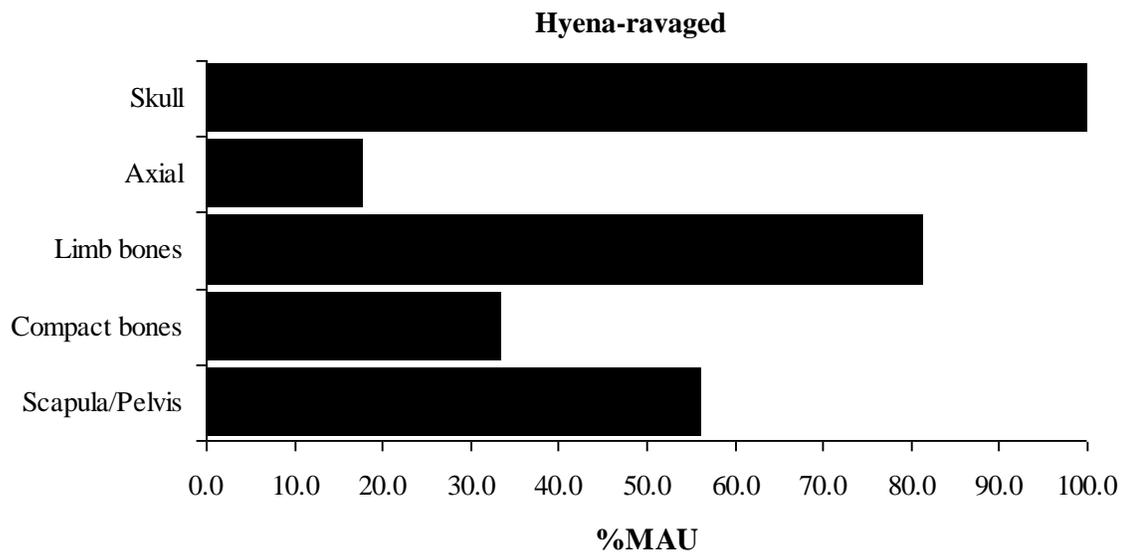
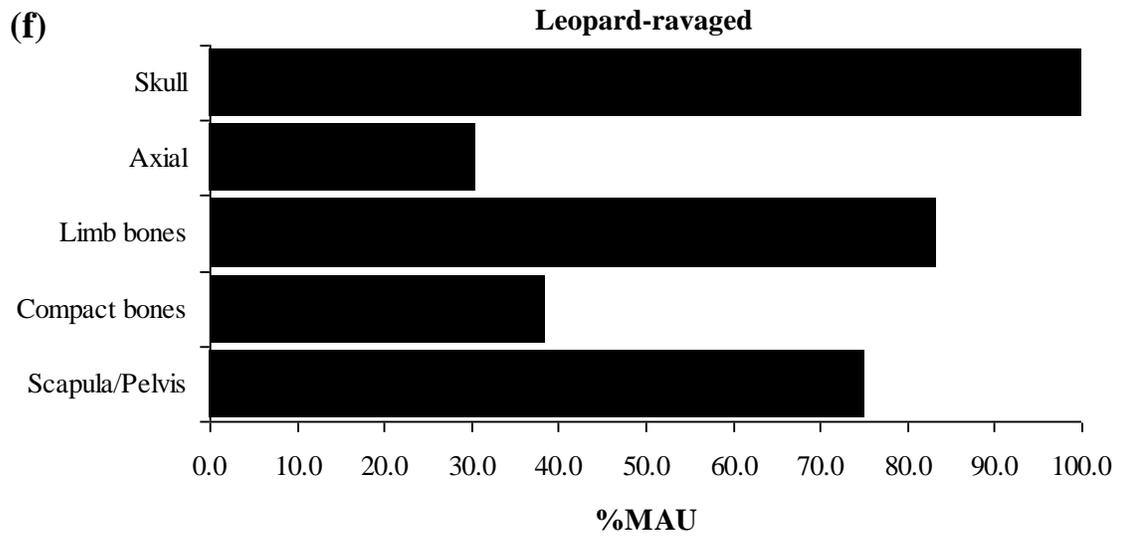
(e)

**Carnivore-only**



**Hammerstone-to-carnivore**





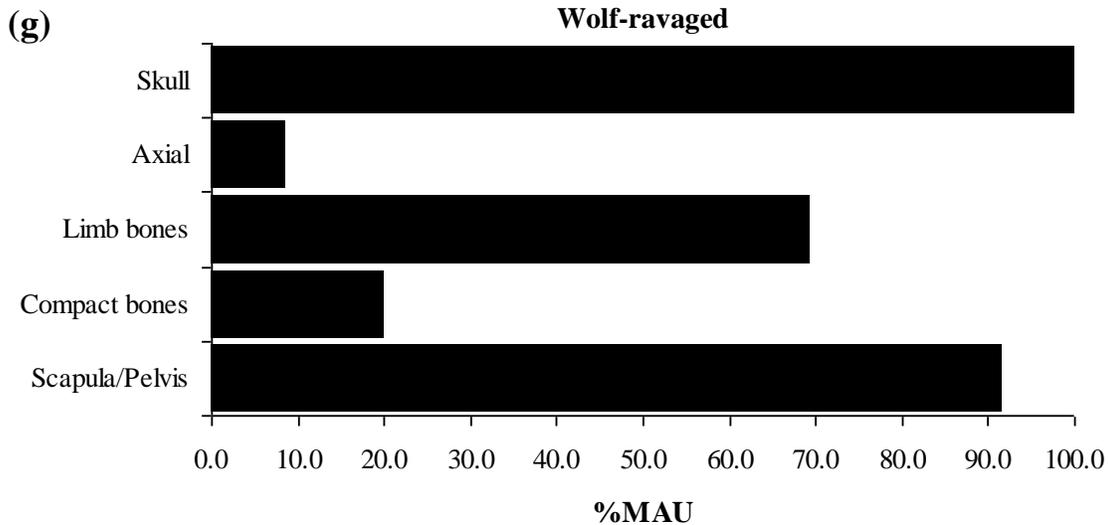


Figure 4.5. Relative representation of skeletal groups for (a) DK 2, (b) DK 3, (c) FLKNN 2, (d) FLKN 5, (e) Capaldo's (1998) naturalistic sample of ravaged African ungulates, (f) Pickering's (2001a, b) experimental sample of leopard- and hyena-ravaged baboon carcasses and (g) Snyder's (1988) experimental sample of wolf-ravaged deer.

preponderance of crania (Figure 4.4 and Table 4.9).<sup>2</sup> This patterning may be due to the fact that the hyenas were exploiting fat-stressed ovicaprids (Lam, 1992: 398). Nevertheless, the hyena den does not show the *overall* low representation of limb bones seen at DK 3 and FLKN 5. The final possibility is that on-site ravaging of complete carcasses deleted not only a majority of the axial bones but a substantial portion of the limb bones. This is probable for the small carcasses at FLKN 5 as hyenas are capable of destroying most of a Size Class 1 carcass (Pobiner and Blumenschine, 2003). The DK 3 medium carcass data could also be interpreted in this way, as the extinct *C. ultra*, which was larger than a modern spotted hyena, may have been capable of destroying the limb bones of medium-sized carcasses. However, this fails to explain the fact that small carcass limb bones at DK 3, which certainly could have been destroyed by *C. ultra*, are not underrepresented. Therefore, it is more likely that the medium carcass data from DK 3 reflect some level of off-site transport of limb bones.

<sup>2</sup> Lam (1992) provides actual MNE values only for crania and limb bones; NISP values were used to estimate skeletal abundances for the remaining elements and therefore their representation is overestimated.

Table 4.9. Shannon evenness index for element representation at the Bed I sites and several modern samples.

	DK 1		DK 2		DK 3		FLKNN 2	
	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>
Sample size	7	24	76	157	35	114	15	66
Evenness	0.461	0.826	0.967	0.994	0.976	0.952	0.880	0.979
	FLKN 5		KFHD 1	Hadza transported assemblages				
	<u>Small</u>	<u>Medium</u>	<u>Small</u>	<u>Small</u>	<u>Medium</u>	<u>Large</u>		
Sample size	121	89	114	211	183	68		
Evenness	0.958	0.993	0.957	0.997	0.998	0.953		

Note: Evenness values calculated using only “high survival” elements. KFHD 1 (= Koobi Fora Hyena Den) data from Lam (1992); Hadza data from Monahan (1998).

The final skeletal profile type is found among the small carcasses from DK 3 and the medium carcasses from DK 2, FLKNN 2 and FLKN 5. The high evenness of these assemblages strongly suggests that complete carcasses were deposited on-site with little or no subsequent transport (Table 4.9). Complete carcass deposition at these sites helps explain a lack of correlation between economic utility and element representation.

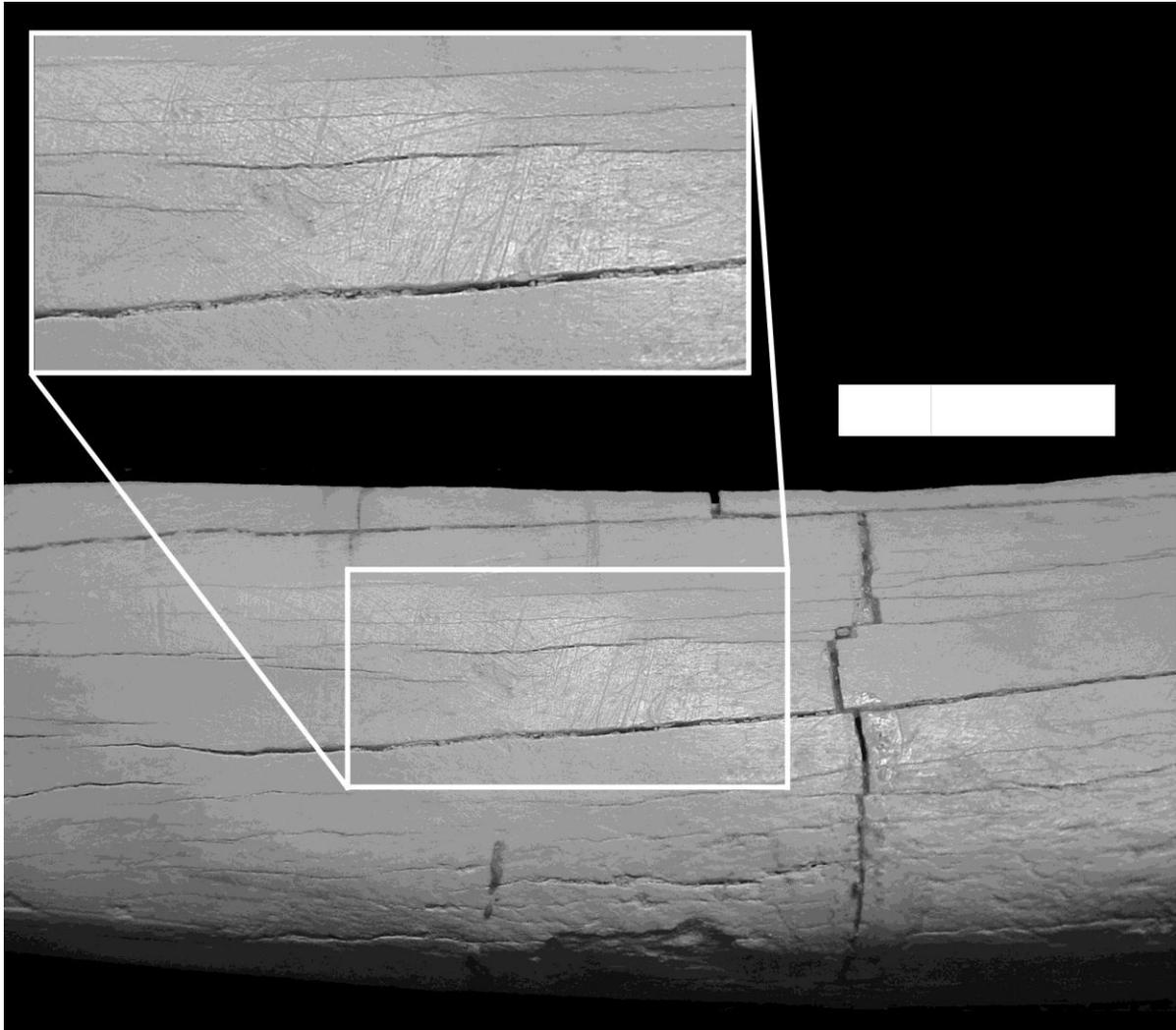
### BONE SURFACE MODIFICATIONS

Tables 4.10–4.13 summarize surface mark frequencies for the Bed I sites. Only one hominid-modified fragment was documented at both DK 1 and FLKN 5 and no hominid modifications were recorded at FLKNN 2 (the cutmarked equid metacarpal identified by Bunn [1982: 139] and Potts [1988: 128] was not available for study); therefore, only tooth mark frequencies are reported for these three assemblages.

Cortical preservation at the Bed I sites is generally very good, which means that a majority of each assemblage is conducive to secure surface mark identification. About 70% of specimens scored for surface preservation had well-preserved cortices at DK (all three levels) and FLKN 5 while at FLKNN 2 almost 60% show good preservation. Therefore, surface mark frequencies at FLKNN 2 may be slightly depressed relative to the other Bed I sites. Sediment abrasion is especially common in

the DK assemblages, where 171 specimens exhibit such damage (e.g., Figure 4.6). As with skeletal element abundances, the remainder of this section considers only the small and medium carcass samples in detail.

Examples of typical cutmarks, percussion marks and tooth marks in the Bed I assemblages are shown in Figures 4.7–4.9. Tooth marks and cutmarks and percussion marks all appear in low frequencies at DK, although carnivore damage is much more abundant than hominid damage (Tables 4.10–4.12). One Size Class 2 metatarsal from Level 2 shows tooth marks overlying cutmarks (Figure 4.10–4.12). One Size Class 2 metatarsal from Level 2 shows tooth marks overlying cutmarks (Figure 4.10), indicating that carnivore bone breakage followed hominid butchery (most likely skinning) in at



least one case.

Figure 4.6. Tibia fragment from DK showing sediment abrasion. Note the random directionality of the marks. Scale bar = 1 cm.

Table 4.10. Tooth mark frequencies by element and carcass size at DK 1.

Element	Small	Medium	Large	Total
Mandible	0/0 (0.0)	0/6 (0.0)	0/0 (0.0)	0/6 (0.0)
Vertebrae	0/4 (0.0)	2/8 (25.0)	0/0 (0.0)	2/12 (16.7)
Innominate	0/1 (0.0)	0/0 (0.0)	0/1 (0.0)	0/2 (0.0)
Ribs	0/4 (0.0)	0/11 (0.0)	0/1 (0.0)	0/16 (0.0)
Scapula	0/0 (0.0)	1/4 (25.0)	0/1 (0.0)	1/5 (20.0)
Humerus	0/0 (0.0)	1/1 (100.0)	0/0 (0.0)	1/1 (100.0)
Radius	1/2 (50.0)	1/3 (33.3)	0/0 (0.0)	2/5 (40.0)
Ulna	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Carpals	0/3 (0.0)	0/5 (0.0)	0/0 (0.0)	0/8 (0.0)
Metacarpal	0/0 (0.0)	3/6 (50.0)	0/0 (0.0)	3/6 (50.0)
Femur	0/0 (0.0)	0/4 (0.0)	0/0 (0.0)	0/4 (0.0)
Patella	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Tibia	0/3 (0.0)	3/7 (42.9)	0/0 (0.0)	3/10 (30.0)
Tarsals	0/1 (0.0)	0/8 (0.0)	0/0 (0.0)	0/9 (0.0)
Metatarsal	0/0 (0.0)	3/4 (75.0)	0/0 (0.0)	3/4 (75.0)
Phalanges	0/6 (0.0)	0/6 (0.0)	0/0 (0.0)	0/12 (0.0)
Sesamoids	0/1 (0.0)	0/5 (0.0)	0/2 (0.0)	0/8 (0.0)
LBS	0/1 (0.0)	1/9 (11.1)	0/0 (0.0)	1/10 (10.0)
Total	1/26 (3.8)	15/87 (17.2)	0/5 (0.0)	16/118 (13.6)

Note: Numerator denotes number of marked specimens, denominator denotes total NISP for each skeletal element, percentage is in parentheses. Codes: LBS = unidentified limb bone fragment.

Table 4.11. Surface mark frequencies by element and carcass size at DK 2.

Element	Small			Medium			Large		
	TM	CM	PM	TM	CM	PM	TM	CM	PM
Mandible	2/11 (18.2)	0/11 (0.0)	0/11 (0.0)	6/37 (16.2)	0/37 (0.0)	0/37 (0.0)	0/4 (0.0)	0/4 (0.0)	0/4 (0.0)
Vertebrae	1/15 (6.7)	0/15 (0.0)	0/15 (0.0)	6/47 (12.8)	0/47 (0.0)	0/47 (0.0)	0/7 (0.0)	0/7 (0.0)	0/7 (0.0)
Innominate	0/6 (0.0)	0/6 (0.0)	0/6 (0.0)	6/25 (24.0)	0/25 (0.0)	0/25 (0.0)	0/4 (0.0)	0/4 (0.0)	0/4 (0.0)
Ribs	1/19 (5.3)	0/19 (0.0)	0/19 (0.0)	4/32 (12.5)	0/32 (0.0)	0/32 (0.0)	3/67 (4.5)	0/67 (0.0)	0/67 (0.0)
Scapula	0/6 (0.0)	0/6 (0.0)	0/6 (0.0)	3/21 (14.3)	0/21 (0.0)	0/21 (0.0)	0/6 (0.0)	0/6 (0.0)	0/6 (0.0)
Humerus	2/6 (33.3)	1/6 (16.7)	0/6 (0.0)	13/44 (29.5)	1/44 (2.3)	0/44 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Radius	5/10 (50.0)	0/10 (0.0)	0/10 (0.0)	8/43 (18.6)	0/43 (0.0)	0/43 (0.0)	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)
Ulna	1/3 (33.3)	1/3 (33.3)	0/3 (0.0)	3/16 (18.8)	0/16 (0.0)	0/16 (0.0)	0/5 (0.0)	0/5 (0.0)	0/5 (0.0)
Carpals	0/9 (0.0)	0/9 (0.0)	0/9 (0.0)	2/17 (11.8)	0/17 (0.0)	0/17 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Metacarpal	2/14 (14.3)	0/14 (0.0)	1/14 (7.1)	11/37 (29.7)	1/37 (2.7)	0/37 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Femur	1/14 (7.1)	0/14 (0.0)	0/14 (0.0)	16/44 (36.4)	0/44 (0.0)	0/44 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Patella	0/4 (0.0)	0/4 (0.0)	0/4 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Tibia	5/17 (29.4)	0/17 (0.0)	0/17 (0.0)	14/73 (19.2)	0/73 (0.0)	1/73 (1.4)	0/5 (0.0)	1/5 (20.0)	0/5 (0.0)
Tarsals	0/16 (0.0)	0/16 (0.0)	0/16 (0.0)	1/12 (8.3)	0/12 (0.0)	0/12 (0.0)	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)
Metatarsal	3/10 (30.0)	1/10 (10.0)	0/10 (0.0)	13/41 (31.7)	0/41 (0.0)	1/41 (2.4)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Phalanges	2/30 (6.7)	0/30 (0.0)	0/30 (0.0)	1/35 (2.9)	0/35 (0.0)	0/35 (0.0)	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)
Sesamoids	0/9 (0.0)	0/9 (0.0)	0/9 (0.0)	1/20 (5.0)	0/20 (0.0)	0/20 (0.0)	0/4 (0.0)	0/4 (0.0)	0/4 (0.0)
LBS	1/23 (4.3)	0/23 (0.0)	0/23 (0.0)	18/109 (16.5)	1/109 (0.9)	2/109 (1.8)	1/24 (4.2)	0/24 (0.0)	0/24 (0.0)
Total	25/216 (11.6)	3/216 (1.4)	1/216 (0.5)	126/654 (19.3)	3/654 (0.5)	4/654 (0.6)	4/120 (3.3)	1/120 (0.8)	0/120 (0.0)

Note: Numerator denotes number of marked specimens, denominator denotes total NISP for each skeletal element, percentage is in parentheses.

Codes: TM = tooth mark; CM = cutmark, PM = percussion mark; LBS = unidentified limb bone fragment.

Table 4.12. Surface mark frequencies by element and carcass size at DK 3.

Element	Small			Medium			Large		
	TM	CM	PM	TM	CM	PM	TM	CM	PM
Mandible	2/6 (33.3)	0/6 (0.0)	0/6 (0.0)	2/27 (7.4)	0/27 (0.0)	0/27 (0.0)	0/6 (0.0)	0/6 (0.0)	0/6 (0.0)
Vertebrae	0/8 (0.0)	0/8 (0.0)	0/8 (0.0)	2/25 (8.0)	0/25 (0.0)	0/25 (0.0)	0/6 (0.0)	0/6 (0.0)	0/6 (0.0)
Innominate	1/2 (50.0)	0/2 (0.0)	0/2 (0.0)	5/12 (41.7)	0/12 (0.0)	0/12 (0.0)	1/2 (50.0)	0/2 (0.0)	0/2 (0.0)
Ribs	0/16 (0.0)	0/16 (0.0)	0/16 (0.0)	4/26 (15.4)	0/26 (0.0)	0/26 (0.0)	0/26 (0.0)	0/26 (0.0)	0/26 (0.0)
Scapula	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)	2/15 (13.3)	0/15 (0.0)	0/15 (0.0)	0/4 (0.0)	0/4 (0.0)	0/4 (0.0)
Humerus	1/5 (20.0)	0/5 (0.0)	0/5 (0.0)	7/33 (21.2)	0/33 (0.0)	0/33 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Radius	1/4 (25.0)	0/4 (0.0)	0/4 (0.0)	6/26 (23.1)	0/26 (0.0)	0/26 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Ulna	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)	2/9 (22.2)	0/9 (0.0)	0/9 (0.0)	1/2 (50.0)	0/2 (0.0)	0/2 (0.0)
Carpals	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)	0/11 (0.0)	0/11 (0.0)	0/11 (0.0)	0/1 (0.0)	0/1 (0.0)	0/1 (0.0)
Metacarpal	2/8 (25.0)	1/8 (12.5)	0/8 (0.0)	1/20 (5.0)	0/20 (0.0)	0/20 (0.0)	1/2 (50.0)	0/2 (0.0)	0/2 (0.0)
Femur	0/8 (0.0)	0/8 (0.0)	0/8 (0.0)	6/35 (17.1)	0/35 (0.0)	1/35 (2.9)	0/4 (0.0)	0/4 (0.0)	0/4 (0.0)
Patella	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Tibia	3/11 (27.3)	0/11 (0.0)	0/11 (0.0)	5/48 (10.4)	0/48 (0.0)	0/48 (0.0)	0/8 (0.0)	0/8 (0.0)	0/8 (0.0)
Tarsals	0/12 (0.0)	0/12 (0.0)	0/12 (0.0)	4/21 (19.0)	0/21 (0.0)	0/21 (0.0)	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)
Metatarsal	1/11 (9.1)	0/11 (0.0)	0/11 (0.0)	12/35 (34.3)	0/35 (0.0)	0/35 (0.0)	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Phalanges	0/17 (0.0)	0/17 (0.0)	0/17 (0.0)	1/8 (12.5)	0/8 (0.0)	0/8 (0.0)	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)
Sesamoids	0/4 (0.0)	0/4 (0.0)	0/4 (0.0)	0/9 (0.0)	0/9 (0.0)	0/9 (0.0)	0/2 (0.0)	0/2 (0.0)	0/2 (0.0)
LBS	2/32 (6.3)	0/32 (0.0)	0/32 (0.0)	3/126 (2.4)	0/126 (0.0)	0/126 (0.0)	1/7 (14.3)	0/7 (0.0)	0/7 (0.0)
Total	13/149 (8.7)	1/149 (0.7)	0/149 (0.0)	62/486 (12.8)	0/486 (0.0)	1/486 (0.2)	4/76 (5.3)	0/76 (0.0)	0/76 (0.0)

Note: Numerator denotes number of marked specimens, denominator denotes total NISP for each skeletal element, percentage is in parentheses.

Codes: TM = tooth mark; CM = cutmark, PM = percussion mark; LBS = unidentified limb bone fragment.

Table 4.13. Tooth mark frequencies by element and carcass size at FLKNN 2 and FLKN 5.

Element	FLKNN 2			FLKN 5			
	Small	Medium	Total	Small	Medium	Large	Total
Mandible	0/2 (0.0)	0/10 (0.0)	0/12 (0.0)	0/24 (0.0)	0/8 (0.0)	0/2 (0.0)	0/34 (0.0)
Vertebrae	0/4 (0.0)	0/14 (0.0)	0/18 (0.0)	3/16 (18.8)	1/27 (3.7)	0/1 (0.0)	4/44 (9.1)
Innominate	0/0 (0.0)	0/2 (0.0)	0/2 (0.0)	4/25 (16.0)	3/7 (42.9)	0/0 (0.0)	7/32 (21.9)
Ribs	0/3 (0.0)	1/39 (2.6)	1/42 (2.4)	3/23 (13.0)	1/22 (4.5)	1/9 (11.1)	5/54 (9.3)
Scapula	1/3 (33.3)	2/7 (28.6)	3/10 (30.0)	2/14 (14.3)	0/12 (0.0)	0/1 (0.0)	2/27 (7.4)
Humerus	1/2 (50.0)	6/14 (42.9)	7/16 (43.8)	7/16 (43.8)	2/28 (7.1)	0/0 (0.0)	9/44 (20.5)
Radius	1/1 (100.0)	7/12 (58.3)	8/13 (61.5)	8/26 (30.8)	1/21 (4.8)	0/0 (0.0)	9/47 (19.1)
Ulna	0/0 (0.0)	6/8 (75.0)	6/8 (75.0)	5/10 (50.0)	2/13 (15.4)	0/0 (0.0)	7/23 (30.4)
Carpals	0/1 (0.0)	0/2 (0.0)	0/3 (0.0)	0/33 (0.0)	0/17 (0.0)	0/0 (0.0)	0/50 (0.0)
Metacarpal	0/0 (0.0)	4/15 (26.7)	4/15 (26.7)	14/24 (58.3)	3/19 (15.8)	0/0 (0.0)	17/43 (39.5)
Femur	1/4 (25.0)	3/7 (42.9)	4/11 (36.4)	4/23 (17.4)	9/30 (30.0)	0/0 (0.0)	13/53 (24.5)
Patella	0/0 (0.0)	0/1 (0.0)	0/1 (0.0)	0/6 (0.0)	0/2 (0.0)	0/0 (0.0)	0/8 (0.0)
Tibia	1/3 (33.3)	8/18 (44.4)	9/21 (42.9)	11/36 (30.6)	6/57 (10.5)	0/1 (0.0)	17/93 (18.3)
Tarsals	0/0 (0.0)	0/1 (0.0)	0/1 (0.0)	2/49 (4.1)	1/28 (3.6)	0/0 (0.0)	3/77 (3.9)
Metatarsal	2/4 (50.0)	6/13 (46.2)	8/17 (47.1)	10/38 (26.3)	4/22 (18.2)	0/1 (0.0)	14/61 (22.9)
Phalanges	0/1 (0.0)	1/6 (16.7)	1/7 (14.3)	0/127 (0.0)	1/21 (4.8)	0/0 (0.0)	1/148 (0.7)
Sesamoids	0/0 (0.0)	0/3 (0.0)	0/3 (0.0)	0/35 (0.0)	0/20 (0.0)	0/0 (0.0)	0/55 (0.0)
LBS	1/4 (25.0)	1/6 (16.7)	2/10 (20.0)	2/68 (2.9)	9/81 (11.1)	0/0 (0.0)	11/149 (7.4)
Total	8/33 (24.2)	45/178 (25.3)	53/211 (25.1)	75/593 (12.6)	43/435 (9.9)	1/15 (6.7)	119/1043 (11.4)

Note: Numerator denotes number of marked specimens, denominator denotes total NISP for each skeletal element, percentage is in parentheses. Codes: LBS = unidentified limb bone fragment.

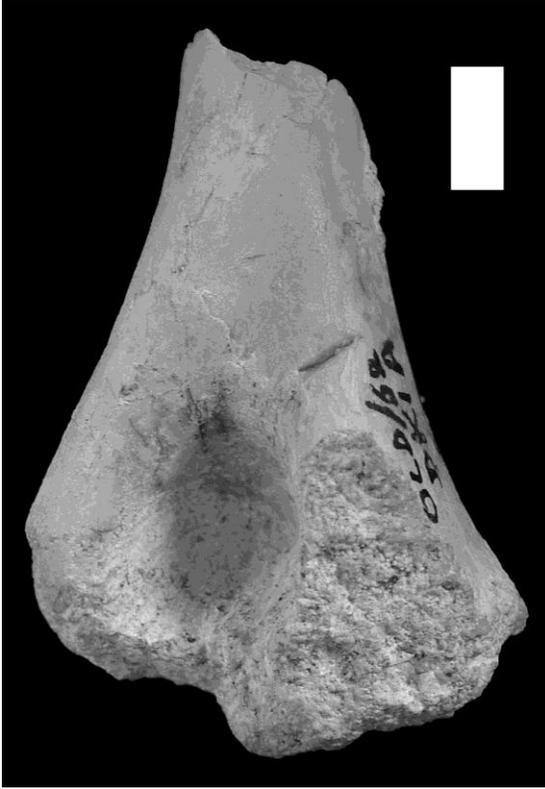


Figure 4.7. Caudal view of a distal bovid humerus from DK showing cutmarks. Scale bar = 1 cm.

The overall incidence of tooth-marking is 25% at FLKNN 2 and 11% at FLKN 5 (Table 4.13). The single cutmarked specimen from FLKN 5 derives from a Size Class 3a humerus. All types of surface damage at the Bed I sites cluster on the appendicular skeleton. Digested pieces occur in all

the assemblages except DK 1. Thirty-two (1.9% of total NISP) and nine (0.7%) were discovered in DK 2 and 3, respectively. Only one piece (0.2%) was identified at FLKNN 2 while FLKN 5 has a total of 54 (3.4%) digested specimens.

Table 4.14 summarizes tooth mark frequencies by limb bone segment. DK 3 shows the lowest overall tooth mark frequencies while DK 1 and 2 and FLKNN 2 have relatively high frequencies. FLKN 5 shows intermediate values. Figures 4.11 and 4.12 display tooth mark

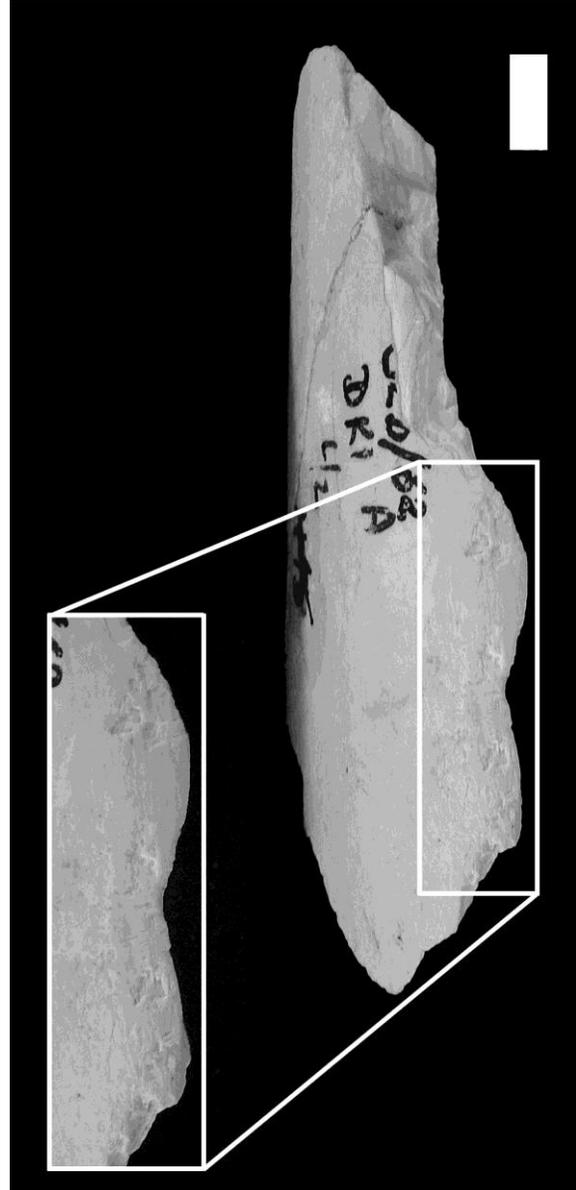


Figure 4.8. Tibia fragment from DK showing percussion marks. Scale bar = 1 cm.

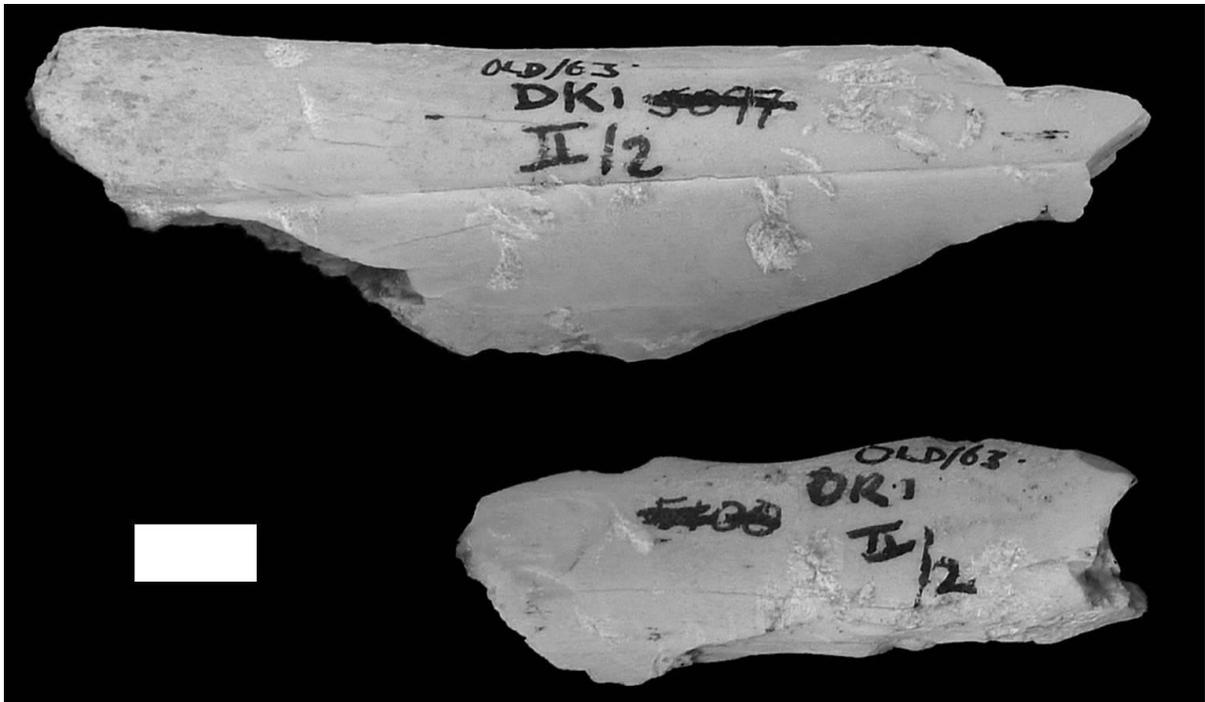


Figure 4.9. Unidentified limb bone (bottom) and metacarpal (top) fragments from DK showing tooth marks. Scale bar = 1 cm.

frequencies on midshaft fragments for the Bed I sites relative to a number of actualistic samples. (Experimental work has demonstrated that epiphyseal and near-epiphyseal tooth mark frequencies are ambiguous indicators of carnivore access to carcasses because these segments retain grease before and after hominid marrow processing [Blumenshine, 1995; Capaldo, 1997].)

The lack of hominid damage and a paucity of other evidence for hominid bone breakage at FLKNN 2 and FLKN 5 (see below) strongly implicate carnivores as the primary modifier of carcasses in these assemblages. Therefore, one would expect tooth mark frequencies to match experimental samples where carnivores enjoyed sole access to flesh and marrow. This expectation is largely met at FLKNN 2, as medium-sized carcasses fall comfortably within the range of “carnivore-only” models. However, tooth mark frequencies on small carcasses at FLKN 5 fall between the ranges of both the “carnivore-only” and “hammerstone-to-carnivore” scenarios. More puzzling is the fact that tooth mark frequencies on medium-sized carcasses at FLKN 5 fall just within the range of experiments where carnivores scavenged demarrowed limb bones. Again, this is unlikely given the absence of hominid bone modifications. However, if felids are considered a primary agent of bone modification

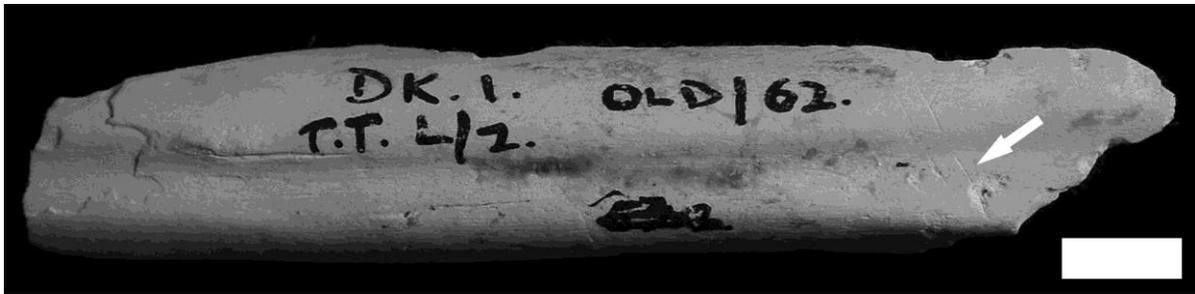


Figure 4.10. Cranial view of a metatarsal fragment from DK 2 showing tooth marks overlying cutmarks (arrow). Scale bar = 1 cm.

the tooth mark data make more sense. In particular, medium-sized felids like cheetahs and leopards are known to tooth-mark limb bones and midshafts in particular in lower frequencies than do hyenas (Domínguez-Rodrigo et al., in press b; Pobiner, 2007; Selvaggio, 1994a). In fact, Figures 4.11 and 4.12 show that felid defleshing followed by bone fragmentation results in very similar midshaft tooth mark frequencies to the “hammerstone-to-carnivore” samples. Tooth mark frequencies on epiphyseal and near-epiphyseal fragments at FLKN 5 are similar to, though not precisely the same as, those generated by leopards and cheetahs (95% confidence intervals = 0–48.5 and 0–34.8, respectively; Domínguez-Rodrigo et al., in press b). At DK, the medium carcasses from Level 1 and the small carcasses from Level 2 fall within “carnivore-only” ranges while the Level 1 small carcasses and the Level 2 medium carcasses lie outside the ranges of all the actualistic models. The Level 3 assemblage is within the range of “hammerstone-to-carnivore” samples.

The fact that felids can produce similar tooth mark frequencies to those generated in “hammerstone-to-carnivore” scenarios means that these data do not necessarily speak directly to the order of *hominid* access to carcasses. Therefore, other evidence, especially hominid-imparted surface modifications and bone breakage, must be brought to bear on the issue. The presence of several percussion marks in DK 2 and a single mark in DK 1 and 3 indicates that limited hominid bone-breaking occurred at these sites. However, percussion mark percentages are far below those expected if hominids had processed most of the limb bones for marrow. Cutmarks also appear in very low frequencies among the Bed I sites, again falling well below those expected if hominids butchered most or all the carcasses. The anatomical location of the cutmarks is largely equivocal in terms of

Table 4.14. Percentage of epiphyseal, near-epiphyseal, and midshaft specimens bearing tooth marks by carcass size at the Bed I sites.

	Small			Medium		
	NISP	NISP TM	%	NISP	NISP TM	%
<b>DK 1</b>						
EP	0	0	0.0	4	3	75.0
NEP	0	0	0.0	2	2	100.0
MSH	3	1	33.3	9	4	44.4
Total	3	1	33.3	15	9	60.0
<b>DK 2</b>						
EP	6	2	33.3	24	12	50.0
NEP	6	4	66.7	31	17	54.8
MSH	17	9	59.9	84	28	33.3
Total	29	15	51.7	139	57	41.0
<b>DK 3</b>						
EP	8	3	37.5	11	1	9.1
NEP	4	0	0.0	19	5	26.3
MSH	19	3	15.8	87	17	19.5
Total	31	6	19.4	117	23	19.7
<b>FLKNN 2</b>						
EP	0	0	0.0	19	11	57.9
NEP	3	3	100.0	8	5	62.5
MSH	0	0	0.0	10	5	50.0
Total	3	3	100.0	37	21	56.8
<b>FLKN 5</b>						
EP	21	13	61.9	5	1	20.0
NEP	8	2	25.0	18	9	50.0
MSH	52	19	36.5	36	6	22.2
Total	81	34	42.0	59	18	30.5

Note: Only green-broken specimens with good surface preservation included. Codes: NISP = number of identified specimens, TM = tooth mark, EP = epiphyseal, NEP = near-epiphyseal, MSH = midshaft.

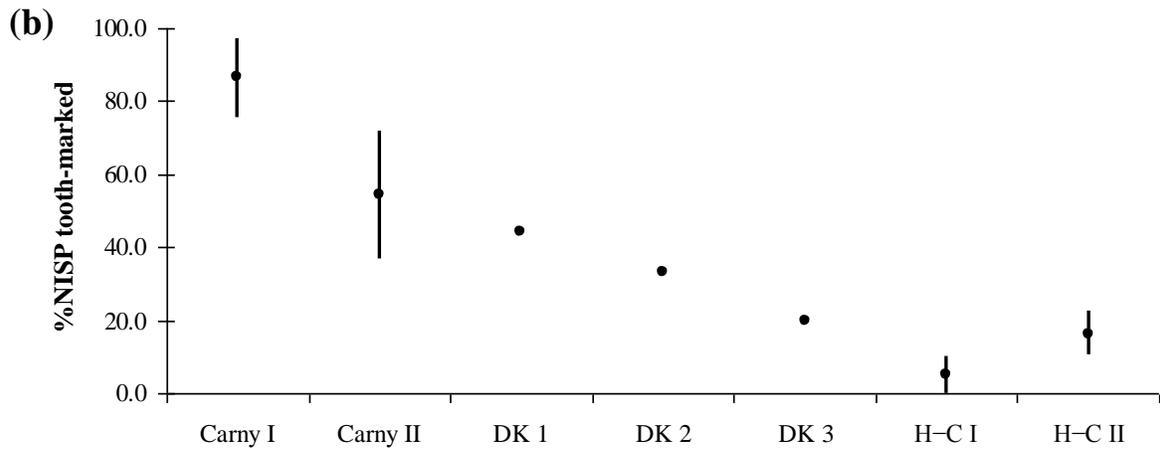
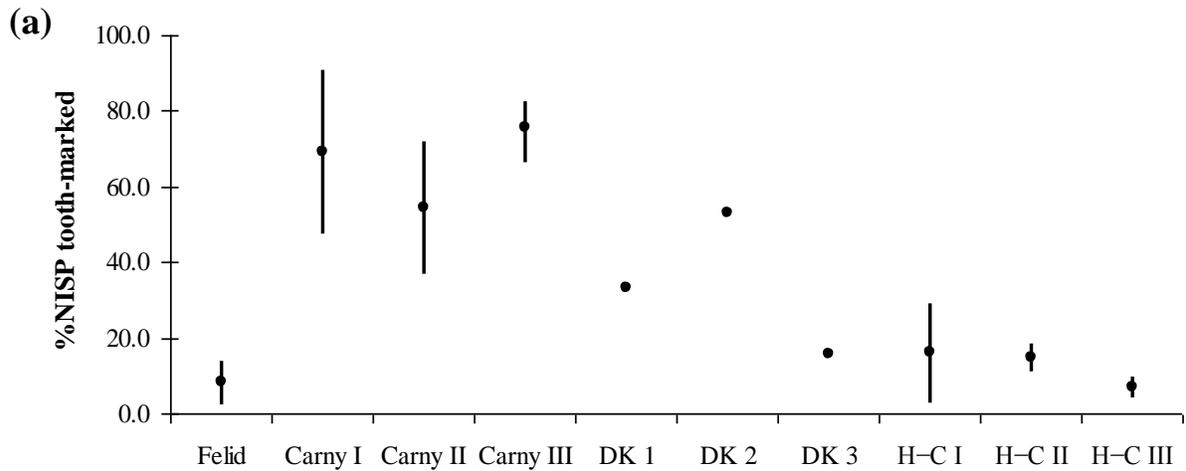


Figure 4.11. Percentage of tooth-marked midshaft specimens at DK for (a) small and (b) medium carcasses compared to the mean and 95% confidence intervals of several actualistic samples. Codes: Felid = felid-consumed carcass followed by hammerstone breakage, Carny = carnivore-only, H-C = hammerstone-to-carnivore. Note: Only fossil specimens with green breakage and good surface preservation are considered. Data from Blumenschine (1995), Capaldo (1997), Domínguez-Rodrigo et al. (in press b), Marean et al. (2000). The range of variation from Marean's experiments ("Carny III" and "H-C III") are somewhat smaller because confidence intervals were calculated by bootstrapping a single sample (Marean et al., 2000: Table 3).

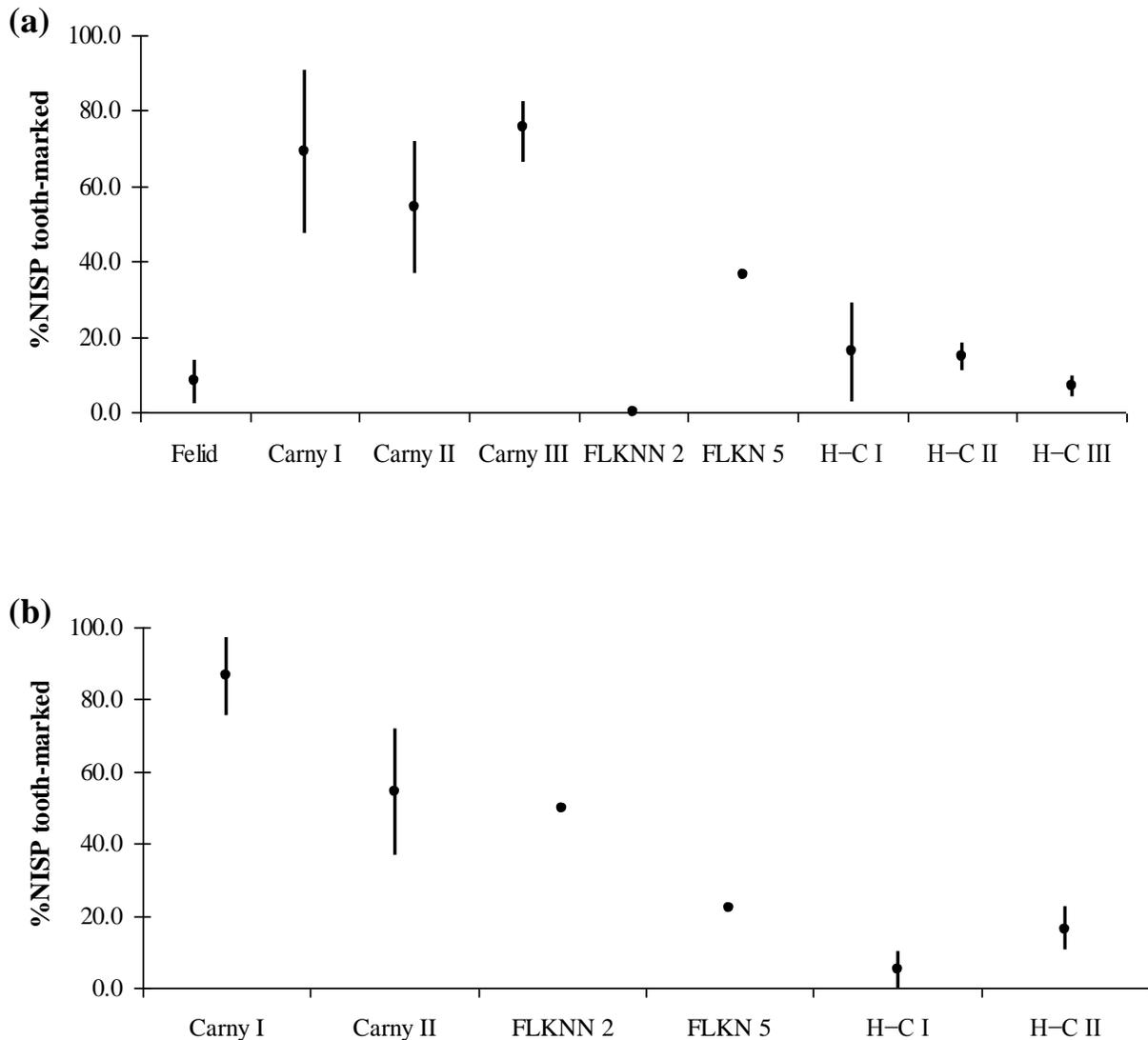


Figure 4.12. Percentage of tooth-marked midshaft specimens at FLKNN 2 and FLKN 5 for (a) small and (b) medium carcasses compared to the mean and 95% confidence intervals of several actualistic samples. Note: For codes and comments see Figure 4.11.

hominid access to carcasses (Table 4.15), although early access to carcasses was gained in some instances.

Table 4.16 summarizes tooth pit dimensions on limb bone diaphyses at the Bed I sites. Only the sample of pits on the DK 2 and FLKNN 2 medium carcasses and the small carcasses from FLKN 5 are large enough to provide reasonable ranges of variation and therefore only these samples are plotted in Figure 4.13. The DK 2 and FLKNN 2 data match well with the ranges of modern carnivores with larger and more robust dentitions like lions and hyenas. Although the samples are

very small, the means of the other DK samples are more consistent with larger carnivores as well. On the other hand, the FLKN 5 small carcass data are similar to pit dimensions created by smaller carnivores such as leopards, cheetahs and jackals.

Table 4.15. Anatomical location of cutmarks in the Bed I assemblages and inferred timing of access.

Assemblage	Element	Size Class	Segment	Section	Interpretation
DK 2	Humerus	2	Near-epiphysis	Near-epiphysis	Early/Late
DK 2	Ulna	2	–	–	Early/Late
DK 2	Metatarsal	2	Midshaft	Midshaft	Early/Late
DK 2	Humerus	3a	Near-epiphysis	Midshaft	Early
DK 2	Metacarpal	3a	Midshaft	Midshaft	Early/Late
DK 2	Upper limb bone	3a	Midshaft	Midshaft	Early
DK 2	Tibia	5	Midshaft	Midshaft	Early?
DK 3	Metacarpal	2	Epiphysis	Near-epiphysis	Early/Late
FLKN 5	Humerus	3a	Epiphysis	Near-epiphysis	Early/Late

Note: Interpretations based on the fact that little or no flesh remains on the midshaft section of upper and intermediate limb bones after felid defleshing (Domínguez-Rodrigo, 1999a). See text for full explanation.

Table 4.16. Summary statistics of tooth pit dimensions by carcass size at the Bed I sites.

	DK 2		DK 3		FLKNN 2		FLKN 5	
	Small	Medium	Small	Medium	Small	Medium	Small	Medium
<b>Length</b>								
N	5	22	2	5	6	27	34	3
Mean	3.4	3.2	2.5	2.7	2.2	3.2	1.9	2.7
S.D.	1.4	1.0	0.9	1.3	0.8	2.0	0.8	1.4
95% CI	1.7–5.2	2.7–3.6	0.0–10.3	1.1–4.2	1.3–3.0	2.5–3.9	1.7–2.2	0.0–6.1
<b>Breadth</b>								
N	5	22	2	5	6	27	34	3
Mean	2.5	2.2	2.0	2.0	1.6	2.2	1.3	2.1
S.D.	1.3	0.7	0.4	0.9	0.5	1.3	0.6	1.2
95% CI	0.9–4.2	1.9–2.5	0.0–5.6	0.9–3.2	1.0–2.1	1.7–2.7	1.1–1.5	0.0–5.0

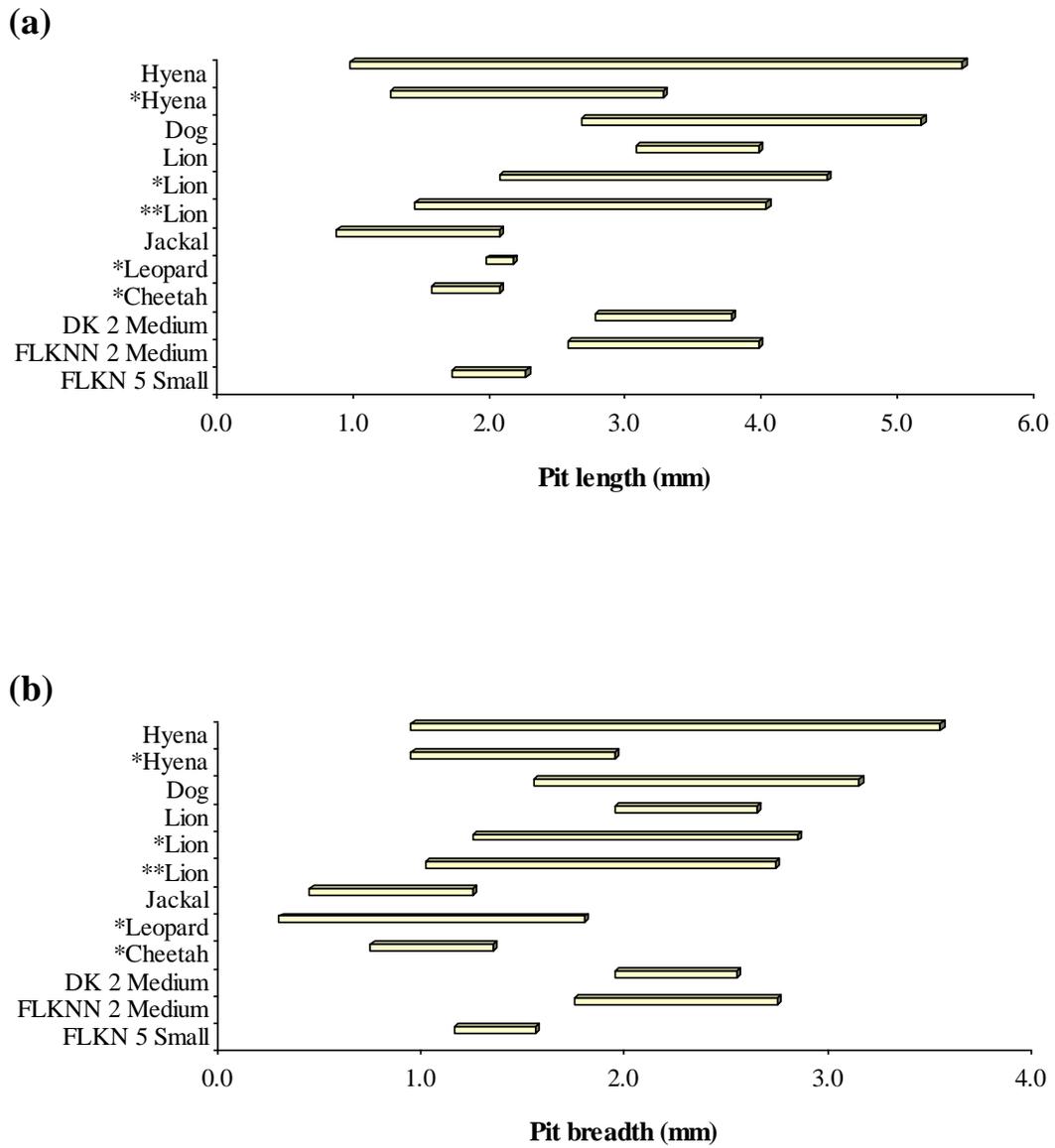


Figure 4.13. Range (95% confidence intervals) of tooth pit (a) lengths and (b) breadths from the Bed I sites and several actualistic samples. Data marked with one asterisk (\*) are from Selvaggio (1994b), data marked with two asterisks (\*\*) from Pobiner (2007). All other actualistic data from Domínguez-Rodrigo and Piqueras (2003).

## FRACTURE PATTERNS

A majority of breakage at the Bed I sites occurred during nutrient extraction (Figure 4.14). The exception to this is the FLKN 5 fauna, which shows a significant frequency of dry breakage. Minor earth movements were apparently common at the FLKN locality and Leakey (1971: 67) noted that this caused much of the fauna to break during fossilization. Other than DK 1, complete limb bones are relatively common at all three sites (Table 4.17). In general limb bones are broken in direct proportion to their nutritional yield; that is, the high-utility humeri and femora were broken more often than lower-utility radii and tibiae, which were in turn broken more often than the lowest-utility metapodials. More unbroken limb bones are found among small carcasses at DK 3 and FLKN 5 while medium carcasses have more unbroken limb bones at DK 2 and FLKNN 2. All three Bed I sites show more Type 3 circumferences than experimental assemblages with intense hyena ravaging (see Figure 4.2).

Table 4.18 lists general measures of fragmentation and 4.19 provides data specific to limb bones for the Bed I sites and several actualistic controls. In general, fragmentation ratios are higher for medium carcasses. The main exception to this is FLKNN 2, where small carcasses are more highly fragmented than are medium carcasses. DK 3 shows the highest limb bone fragmentation. The actualistic samples indicate that human marrow processing creates the most comminuted assemblages followed by hyenas and lions. Leopards, cheetahs, dogs and jackals all produce lower fragmentation ratios. In terms of limb bone fragmentation, the small carcass samples for the Bed I sites are far lower than the hammerstone-only experimental assemblages. They also fall below the open-air hyena assemblages and above those created by carnivores with less robust dentitions (leopards, dogs and jackals) (Figure 4.15). However, they are tightly bracketed by the hyena den and Kua assemblages. The medium carcass sample from all the Bed I sites is well below the hammerstone-generated Kua assemblage. The low fragmentation of the medium carcasses from FLKNN 2 matches well with the experimental lion sample while the DK 3 value is close to experimental hammerstone-only assemblages.

Table 4.17. Incidence  
of complete limb bones by carcass size at the Bed I sites.

Element	Small	Medium	Total
<b>DK 2</b>			
Humerus	0/4 (0.0)	1/25 (4.0)	1/29 (3.4)
Radius	1/8 (12.5)	2/21 (19.0)	3/29 (10.3)
Metacarpal	0/11 (0.0)	5/20 (25.0)	5/31 (16.1)
Femur	0/8 (0.0)	1/23 (4.3)	1/31 (3.2)
Tibia	0/10 (0.0)	1/30 (3.3)	1/40 (2.5)
Metatarsal	0/6 (0.0)	3/23 (13.0)	3/29 (10.3)
Total	1/47 (2.1)	15/142 (10.6)	16/189 (8.5)
<b>DK 3</b>			
Humerus	0/5 (0.0)	1/18 (5.6)	1/23 (4.3)
Radius	0/2 (0.0)	0/13 (0.0)	0/15 (0.0)
Metacarpal	0/6 (0.0)	0/9 (0.0)	0/15 (0.0)
Femur	2/6 (33.3)	1/17 (5.9)	3/23 (13.0)
Tibia	1/6 (16.7)	3/22 (13.6)	4/28 (14.3)
Metatarsal	1/7 (14.3)	2/16 (12.5)	3/23 (13.0)
Total	4/32 (12.5)	7/95 (7.4)	11/127 (8.7)
<b>FLKNN 2</b>			
Humerus	0/2 (0.0)	1/13 (7.7)	1/15 (6.7)
Radius	0/1 (0.0)	4/12 (33.3)	4/13 (30.8)
Metacarpal	0/0 (0.0)	8/13 (61.5)	8/13 (61.5)
Femur	0/3 (0.0)	1/5 (20.0)	1/8 (12.5)
Tibia	0/3 (0.0)	2/9 (22.2)	2/12 (16.7)
Metatarsal	0/4 (0.0)	2/8 (25.0)	2/12 (16.7)
Total	0/13 (0.0)	17/60 (28.3)	17/73 (23.3)
<b>FLKN 5</b>			
Humerus	2/13 (15.4)	0/14 (0.0)	2/27 (7.4)
Radius	2/19 (10.5)	1/10 (10.0)	3/29 (10.3)
Metacarpal	3/17 (17.6)	6/13 (46.2)	9/30 (30.0)
Femur	0/10 (0.0)	0/12 (0.0)	0/22 (0.0)
Tibia	1/23 (4.3)	1/17 (5.9)	2/40 (5.0)
Metatarsal	10/20 (50.0)	4/16 (25.0)	14/36 (38.9)
Total	18/102 (17.6)	12/82 (14.6)	30/184 (16.3)

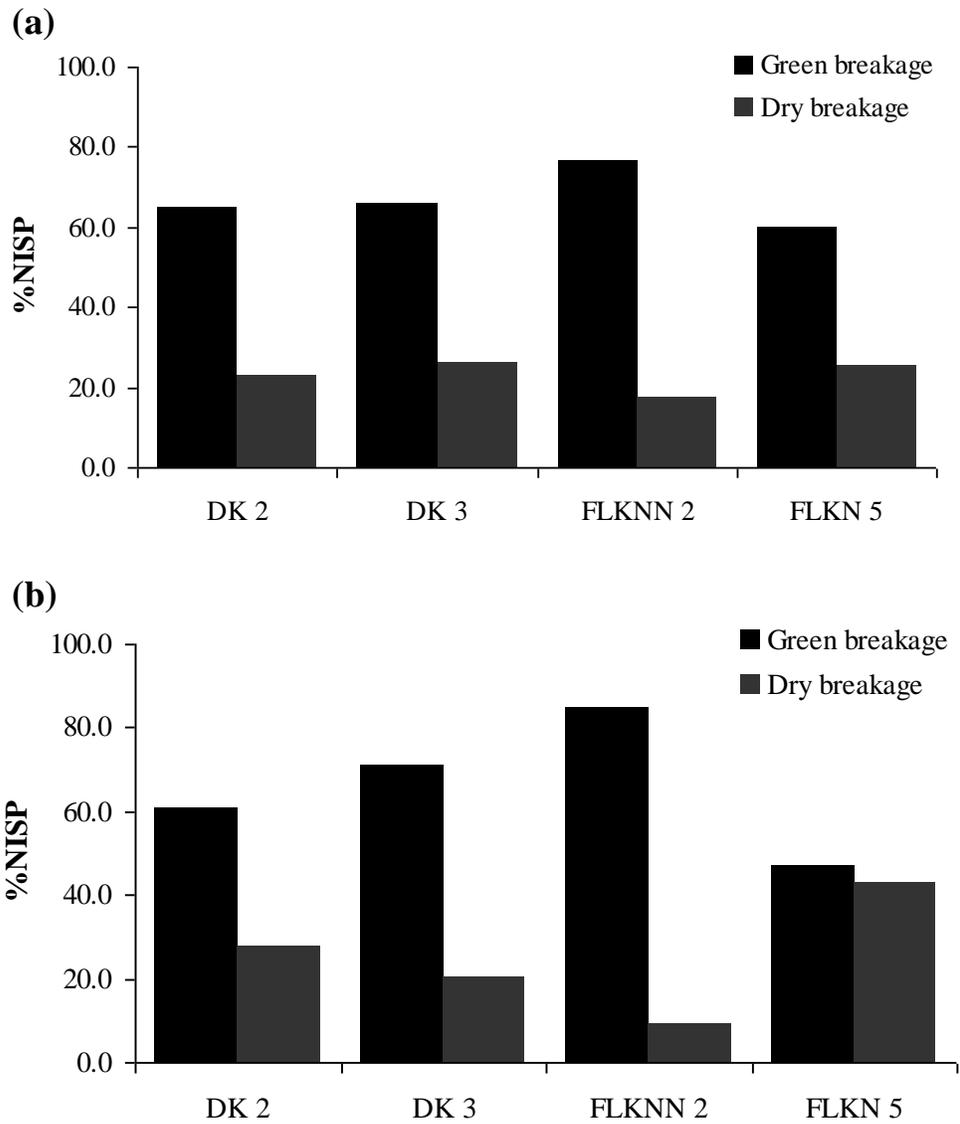


Figure 4.14. Percentage of green and dry breakage on limb bones for (a) small and (b) medium carcasses in the Bed I sites. Note: Specimens with recent breakage are not included, therefore values may not add to 100%.

Actualistic research demonstrates that hyena ravaging consistently results in the highest levels of epiphyseal destruction, whether or not limb bones are first processed for marrow by humans. Lion processing of small carcasses can also result in similarly high epiphyseal loss. Hammerstone-generated experiments can also show relatively low epiphysis-to-shaft ratios; however, this is due not to epiphyseal destruction but to the fact that hammerstone breakage results in a disproportionately high number of shaft fragments. Other than DK 1, the Bed I assemblages show higher rates of epiphyseal survival than seen among assemblages heavily ravaged by hyenas in experimental and open-air naturalistic contexts (Figure 4.16). For small carcasses, all the assemblages are below the hammerstone-broken Kua assemblage. DK 3 and FLKN 5 are close to the values produced by medium-sized felids and jackals. The medium carcass sample from FLKNN 2 is conspicuous in its high epiphyseal representation. The other sites fall between the hyena, lion and hammerstone assemblages.

Table 4.20 provides summary statistics for fracture plane angles at the Bed I sites. Because only a handful of transverse planes >4 cm were recorded only the data from longitudinal and oblique planes are summarized here. Figures 4.17 and 4.18 show the distribution of angles in the Bed I sites in relation to experimentally derived ranges for dynamic and static loading. The DK assemblages, especially Level 2, have a substantial number of fracture angles completely outside the carnivore range. Most of the angles at FLKNN 2 fall within the carnivore range of variation. FLKN 5 is intermediate between DK and FLKNN 2, although a majority of the angles still fall within the carnivore range.

Of those notches complete enough to provide both ratios, many of them fall within or below the ranges of carnivore-created notches (Figure 4.19). For medium carcasses, the fact that the carnivore and hammerstone ranges overlap extensively is largely due to the very small sample size of experimental hammerstone-generated notches ( $n = 3$ ; Capaldo and Blumenschine, 1994: Table 4). Therefore, the two DK 3 outliers in Figure 4.19 are probably consistent with hammerstone breakage.

Table 4.18. Fragmentation indices by carcass size for the Bed I sites and several actualistic samples.

	Small		Medium	
	<u>NISP:MNE</u>	<u>NISP:MNI</u>	<u>NISP:MNE</u>	<u>NISP:MNI</u>
<b>Olduvai Bed I</b>				
DK 1	1.34	15.67	1.16	17.21
DK 2	1.23	30.45	1.10	30.67
DK 3	1.06	21.58	1.28	25.00
FLKNN 2	4.17	20.83	1.00	15.65
FLKN 5	1.12	33.04	1.01	30.58
<b>Carnivore-Experimental</b>				
Brown hyena	2.21	-	-	-
Spotted hyena	5.17	-	1.71	-
Spotted hyena II	-	-	1.02	-
Lion	-	-	1.02	-
Lion II	1.56	-	1.02	-
Lion-Spotted hyena	-	-	1.01	-
Leopard	1.00	-	-	-
Leopard II	1.00	-	-	-
Cheetah	1.05	-	-	-
Dog	1.08	-	-	-
Jackal	1.07	-	1.10	-
Jackal II	1.11	-	-	-
<b>Carnivore-Dens</b>				
Syokimau (Spotted hyena)	-	-	-	13.90
KFHD 1 (Spotted hyena)	-	25.26	-	11.00
<b>Hunter-gatherer</b>				
Khwee	-	-	-	94.70
Kua	1.98	58.14	3.57	257.40

Data sources: Bartram and Marean (1999: Tables 2 and 3), Bunn (1982: Table 3.11), Lam (1992: Table 1), Pobiner (2007: Tables 4.2 and 4.3) and Richardson (1980: Figure 4). Note: The Syokimau den consists of Size Class 1–5 carcasses; however, a vast majority of the skeletal material derives from Size Class 3 cows (Bunn, 1982; personal observations). Similarly, the Khwee assemblage consists of Size Class 1–4 carcasses; however, a vast majority of the skeletal material derives from Size Class 4 eland (Bunn, 1982).

Table 4.19. Limb bone fragmentation indices by carcass size for the Bed I sites and several actualistic samples.

	Small		Medium	
	NISP:MNE	EP:SH	NISP:MNE	EP:SH
<b>Olduvai Bed I</b>				
DK 1	1.00	0.00	1.79	0.61
DK 2	1.78	0.46	2.36	0.45
DK 3	2.22	0.68	3.01	0.31
FLKNN 2	1.92	0.38	1.35	1.37
FLKN 5	1.98	0.77	2.43	0.42
<b>Carnivore-Experimental</b>				
Hyena	4.90	–	–	–
Spotted hyena	3.86	0.02	6.45	0.25
Lion-Spotted hyena	–	–	1.01	0.43
Lion	–	0.05	–	0.71
Leopard	1.00	0.70	–	–
Cheetah	–	0.67	–	–
Dog	1.01	–	–	–
Jackal	1.03	0.67	1.04	–
Carnivore-only I	–	0.03	–	0.02
Carnivore-only II	–	0.08	–	–
<b>Carnivore-Dens</b>				
Syokimau (Spotted hyena)	–	–	–	0.63
KFHD 1 (Spotted hyena)	1.60	–	–	–
<b>Human-Experimental</b>				
Hammerstone-only I	–	0.36	–	0.50
Hammerstone-only II	–	–	3.08	0.42
Hammerstone-only III	–	–	4.13	0.70
Hammerstone-only IV	12.03	0.20	–	–
HS-C I	7.82	0.05	–	–
HS-C II	–	0.01	–	0.03
HS-C III	–	0.11	–	–
<b>Hunter-gatherer</b>				
Kua	2.68	1.23	9.98	0.67

Data sources: Bartram and Marean (1999: Table 3), Blumenschine (1995: Table 1), Bunn (1982: Tables 3.4 and 3.11; 1989: Table 2), Capaldo (1997: Table 7, 1998: Tables 10 and 11), Lam (1992: Table 3), Marean (data cited in Monahan [1996a: Table 3]), Pickering and Egeland (2006), Pobiner (2007: Tables 4.5 and 4.6), Richardson (1980: Figure 4) and Selvaggio (1994a: Table 1). Note: The data presented here differ slightly from those in Pickering and Egeland (2006), as only fragments  $\geq 2$  cm (and not  $\geq 1$  cm as in Pickering and Egeland [2006]) are considered here.

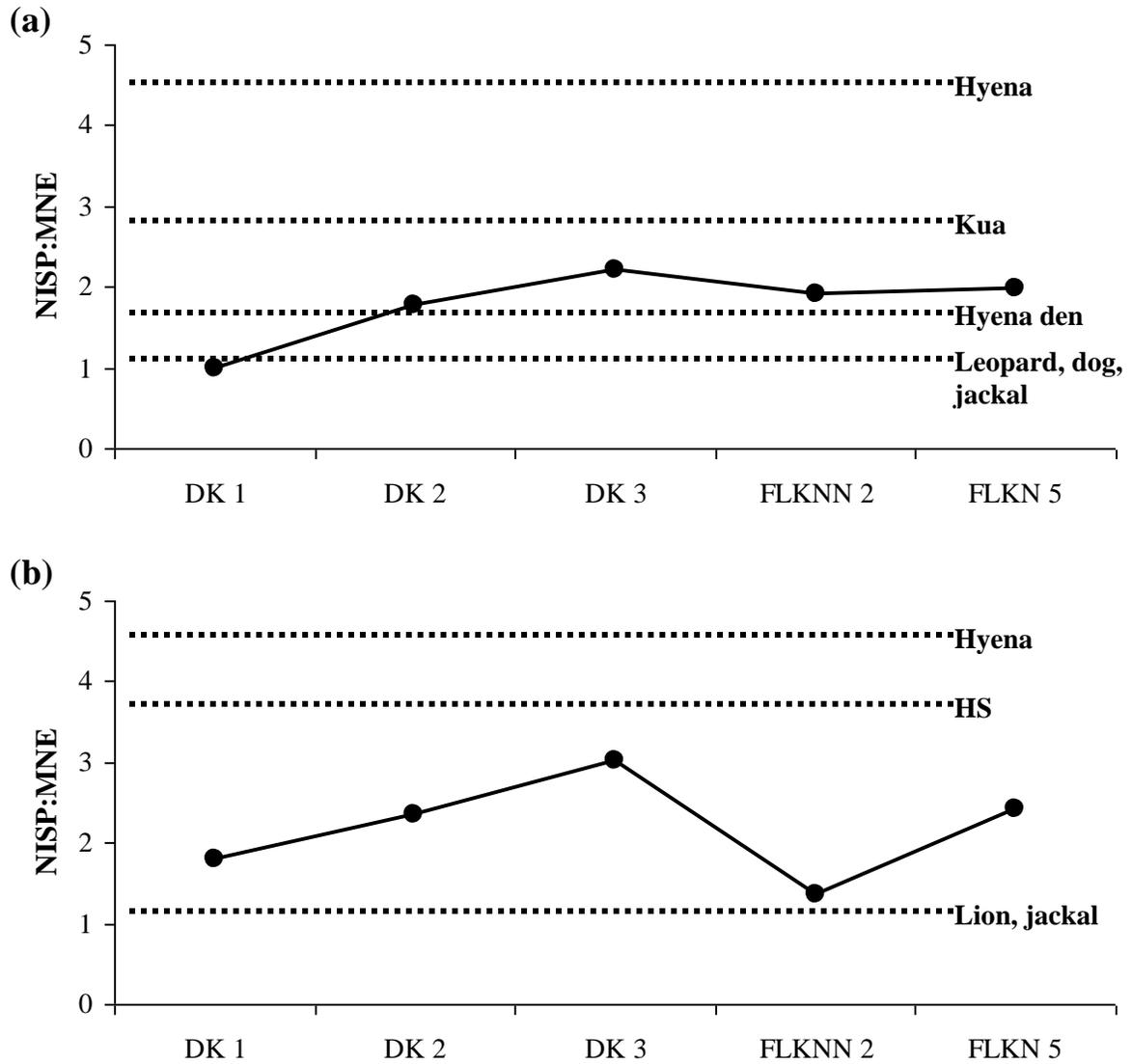


Figure 4.15. Limb bone fragmentation ratios for (a) small and (b) medium carcasses from the Bed I sites relative to actualistic controls. Codes: HS = Hammerstone-only.

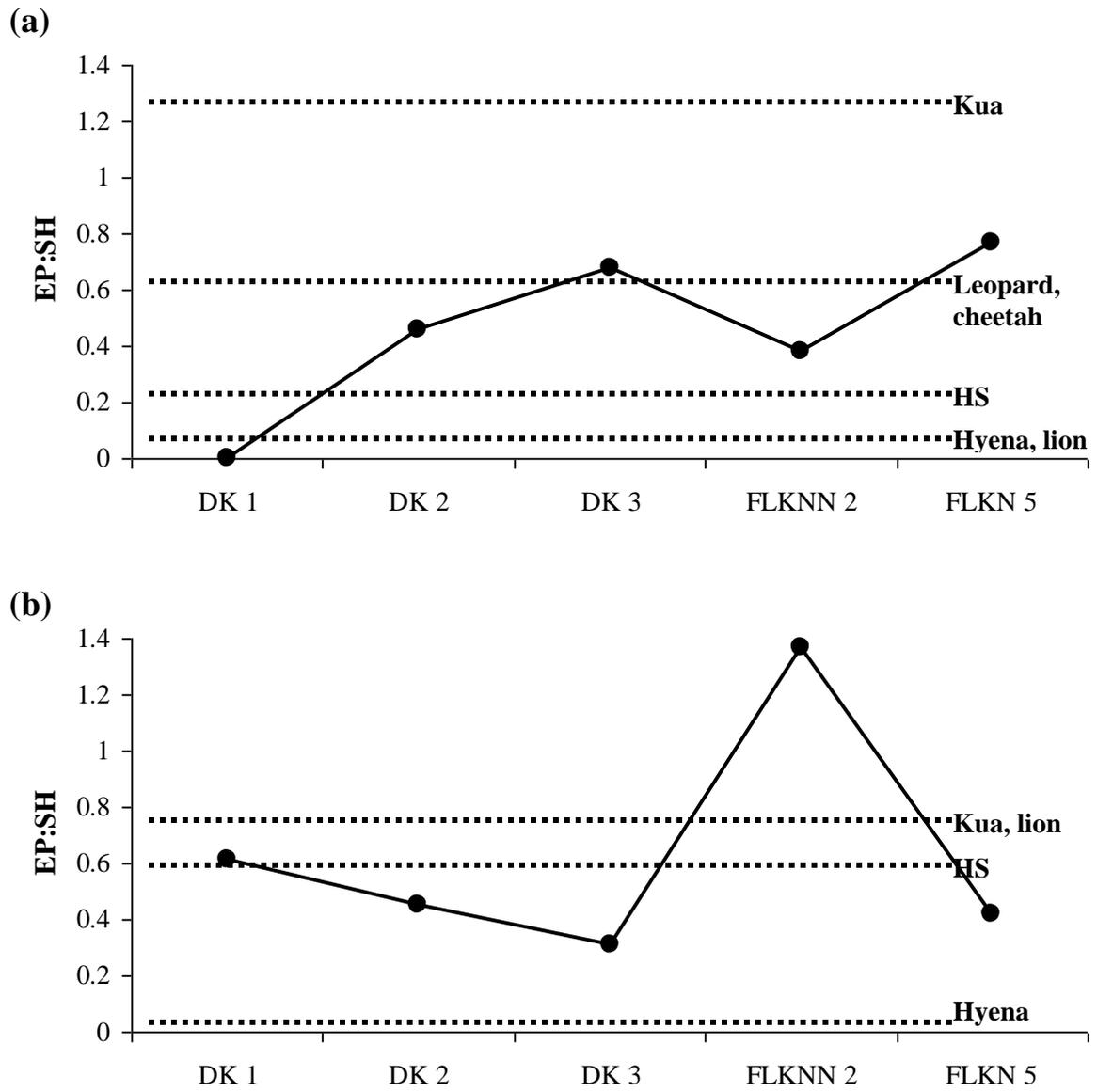


Figure 4.16. Epiphysis-to-shaft ratios for (a) small and (b) medium carcasses from the Bed I sites relative to actualistic controls. Codes: HS = Hammerstone-only.

Table 4.20. Summary statistics for fracture angles by carcass size from non-metapodial limb bone fragments in the Bed I assemblages.

	DK 2		DK 3		FLKNN 2		FLKN 5	
	Small	Medium	Small	Medium	Small	Medium	Small	Medium
<b>Long. &lt;90°</b>								
N	4	21	0	14	2	4	4	10
Mean	83.8	77.7	–	79.9	88.0	78.5	98.5	73.70
S.D.	3.2	7.2	–	11.3	1.4	5.1	7.7	11.67
95% CI	78.7–88.8	74.5–81.0	–	73.4–86.4	75.3–100.7	70.4–86.6	86.2–110.8	65.35–82.05
<b>Long. &gt;90°</b>								
N	2	25	0	13	0	8	8	8
Mean	98.5	104.4	–	99.3	–	103.4	78.5	99.00
S.D.	7.8	10.2	–	8.3	–	9.7	8.5	11.21
95% CI	28.6–168.4	100.2–108.7	–	94.3–104.3	–	95.2–111.5	71.5–85.6	89.63–108.37
<b>Obl. &lt;90°</b>								
N	3	24	2	20	0	12	5	13
Mean	76.0	71.5	82.5	68.9	–	76.3	73.6	68.15
S.D.	11.4	12.1	9.2	18.1	–	13.5	14.2	21.53
95% CI	47.8–104.2	66.0–77.0	0.0–165.1	60.4–77.4	–	67.8–84.9	56.0–91.2	55.14–81.16
<b>Obl. &gt;90°</b>								
N	1	42	5	27	2	9	6	13
Mean	129.0	111.8	110.4	110.3	112.5	105.0	113.2	102.62
S.D.	–	13.6	12.1	13.0	13.4	10.3	18.4	11.47
95% CI	–	107.5–116.0	85.4–125.4	105.2–115.8	0.0–180.0	97.0–112.8	93.8–132.5	95.69–109.55

Note: Data for DK 1 not listed as a total of only two angles were measured from this level.

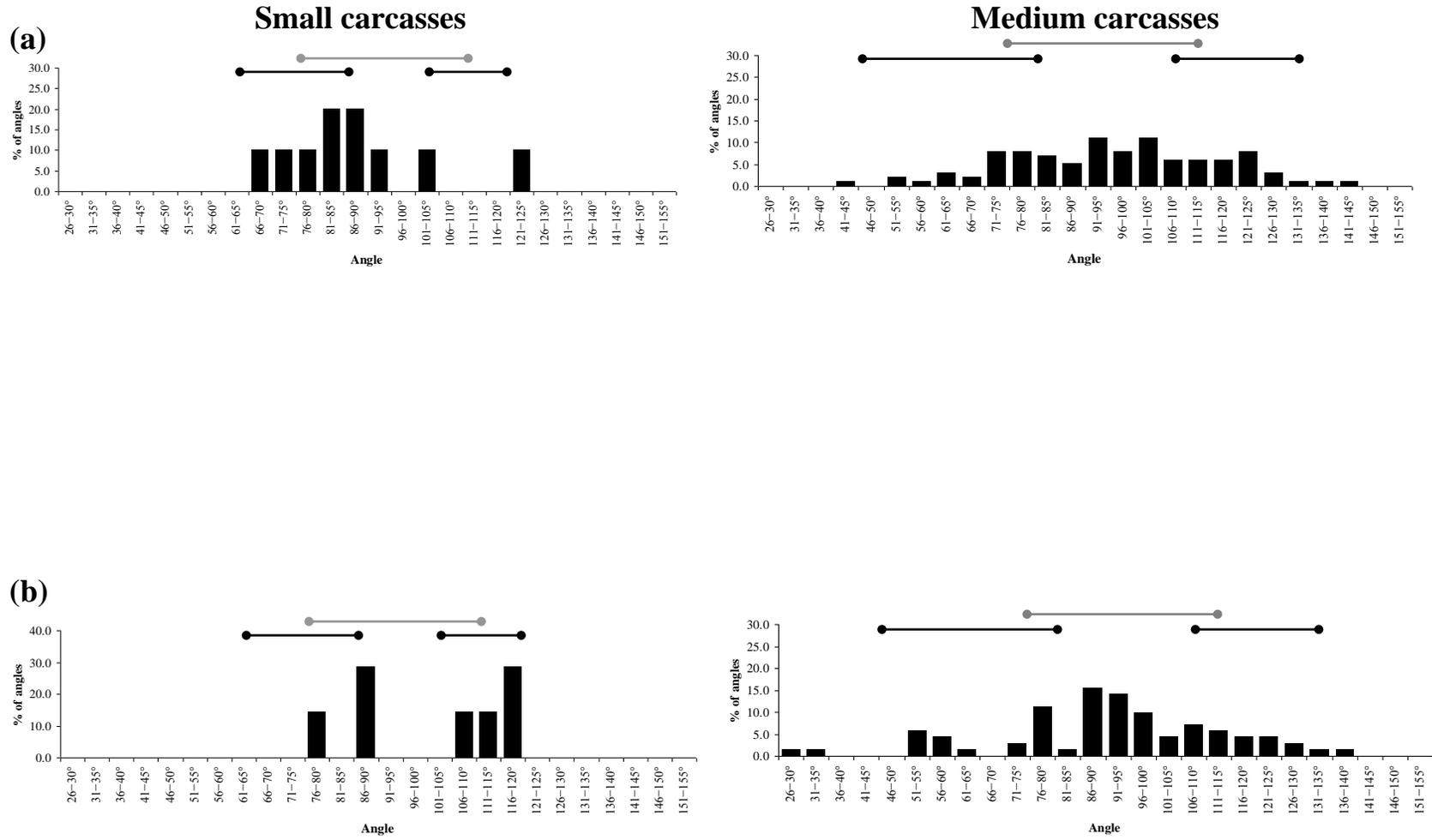


Figure 4.17. Distribution of longitudinal and oblique fracture angles from (a) DK 2 and (b) DK 3. Note: Grey line denotes 95% confidence intervals of experimental static loading angles, black line denotes 95% confidence intervals of experimental dynamic loading angles.

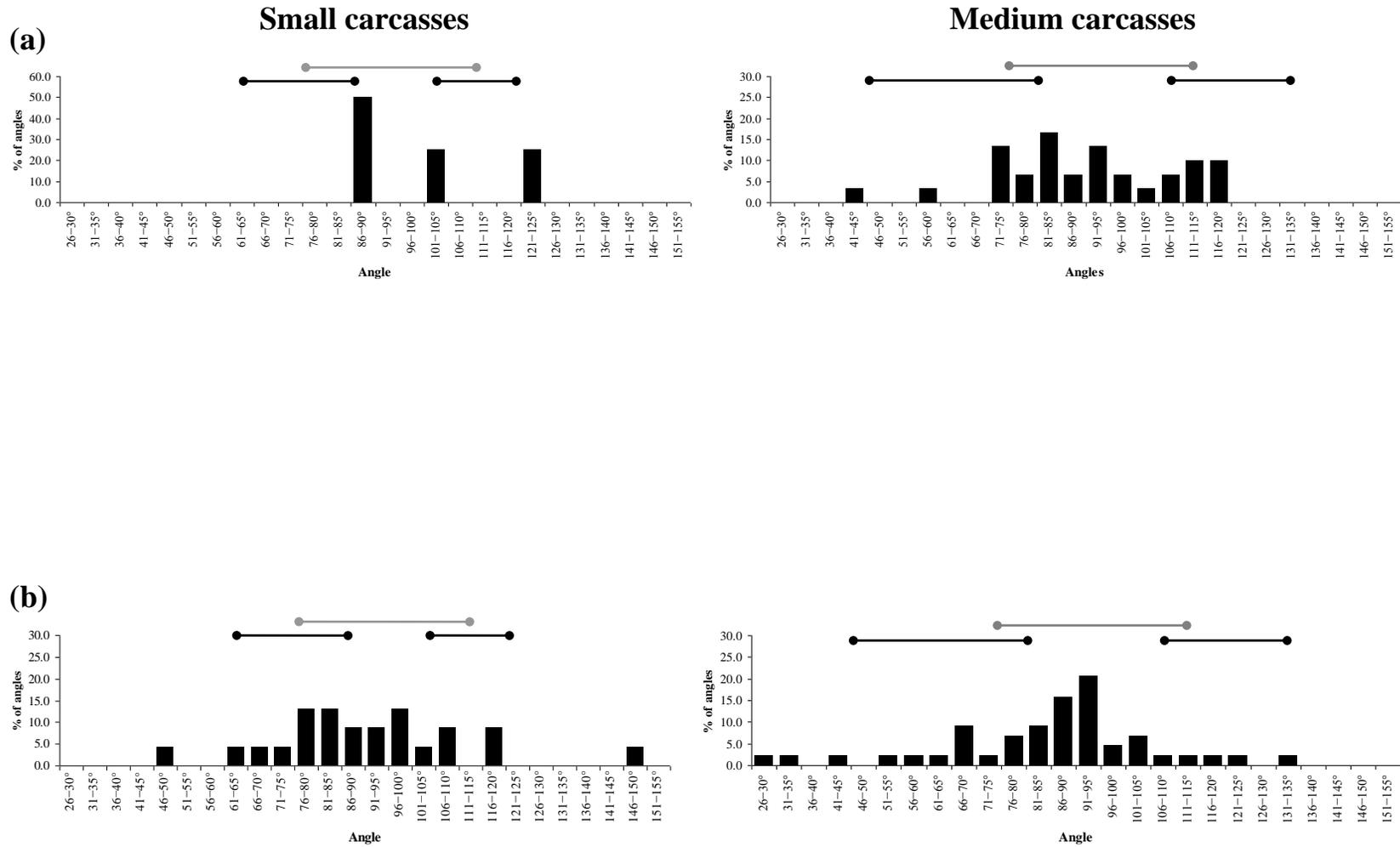


Figure 4.18. Distribution of longitudinal and oblique fracture angles from (a) FLKNN 2 and (b) FLKN 5. Note: Grey line denotes 95% confidence intervals of experimental static loading angles, black line denotes 95% confidence intervals of experimental dynamic loading angles.

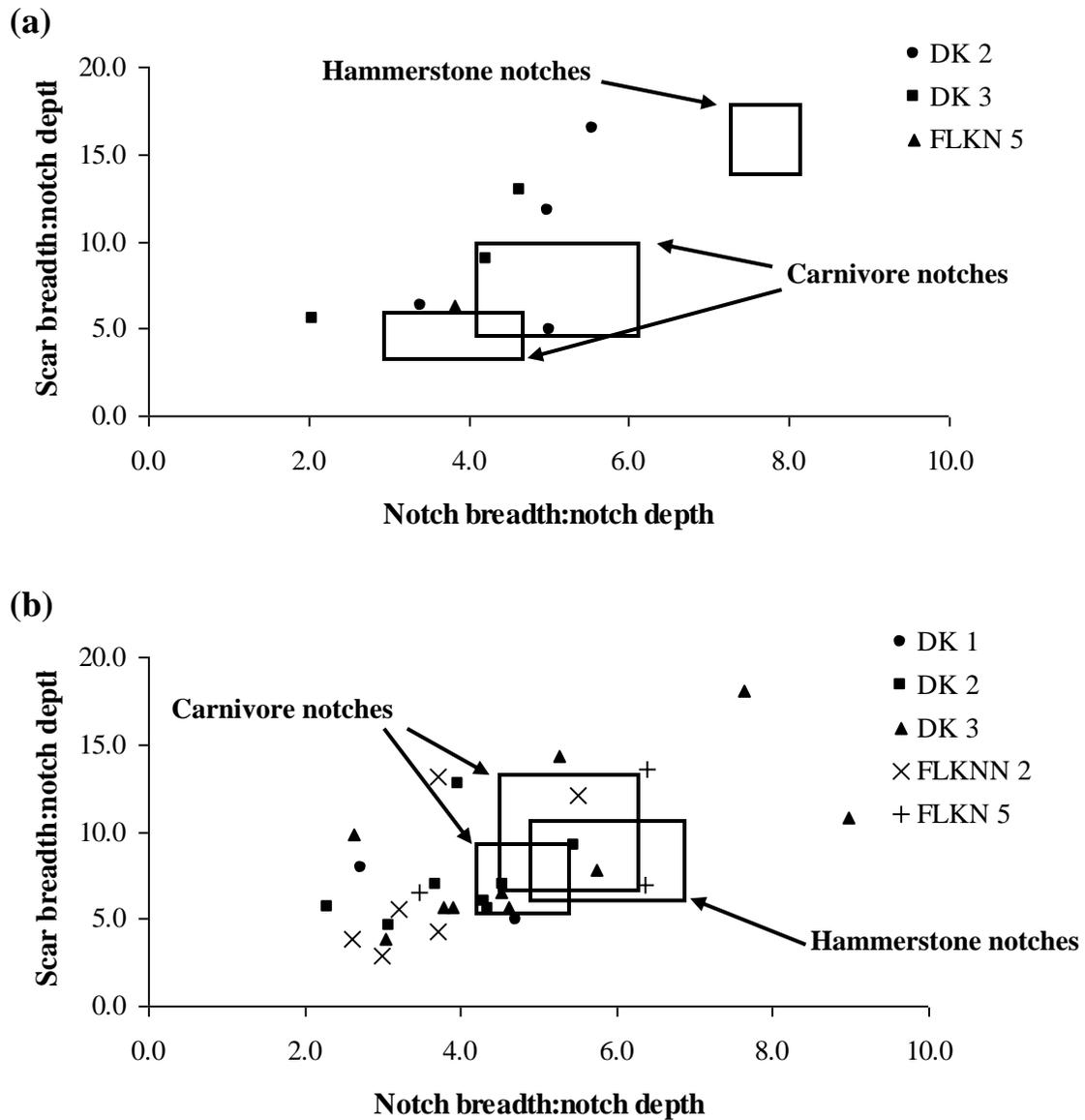


Figure 4.19. Notch dimensions on specimens from (a) small and (b) medium carcasses at the Bed I sites. Boxes represent 95% confidence intervals of notch breadth:notch depth and scar breadth:notch depth ratios for experimental assemblages (Capaldo and Blumenchine, 1994) and a sample of notches from a hyena den in the Masaai Mara (Egeland et al., unpublished data).

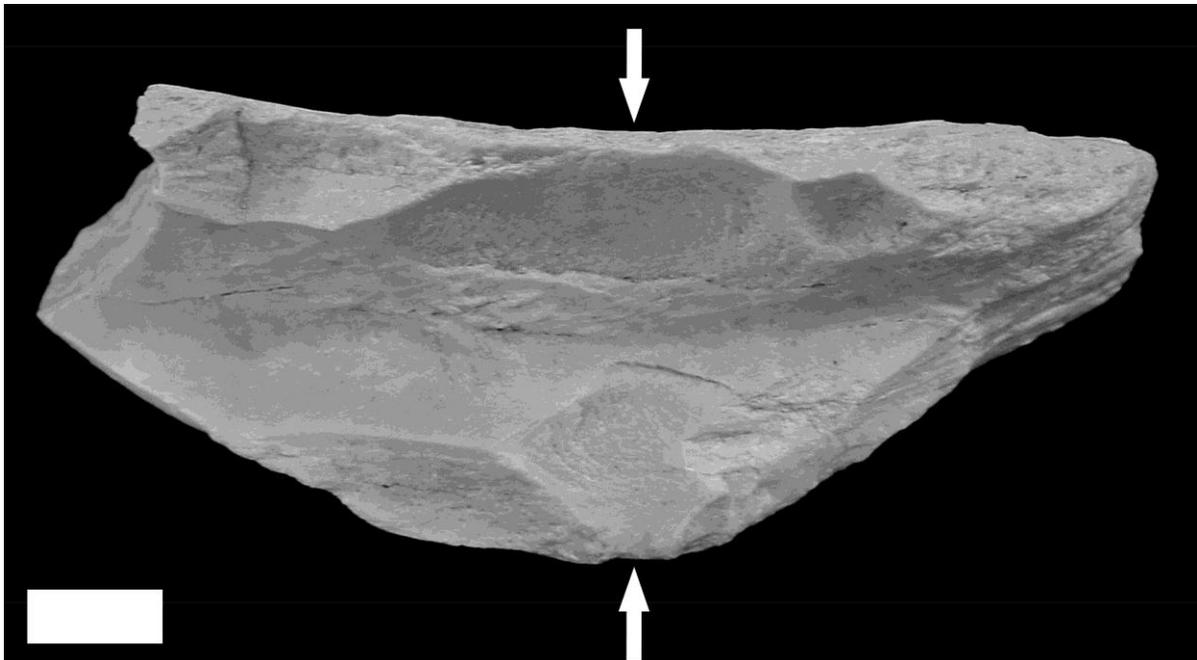


Figure 4.20. Medullary view of opposing notches (arrows) on a Size Class 3 femur from DK 2. Scale bar = 1cm.

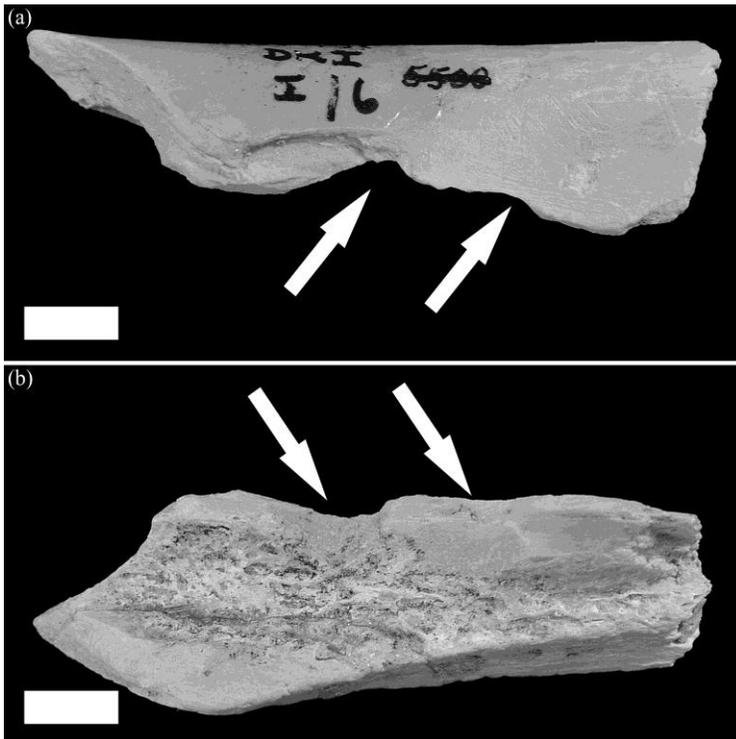


Figure 4.21. (a) Cortical and (b) medullary views of an Incomplete Type C notch (arrows) on a Size Class 3 intermediate (i.e., radius or tibia) limb bone from DK 2. Scale bar = 1cm.

A much higher frequency of notched fragments are tooth-marked than are percussion-marked (Table 4.21). In fact, notched specimens are tooth-marked at rates equal to or greater than the modern hyena den assemblage from Masaai Mara. Opposing complete and Incomplete Type C notches are present (e.g., Figures 4.20 and 4.21) but not common in the Bed I assemblages.

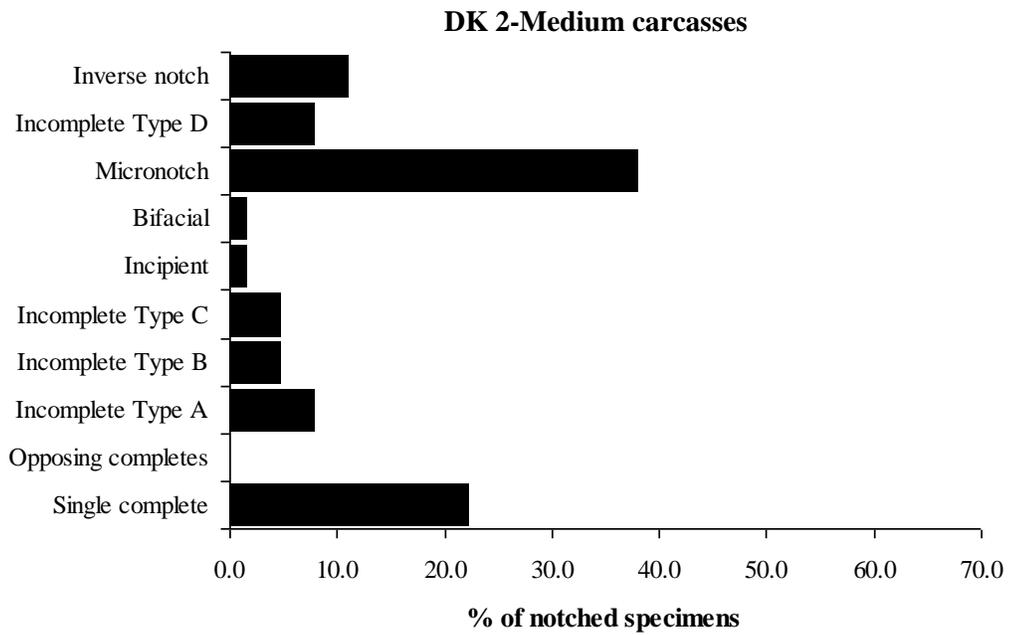
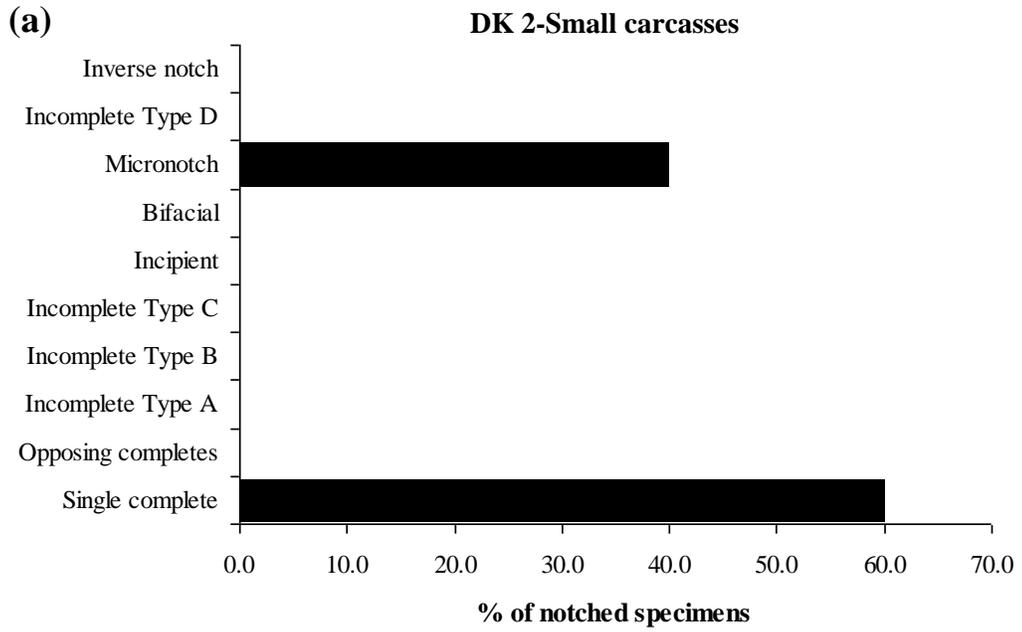
A relatively high frequency of micronotches is evident at all three

Bed I sites, which is very similar to the Masaai Mara hyena den assemblage (Figure 4.22), which has a substantial representation of opposing complete and Incomplete Type C notches. Incipient notches (e.g., Figure 4.23), which are associated mainly, though not exclusively, with hammerstone breakage, are also present in low frequencies.

Table 4.21. Surface mark frequencies on notched specimens from the Bed I sites and several actualistic samples.

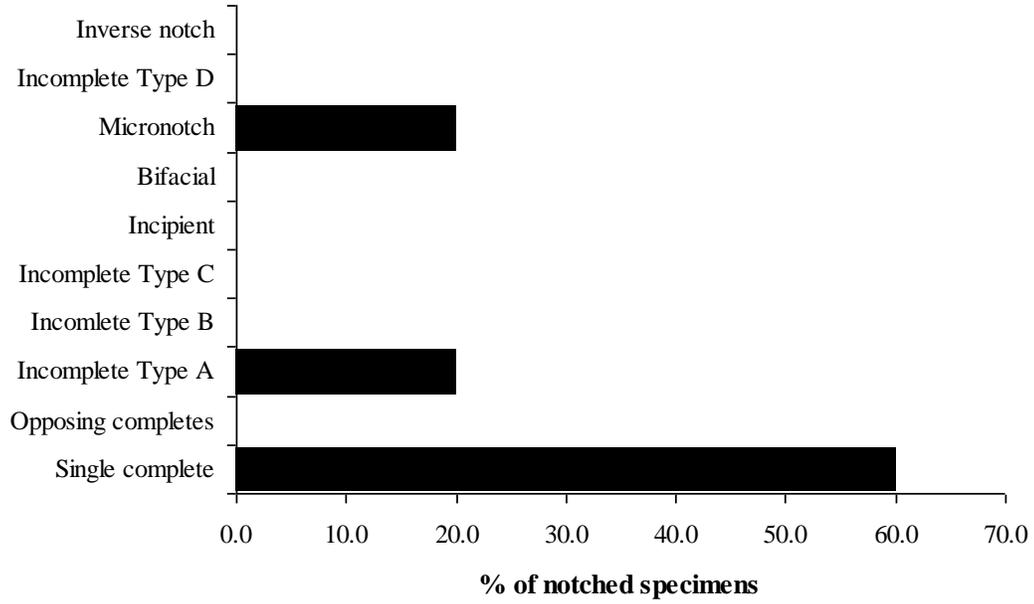
	NISP notched	NISP TM	%	NISP PM	%
<b>DK 1</b>					
Small carcasses	–	–	–	–	–
Medium carcasses	5	3	60.0	–	–
Total	5	3	60.0	–	–
<b>DK 2</b>					
Small carcasses	6	5	83.3	–	–
Medium carcasses	27	10	37.0	1	3.7
Total	33	15	45.5	1	3.0
<b>DK 3</b>					
Small carcasses	4	1	25.0	–	–
Medium carcasses	17	7	41.2	–	–
Total	34	15	44.1	–	–
<b>FLKNN 2</b>					
Small carcasses	2	2	100.0	–	–
Medium carcasses	9	6	66.7	–	–
Total	11	8	72.7	–	–
<b>FLKN 5</b>					
Small carcasses	5	2	40.0	–	–
Medium carcasses	13	7	53.8	–	–
Total	18	9	50.0	–	–
<b>Masaai Mara hyena den</b>					
Small carcasses	56	21	37.5	–	–
Medium carcasses	67	29	43.3	–	–
Total	123	50	40.7	–	–
<b>Experimental carnivore</b>					
Medium carcasses	45	35	77.8	–	–
<b>Experimental percussion I</b>					
Small carcasses	90	–	–	58	64.4
<b>Experimental percussion II</b>					
Small carcasses	27	–	–	13	48.1

Note: Only specimens with normal notches included. Data sources: Blumenschine and Selvaggio (1991: Tables 1a and 1b) and Pickering and Egeland (2006: Table 1).

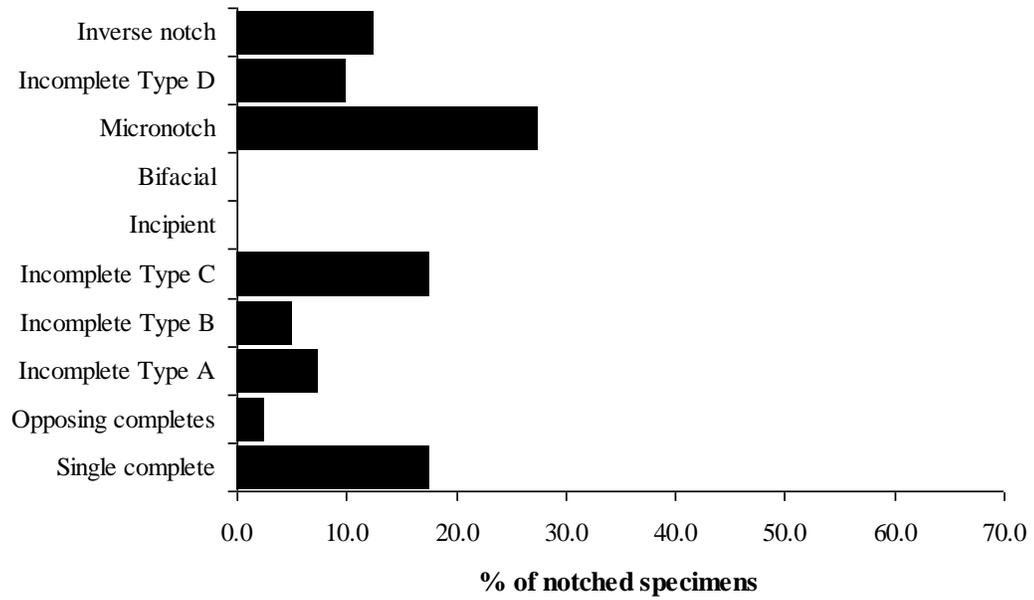


**(b)**

**DK 3-Small carcasses**

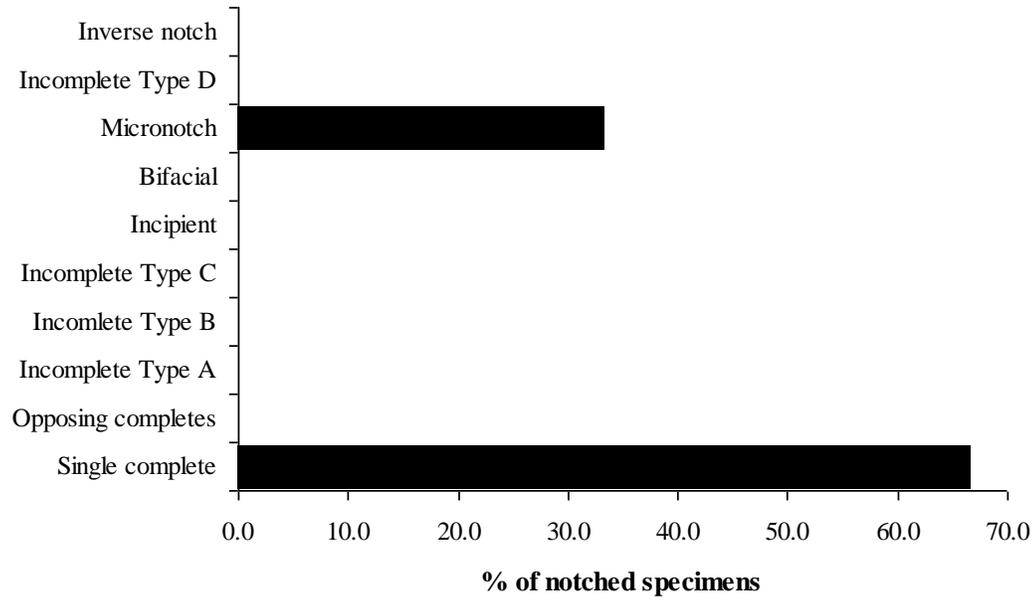


**DK 3-Medium carcasses**

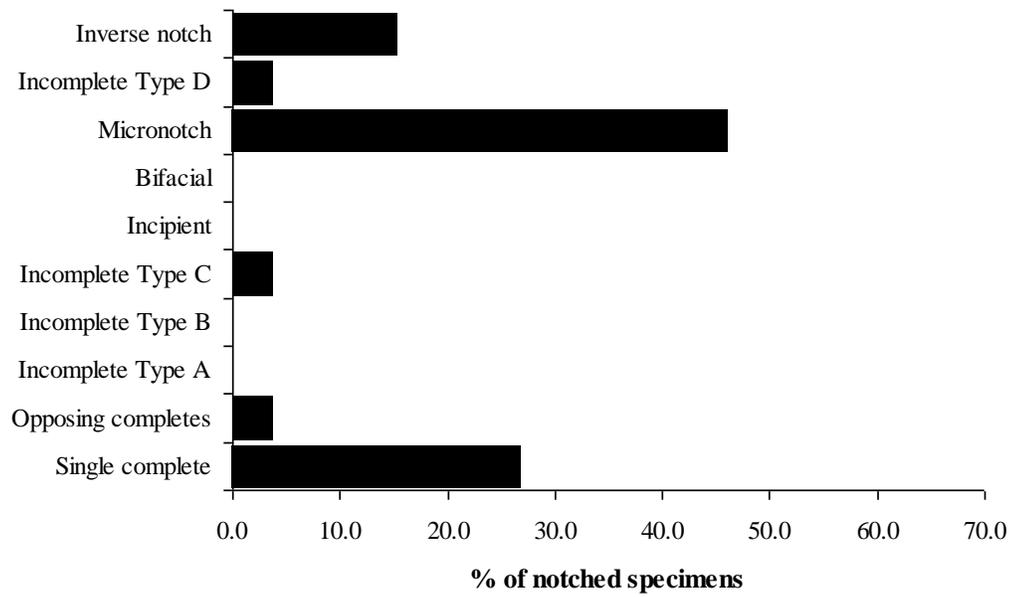


(c)

**FLKNN 2-Small carcasses**

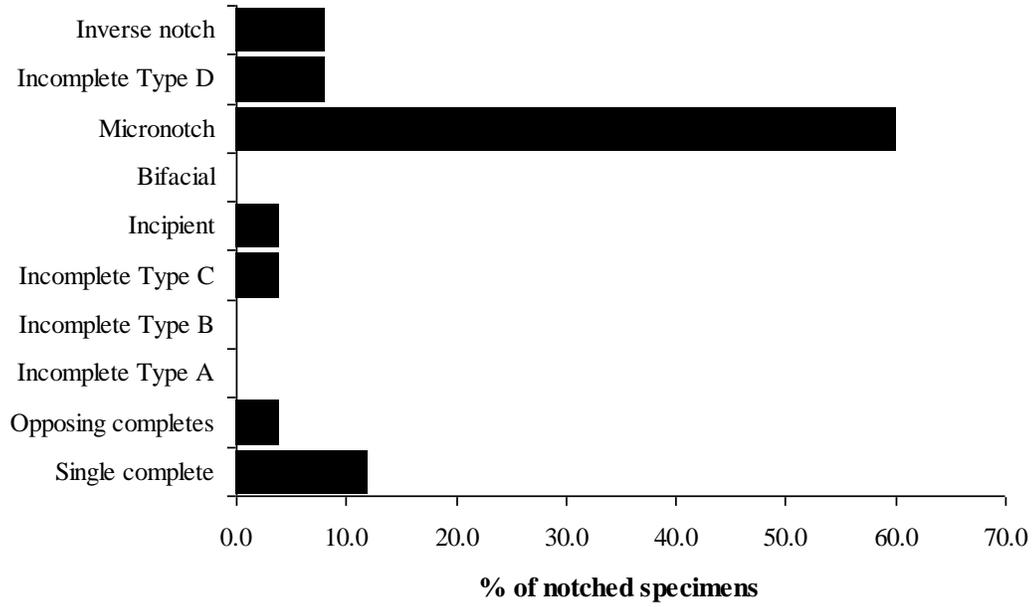


**FLKNN 2-Medium carcasses**

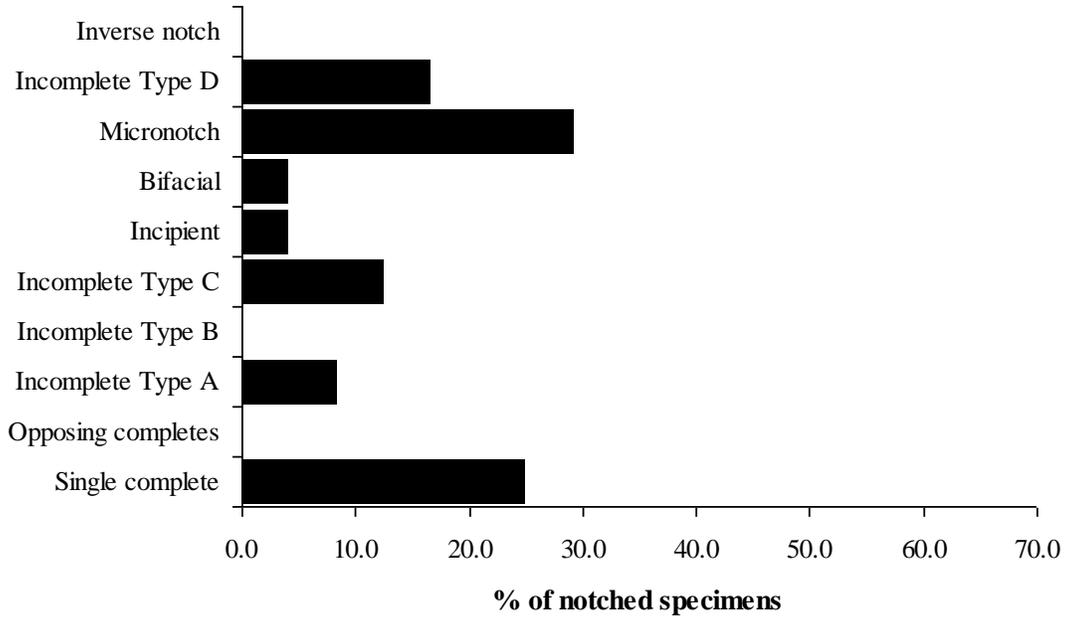


(d)

**FLKN 5-Small carcasses**



**FLKN 5-Medium carcasses**



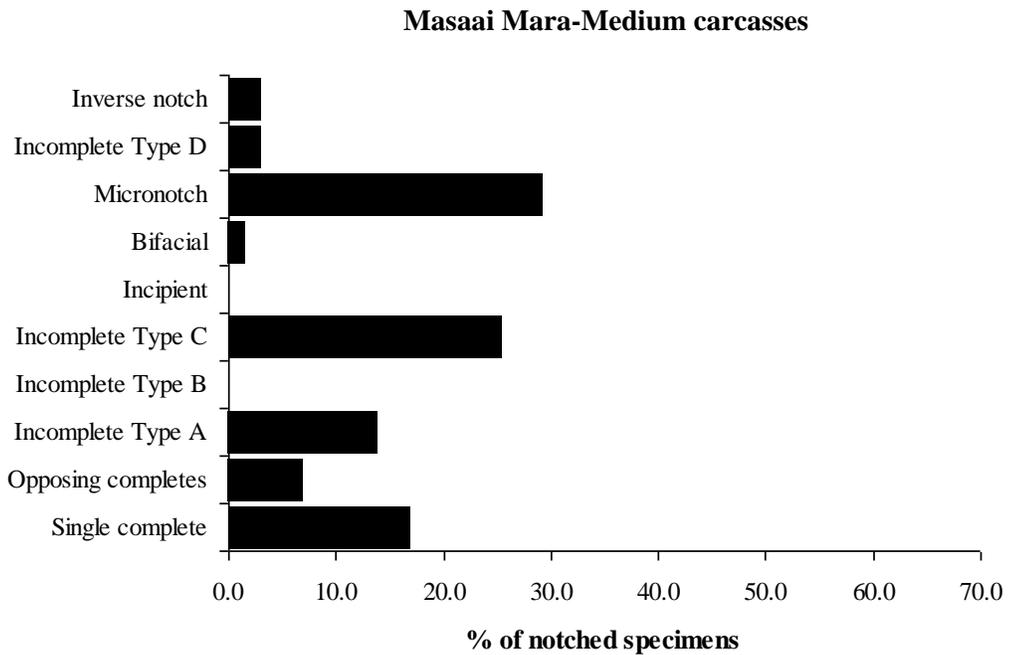
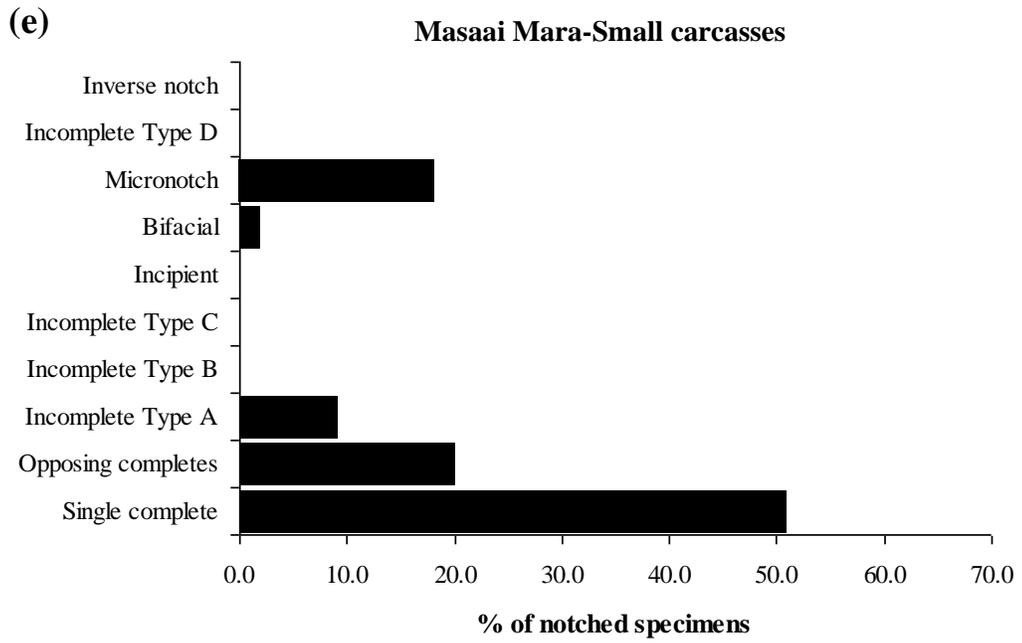


Figure 4.22. Frequency of notch types from (a) DK 2, (b) DK 3, (c) FLKNN 2, (d) FLKN 5 and (e) Masaai Mara hyena den.

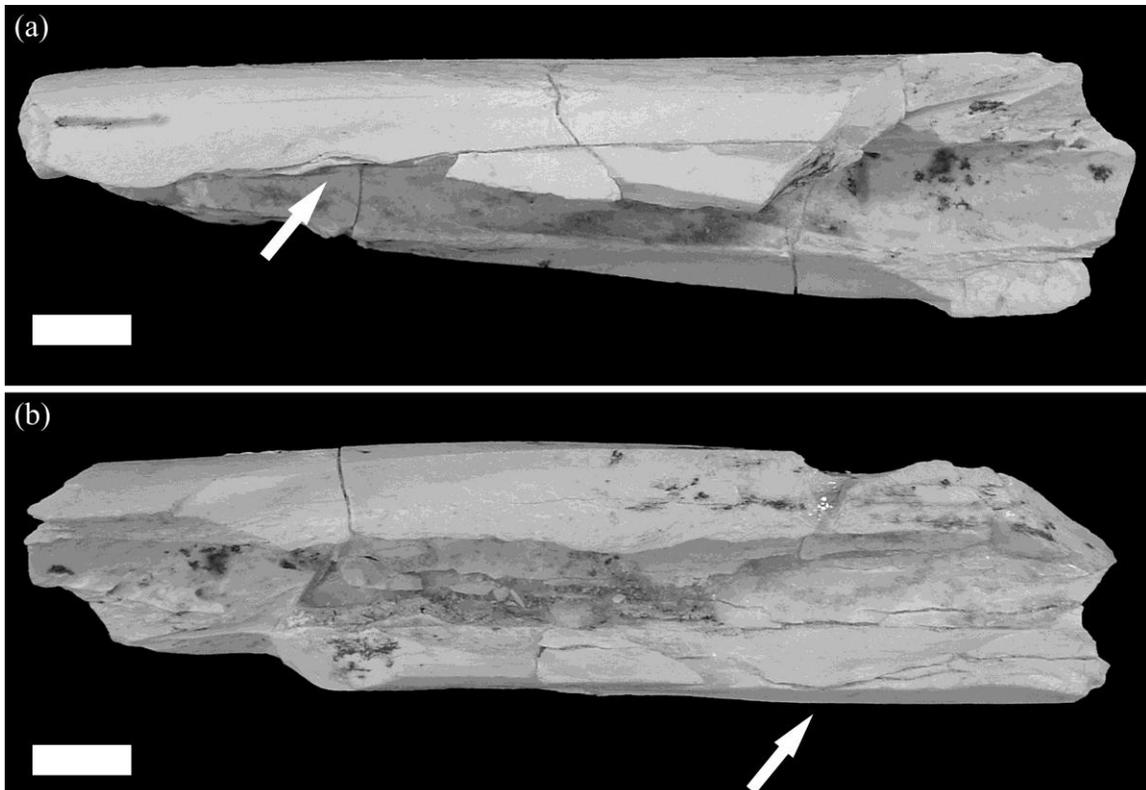


Figure 4.23. (a) Cortical and (b) medullary views of an incipient notch with a partially detached flake (arrows) on a Size Class 3a tibia from DK 2. Scale bar = 1 cm.

### MORTALITY ANALYSIS

Table 4.22 provides the frequency occurrence (in terms of MNI) of each age class by size and bovid taxon. The taxon data are based only on diagnostic dental material while the Size Class totals include both the dental material and taxonomically non-diagnostic unfused elements. These totals therefore partially compensate for differential destruction of juvenile dentitions. What stands in from these data is the relatively high representation of old-aged individuals among the Size Class 1 Antilopini. This is in contrast to the medium carcass sample (mainly alcelaphines), which is dominated by juvenile and especially adult individuals. Also interesting is the fact that tribes Bovini, Hippotragini, Reduncini and Tragelaphini are represented almost exclusively by juveniles at most of the Bed I sites. Sample sizes permit a systematic ternary analysis of the FLKN 5 assemblage and the medium carcass samples from DK 2 and 3. Four ternary diagrams are plotted in Figure 4.24. The top

two show data for modern African carnivores preying upon small- and medium-sized animals. For small animals lions, wild dogs and leopards concentrate on adult individuals while cheetahs take a higher frequency of juvenile individuals. Lions seem to concentrate on adult individuals from medium-sized animals while wild dogs mainly hunt and kill juveniles. The small sample sizes from the Olduvai sites are clearly shown in the large area encompassed by the 95% confidence intervals. The FLKN 5 small carcass sample appears to have slightly more old individuals than the modern comparative data, although it cannot be statistically distinguished from any of carnivore profiles. The medium carcass samples from DK and FLKN 5 show slightly more juvenile but less old individuals than the lion data but, again, cannot be statistically distinguished.

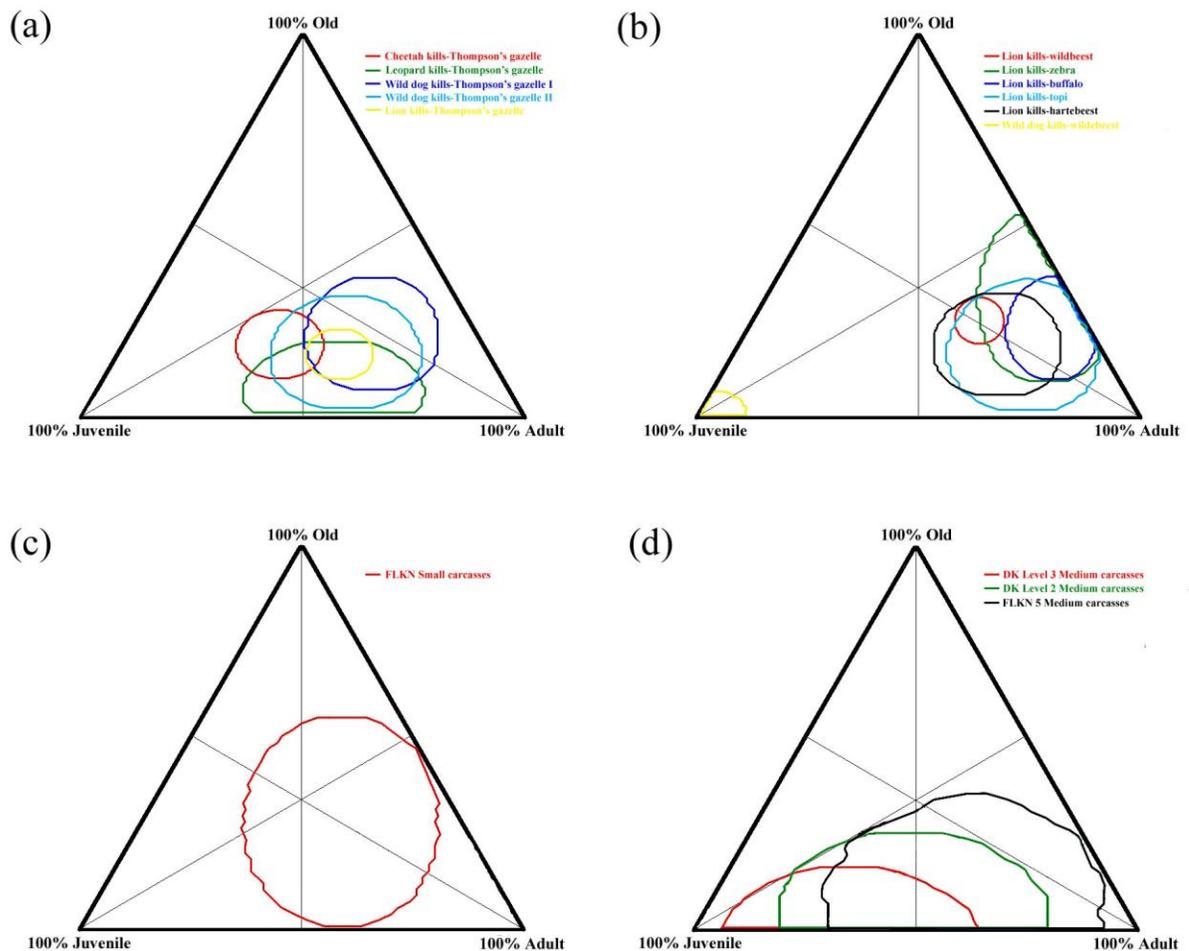


Figure 4.24. Triangular diagrams with 95% confidence intervals of mortality profiles for (a) modern carnivore kills of small animals, (b) modern carnivore kills of medium animals, (c) small carcasses from FLKN 5 and (d) medium carcasses from DK 2, DK 3 and FLKN 5.

Table 4.22. Frequency of juvenile, adult and old-aged individuals in the Bed I sites.

Size/Taxon	DK 1			DK 2			DK 3		
	Juvenile (%)	Adult (%)	Old (%)	Juvenile (%)	Adult (%)	Old (%)	Juvenile (%)	Adult (%)	Old (%)
Antilopini	0 (0.0)	1 (100.0)	0 (0.0)	1 (20.0)	1 (20.0)	3 (60.0)	1 (33.3)	1 (33.3)	1 (33.3)
Alcelaphini	1 (33.3)	0 (0.0)	2 (66.7)	2 (33.3)	4 (66.7)	0 (0.0)	3 (37.5)	5 (62.5)	0 (0.0)
Bovini	–	–	–	–	–	–	2 (100.0)	0 (0.0)	0 (0.0)
Hippotragini	–	–	–	1 (50.0)	1 (50.0)	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)
Reduncini	1 (100.0)	0 (0.0)	0 (0.0)	1 (50.0)	1 (50.0)	0 (0.0)	–	–	–
Tragelaphini	0 (0.0)	2 (100.0)	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)	2 (100.0)	0 (0.0)	0 (0.0)
Small total	2 (66.7)	1 (33.3)	0 (0.0)	3 (42.9)	1 (14.3)	3 (42.9)	2 (50.0)	1 (25.0)	1 (25.0)
Medium total	3 (42.9)	2 (28.6)	2 (28.6)	7 (53.8)	6 (46.2)	0 (0.0)	8 (61.5)	5 (38.5)	0 (0.0)

Size/Taxon	FLKNN 2			FLKN 5		
	Juvenile (%)	Adult (%)	Old (%)	Juvenile (%)	Adult (%)	Old (%)
Antilopini	–	–	–	3 (15.0)	12 (60.0)	5 (25.0)
Alcelaphini	–	–	–	2 (28.6)	5 (71.4)	0 (0.0)
Bovini	–	–	–	–	–	–
Hippotragini	–	–	–	–	–	–
Reduncini	3 (37.5)	5 (62.5)	0 (0.0)	–	–	–
Tragelaphini	–	–	–	1 (100.0)	0 (0.0)	0 (0.0)
Small total	2 (100.0)	0 (0.0)	0 (0.0)	5 (22.7)	12 (54.5)	5 (22.7)
Medium total	3 (37.5)	5 (62.5)	0 (0.0)	3 (37.5)	5 (62.5)	0 (0.0)

Note: The taxon totals may not equal the carcass size totals because of the use of unfused, but taxonomically non-diagnostic, elements in calculating the latter.

## CHAPTER 5 BED II ZOOARCHAEOLOGY AND TAPHONOMY

This chapter summarizes pertinent zooarchaeological and taphonomic data for the Bed II faunas. More detailed data, particularly for skeletal part frequencies, are located in the Appendices.

### GENERAL ASSEMBLAGE COMPOSITION

Table 5.1. Number of identified specimens (NISP) by taxon at the Bed II sites.

Taxon	FC West		TK LF		TK UF		BK	
	NISP	%	NISP	%	NISP	%	NISP	%
Bovidae	21	43.8	22	47.8	38	48.7	1092	79.0
Suidae	2	4.2	1	2.2	0	0.0	32	2.3
Equidae	18	37.5	21	45.7	29	37.2	178	12.9
Proboscidean	0	0.0	0	0.0	0	0.0	9	0.7
Hippopotamidae	6	12.5	2	4.3	8	10.3	17	1.2
Giraffidae	1	2.1	0	0.0	1	1.3	15	1.1
Rhinocerotidae	0	0.0	0	0.0	2	2.6	2	0.1
Primates	0	0.0	0	0.0	0	0.0	16	1.2
Carnivora	0	0.0	0	0.0	0	0.0	22	1.6

The FC West Occupation Floor consists of a total of 95 specimens while a total of 80 and 135 specimens were examined from the TK Lower Floor (LF) and Upper Floor (UF), respectively. BK is by far the largest of the three sites with a total NISP of 2,479. Equids are more common in the Bed II sites and, in fact, are as well represented as bovids at all but BK (Table 5.1). At least five large mammal individuals are present at FC West, four at TK LF and 10 at TK UF (Table 5.2). BK has a total MNI of 50. The FC West and TK assemblages are composed exclusively of medium- and large-sized animals while Size Class 2/3a alcelaphines make up 38% of the total MNI at BK. Most of the non-bovid taxa at FC West and TK LF are represented only by isolated skull remains (mostly teeth); this contrasts with the more complete representation of the bovids in these assemblages (Table 5.3). Hippopotamuses at TK UF and giraffids and suids at BK are represented by several body parts.

Table 5.2. Minimum number of large mammal individuals (MNI) represented at the Bed II sites.

Taxon	FC West	TK LF	TK UF	BK
<i>Hippotragus gigas</i>	–	–	1	2
<i>Pelorovis oldowayensis</i>	–	–	1	3
Size 2/3a Alcelaphini	–	–	–	19
Size 3 Alcelaphini	2	–	–	–
Size 3a Alcelaphini	–	2	4	–
Size 3b Alcelaphini	–	–	1	–
Size 3b/4 Alcelaphini	–	–	–	10
Size 4 Alcelaphini	1	–	–	–
Size 1 Antilopini	–	–	–	2
Size 3b Tragelaphini	–	–	–	1
Size 4 Tragelaphini	–	–	–	1
Size 4 Bovini	–	–	–	4
Rhinocerotidae	–	–	1	1
Size 3 Suidae	–	1	–	–
Hippopotamidae	–	1	1	–
<i>Hippopotamus gorgops</i>	1	–	–	1
Giraffidae	1	–	1	–
<i>Libytherium sp.</i>	–	–	–	1
<i>Sivatherium sp.</i>	–	–	–	2
<i>Panthera leo</i>	–	–	–	2
<i>Crocuta crocuta</i>	–	–	–	1
Total	5	4	10	50

Table 5.3. Number of identified specimens (NISP) by ungulate group and skeletal element at the Bed II sites.

Element	Bovidae	Suidae	Proboscidean	Hippopotamidae	Giraffidae	Rhinocerotidae
<b>FC West</b>						
Cranium	–	–	–	–	–	–
Teeth	4	2	–	5	1	–
Mandible	–	–	–	–	–	–
Vertebrae	–	–	–	–	–	–
Ribs	–	–	–	–	–	–
Innominate	–	–	–	–	–	–
Scapula	1	–	–	–	–	–
Humerus	2	–	–	–	–	–
Radio-ulna	1	–	–	–	–	–
Carpals/Tarsals	3	–	–	–	–	–
Metacarpal	3	–	–	–	–	–
Femur	1	–	–	–	–	–
Tibia	–	–	–	–	–	–
Metatarsal	3	–	–	–	–	–
Patella	–	–	–	–	–	–
Phalanges	–	–	–	1	–	–
Sesamoids	–	–	–	–	–	–
Metapodial	2	–	–	–	–	–
Limb bone shaft	–	–	–	–	–	–
<b>TK LF</b>						
Cranium	–	–	–	–	–	–
Teeth	2	1	–	–	–	–
Mandible	1	–	–	1	–	–
Vertebrae	1	–	–	–	–	–
Ribs	–	–	–	–	–	–
Innominate	–	–	–	–	–	–
Scapula	–	–	–	–	–	–
Humerus	1	–	–	–	–	–
Radio-ulna	4	–	–	–	–	–
Carpals/Tarsals	3	–	–	–	–	–
Metacarpal	1	–	–	–	–	–
Femur	1	–	–	–	–	–
Tibia	2	–	–	–	–	–
Metatarsal	2	–	–	1	–	–
Patella	1	–	–	–	–	–
Phalanges	–	–	–	–	–	–
Sesamoids	2	–	–	–	–	–
Metapodial	1	–	–	–	–	–
Limb bone shaft	–	–	–	–	–	–

Table 5.3. cont.

Element	Bovidae	Suidae	Proboscidean	Hippopotamidae	Giraffidae	Rhinocerotidae
<b>TK UF</b>						
Cranium	3	–	–	1	–	–
Teeth	22	–	–	2	1	–
Mandible	–	–	–	–	–	–
Vertebrae	–	–	–	–	–	–
Ribs	–	–	–	–	–	–
Innominate	1	–	–	–	–	–
Scapula	–	–	–	–	–	–
Humerus	4	–	–	–	–	–
Radio-ulna	2	–	–	–	–	1
Carpals/Tarsals	–	–	–	2	–	–
Metacarpal	–	–	–	2	–	–
Femur	4	–	–	1	–	–
Tibia	1	–	–	–	–	–
Metatarsal	1	–	–	1	–	–
Patella	–	–	–	–	–	–
Phalanges	–	–	–	–	–	–
Sesamoids	–	–	–	–	–	–
Metapodial	–	–	–	–	–	–
Limb bone shaft	–	–	–	–	–	–
<b>BK</b>						
Cranium	56	–	–	–	–	–
Teeth	149	2	–	1	–	–
Mandible	58	2	–	–	1	–
Vertebrae	28	3	–	1	3	–
Ribs	12	4	1	–	–	–
Innominate	17	–	–	–	–	–
Scapula	7	1	–	–	–	1
Humerus	96	2	–	–	2	1
Radio-ulna	96	2	–	–	1	–
Carpals/Tarsals	58	3	–	2	5	–
Metacarpal	59	–	–	–	1	–
Femur	105	–	–	–	1	–
Tibia	119	3	–	–	1	–
Metatarsal	86	–	–	–	–	–
Patella	7	–	–	–	–	–
Phalanges	23	9	–	1	–	–
Sesamoids	21	–	–	–	–	–
Metapodial	20	1	–	–	–	–
Limb bone shaft	75	–	8	–	–	–

## SITE INTEGRITY

All three Bed II sites are extremely deficient in specimens <4 cm (Figure 5.1). At FC West six specimens (6.3% of total NISP) show polishing damage due to long distance water transport. TK LF has three specimens (3.8%) and BK 74 (3.0%) with such damage. As Monahan (1996a: 87) has noted, there is lateral variation in polishing damage at BK. For example, highly rounded pieces are particularly common in Excavation Unit 7 (e.g., Figure 5.2). Specimen size distributions for the Bed II sites are consistent with site formation analyses of the lithics, which classify FC West as a slightly transported assemblage with some winnowing and TK UF as a lag assemblage (Petraglia and Potts, 1994). It is therefore likely that water action played some role in the accumulation and dispersal of faunal material at the Bed II sites. Because most of the very small fragments will most likely be skeletally non-identifiable, the lack of such specimens will affect three datasets: (1) find density will be artificially depressed; (2) surface mark frequencies may be higher without the inclusion of the smallest pieces; and (3) epiphysis-to-shaft ratios could be lower than reported if shaft specimens were selectively removed (either through water action or excavation biases). MNE estimates are probably not affected greatly by the absence of very small fragments.

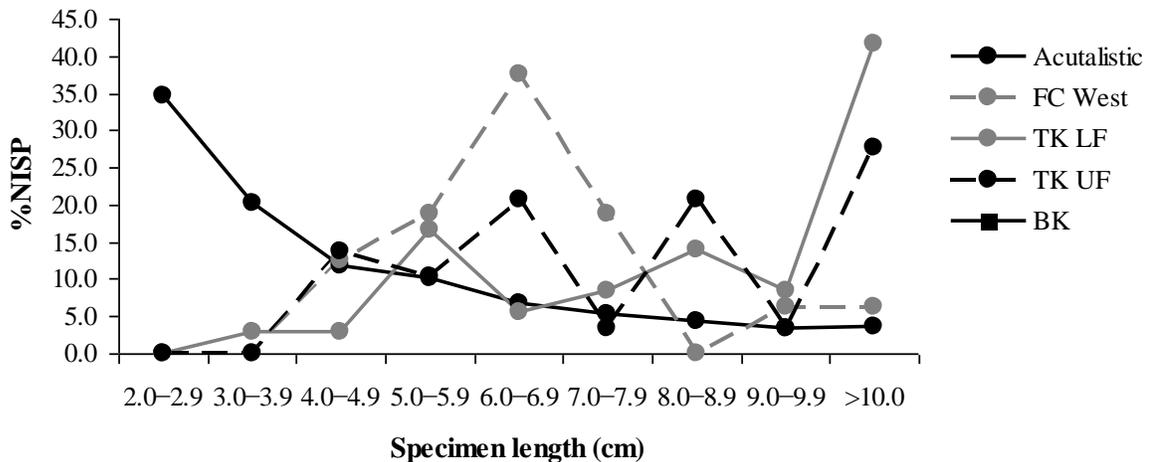


Figure 5.1. Distribution of limb bone fragment sizes for the Bed II sites compared to an actualistic sample from Pickering and Egeland (2006).

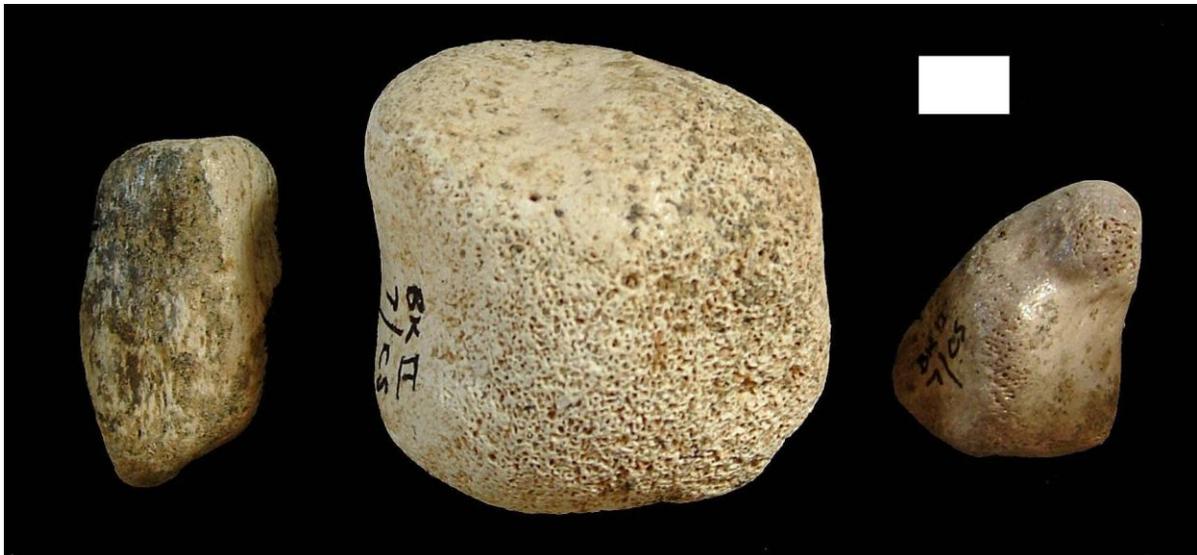


Figure 5.2. Examples of heavily rolled specimens from BK. Scale bar = 1 cm.

A predominance of Bunn's (1982, 1983a) Type 1 circumferences is evident at all three Bed II sites (Figure 5.3). As with the Bed I sites, although this suggests complete retention of limb bone shaft fragments, it is possible that some of the smaller fragments were either removed by water action or discarded because of unsystematic sediment screening. Nevertheless, the high frequency of limb bone shaft fragments should provide relatively accurate MNE estimates. Despite extensive effort, no refitting sets were found at either FC West or TK. No new refitting sets were added to the nine (21 total specimens) previously identified by Monahan (1996b: 221). The number of refits at BK is surprising given the evidence for water activity and the fact that Leakey lumped several vertical units together. Although these issues must be kept in mind when interpreting site formation, the refitting data suggest a relatively high degree of integrity for at least a portion of the BK assemblage.

#### ***Exposure and accumulation times***

All five subaerial weathering stages are represented at the Bed II sites (Table 5.4). When only limb bone shafts and small compact bones are considered, stages 0 through 2 are the most common. However, only BK shows a predominance of unweathered (i.e., stage 0) specimens while the other Bed II sites exhibit a more even representation of weathering stages.

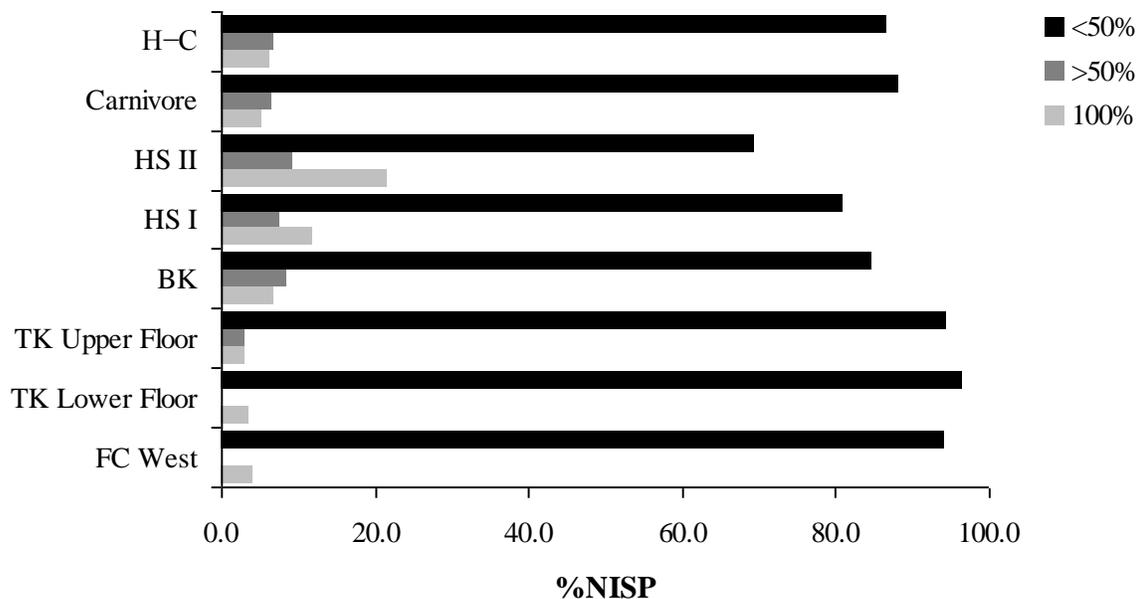


Figure 5.3. Percentage of Bunn's (1982, 1983a) circumference types from the Bed II sites and several actualistic samples. Note: fossil data include only green-brown specimens; Abbreviations: HS-C = hammerstone-to-carnivore; Carnivore = carnivore only; HS = hammerstone-only; HS-C, HS I, and Carnivore data from Marean et al., (2004); HS II data from Pickering and Egeland (2006).

It is clear that BK reflects a very short exposure time relative to the other Bed II sites (see also Monahan, 199a: 218). This means that even if the BK assemblage samples several depositional events, sedimentation and burial occurred rapidly. It is therefore difficult to say if carcass accumulation rates were high over a short period of time or relatively constant over a longer period of time with high sedimentation rates. The three paleosol assemblages from FC West and TK show longer exposure times as would be expected on a stable land surface.

Table 5.4. Maximum weathering stage data for the Bed II sites.

Stage	FC West		TK LF		TK UF		BK	
	NISP	%	NISP	%	NISP	%	NISP	%
0	4	18.2	5	27.8	3	30.0	644	70.6
1	11	50.0	3	16.7	2	20.0	214	23.5
2	4	18.2	8	44.4	2	20.0	35	3.8
3	3	13.6	2	11.1	2	20.0	17	1.9
4	0	0.0	0	0.0	0	0.0	0	0.0
5	0	0.0	0	0.0	1	10.0	2	0.2

Note: Only limb bone shaft fragments and compact bones included.

## SKELETAL ELEMENT ABUNDANCES

Tables 5.5 and 5.6 provide element abundances as measured by NISP and MNE, respectively, for three size groupings (small, medium, large). For FC West and TK only medium carcasses are considered in the remainder of the chapter while all three size grouping are dealt with for BK (see Appendices for complete datasets). Limb bone MNEs by portion are summarized in Figure 5.4 (only BK data graphed). As with the Bed I sites, the low representation of limb bone epiphyses is accompanied by a paucity of axial bones (Figure 5.5). A significant positive relationship between skeletal part representation and density is evident at all three sites (Table 5.7). The fact that many elements are not represented at all at FC West and TK may explain the weaker (though statistically significant) relationships at these sites. The Bed II skeletal profiles are similar to actualistic samples of carnivore-ravaged assemblages where skulls and limb elements are best represented (Figure 5.6). Compact bone representation is also very low at the Bed II sites, mirroring Capaldo's (1998) heavily ravaged sample of ungulate carcasses. Given the evidence for fluvial activity at the Bed II sites, it is possible that water transport can at least partially account for the low frequencies of ribs, vertebrae and perhaps compact bones, which are known to be easily moved through water flow (Voohties, 1969).

Among the Bed II sites, the FUI and MUI are significantly correlated with element representation only for small carcasses at BK (high survival elements only). The marrow index is significantly correlated with element representation for medium carcasses at TK UF and small carcasses at BK (Table 5.8). Although economic utility is not correlated with skeletal element representation among medium carcasses at BK, meaty and marrow-rich upper and intermediate limb bones still predominate over resource-poor metapodials (see also Monahan, 1996a: 199-201; 1996b: 110).

All three Bed II sites have relatively low evenness values (calculated only for high survival elements; Table 5.9). The low sample sizes from FC West and TK make patterning difficult to identify. However, it is interesting to note the similarities between these assemblages and a Hadza

Table 5.5. Number of identified specimens (NISP) by skeletal element and carcass size for the Bed II sites.

Element	FC West			TK LF			TK UF			BK		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Cranium	–	2	3	–	–	–	–	14	2	26	63	53
Mandible	–	2	2	–	4	–	–	8	1	32	84	33
Vertebrae	–	2	–	–	1	3	–	–	2	16	46	21
Innominate	–	1	1	–	–	1	–	3	1	6	21	6
Ribs	–	1	1	–	–	–	–	1	3	18	70	95
Scapula	–	1	1	–	–	1	–	2	1	3	20	10
Humerus	–	3	–	1	1	–	–	3	1	29	82	24
Radius	–	1	–	–	3	2	–	3	1	18	58	28
Ulna	–	–	–	–	–	–	–	–	–	4	12	4
Carpals	–	1	1	–	–	–	–	–	2	3	10	4
Metacarpal	–	3	–	–	1	–	–	–	–	18	35	8
Femur	–	1	1	1	–	1	–	4	1	38	61	27
Patella	–	–	–	–	1	–	–	–	–	3	2	2
Tibia	–	1	–	–	4	3	–	4	–	38	100	32
Tarsals	1	1	1	–	1	–	–	–	1	12	20	18
Metatarsal	–	2	2	–	2	–	–	1	–	23	53	11
Phalanges	–	–	1	–	–	–	–	–	–	8	12	7
Sesamoids	–	–	1	–	–	–	–	–	–	3	17	2
Total	1	22	15	2	18	11	–	43	16	297	767	385

Table 5.6. Minimum number of elements (MNE) estimates by carcass size for the Bed II sites.

Element	FC West			TK LF			TK UF			BK		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Cranium	–	1	2	–	–	–	–	5	2	8	13	11
Mandible	–	1	2	–	2	–	–	5	1	9	21	10
Vertebrae	–	2	–	–	1	3	–	–	2	9	29	16
Innominate	–	1	1	–	–	1	–	3	1	6	11	3
Ribs	–	1	1	–	–	–	–	1	3	4	13	20
Scapula	–	1	1	–	–	1	–	1	1	1	11	5
Humerus	–	3	–	1	1	–	–	3	1	21	35	10
Radius	–	1	–	–	2	1	–	2	1	13	28	16
Ulna	–	–	–	–	–	–	–	–	–	4	7	3
Carpals	–	1	1	–	–	–	–	–	2	3	10	4
Metacarpal	–	1	–	–	1	–	–	–	–	8	13	6
Femur	–	1	1	1	–	1	–	4	1	22	23	11
Patella	–	–	–	–	1	–	–	–	–	3	2	2
Tibia	–	1	–	–	2	2	–	3	–	18	34	12
Tarsals	1	1	1	–	1	–	–	–	1	10	18	19
Metatarsal	–	2	1	–	1	–	–	1	–	12	13	3
Phalanges	–	–	1	–	–	–	–	–	–	8	9	4
Sesamoids	–	–	1	–	–	–	–	–	–	3	16	2
Total	1	18	13	2	12	9	–	28	16	162	306	156

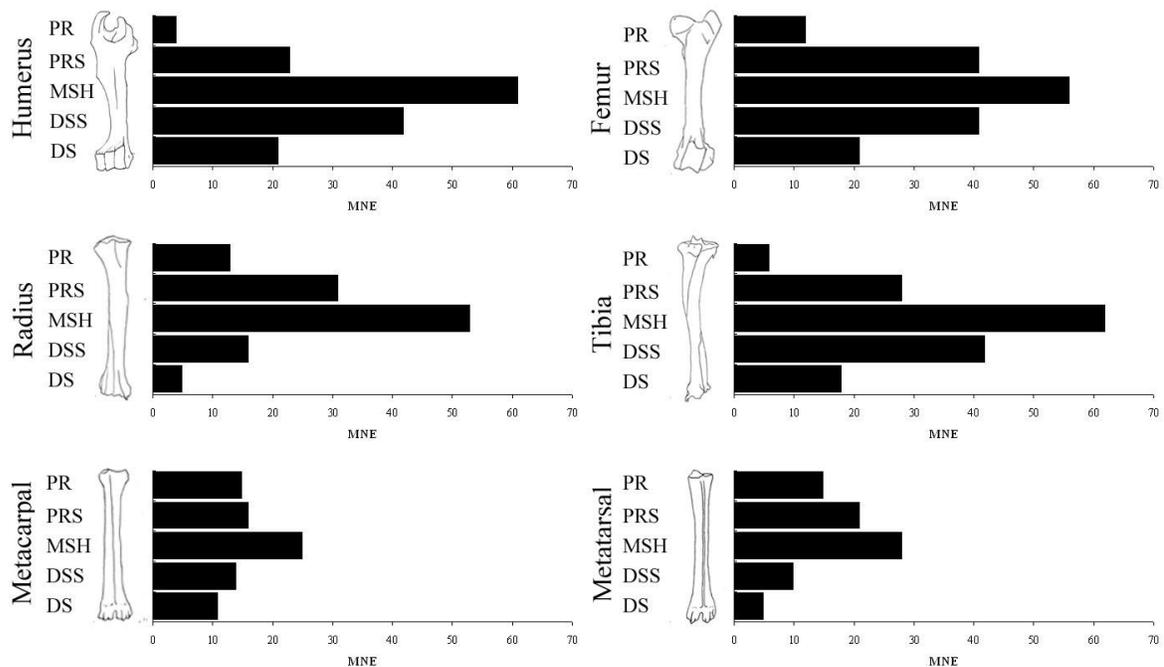
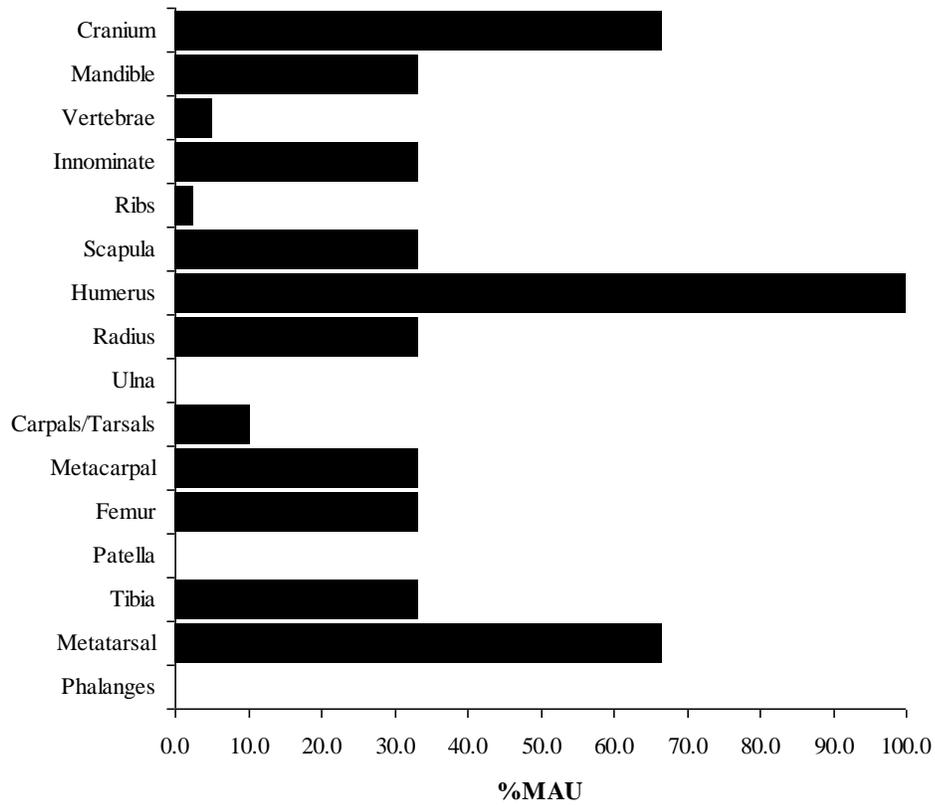


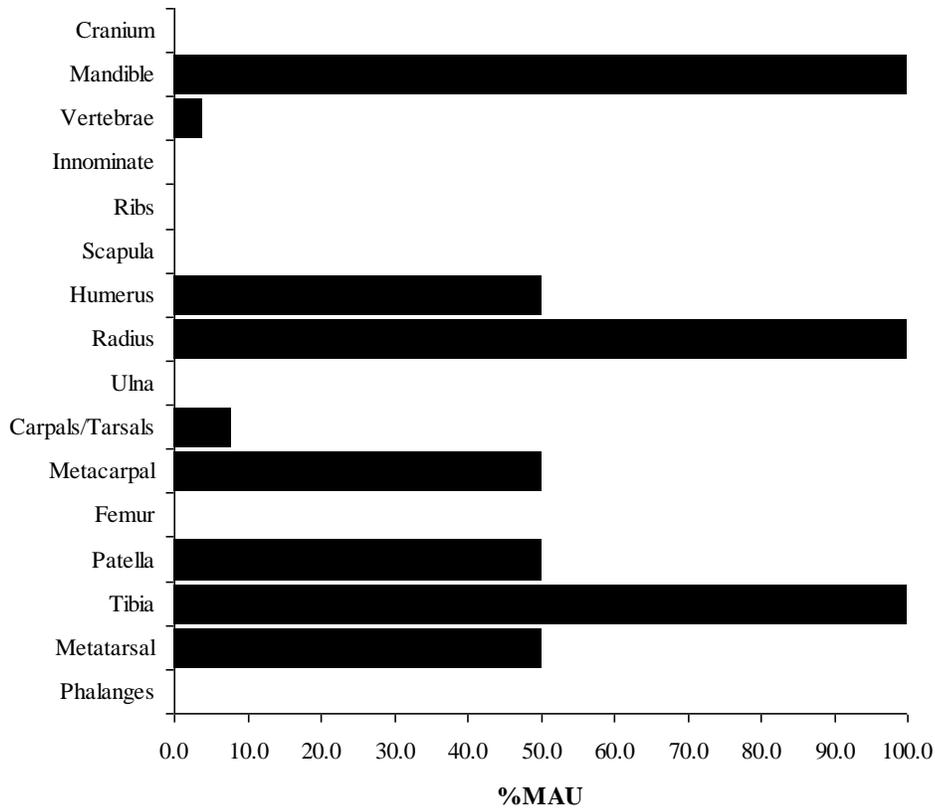
Figure 5.4. Limb bone MNEs (all Size Classes combined) by portion for BK. Codes: PR = proximal, PRS = proximal shaft, MSH = midshaft, DSS = distal shaft, DS = distal.

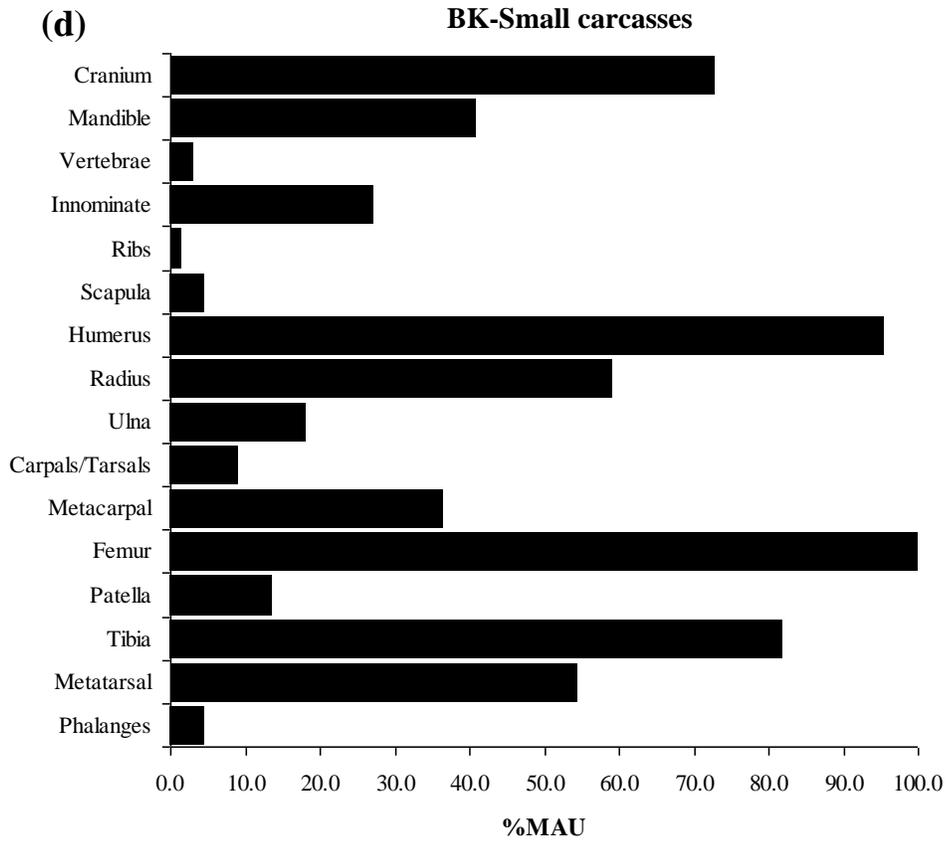
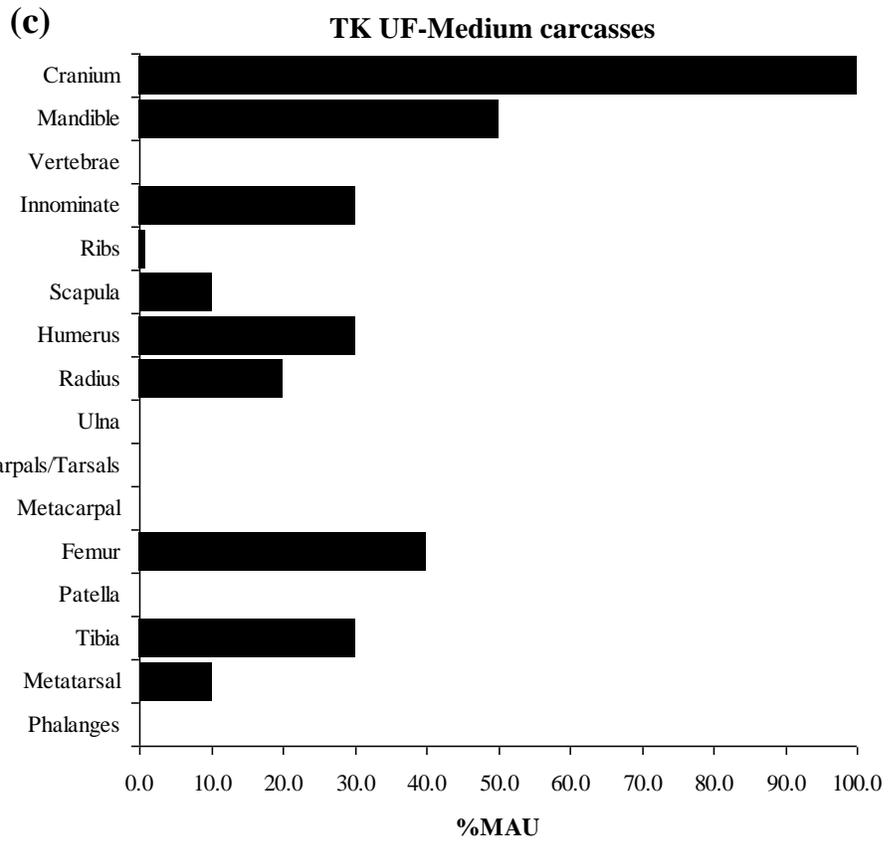
intercept hunting blind reported on by Lupo (2001). This location was utilized by the Hadza during the dry season to take prey repeatedly drawn to a perennial water source. Bone assemblages form when carcasses are dragged to nearby shady spots for butchery, partial consumption and discard. It appears that the low evenness values for the ethnoarchaeological assemblage stem from the differential transport of various skeletal parts back to base camps, which are typically no more than 5 km away (Bunn et al., 1988: 420; O’Connell et al., 1992: 329). There is little direct evidence linking hominids to the faunas from FC West or TK (see below); therefore, it is safe to say only that these sites represent areas from which carcass parts were transported away. Evenness values for small and large animals at BK are suggestive of incomplete carcass representation, while the medium carcass sample falls at the cusp of incomplete and complete representation. Although crania are relatively well represented, it is the variable representation of limb bones that seems to be driving the general unevenness of the small and medium carcass samples; specifically, upper limb bones, and, to

**(a)** FC West-Medium carcasses



**(b)** TK LF-Medium carcasses





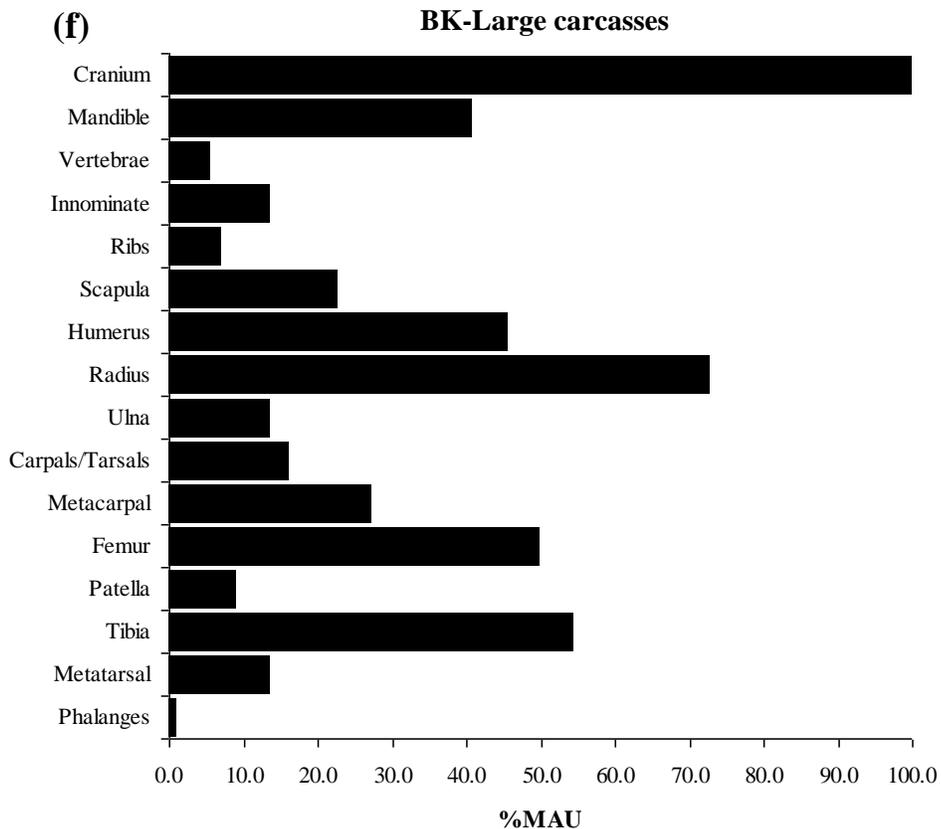
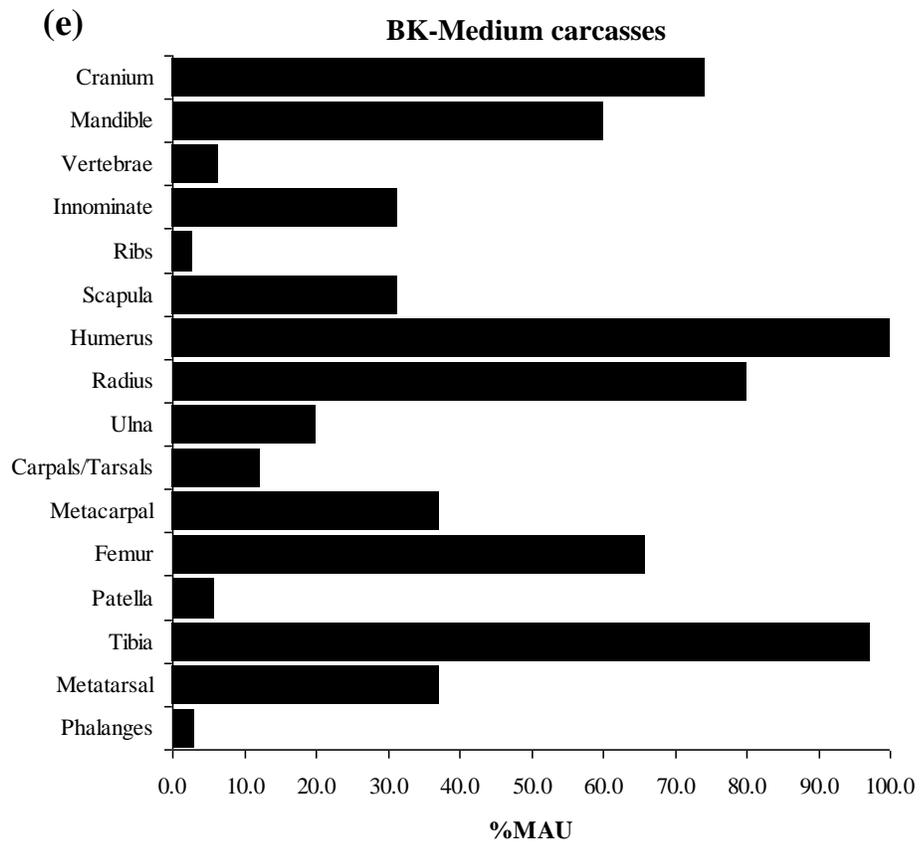


Figure 5.5. %MAU values by skeletal element for (a) medium carcasses at FC West (b) medium carcasses at TK LF (c) medium carcasses at TK UF (d) small carcasses at BK (e) medium carcasses at BK and (f) large carcasses at BK.

Table 5.7. Regression and Spearman's statistics for the relationship between %MAU and density.

	FC West	TK LF	TK UF	BK		
	<u>Medium</u>	<u>Medium</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Large</u>
R <sup>2</sup>	<b>0.48</b>	<b>0.41</b>	<b>0.41</b>	<b>0.65</b>	<b>0.67</b>	<b>0.45</b>
F	<b>12.23</b>	<b>8.29</b>	<b>8.26</b>	<b>29.56</b>	<b>33.86</b>	<b>31.68</b>
P	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>
r <sub>s</sub>	<b>0.48</b>	<b>0.38</b>	<b>0.35</b>	<b>0.64</b>	<b>0.68</b>	<b>0.62</b>
P	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>

Note: Significant values expressed in bold.

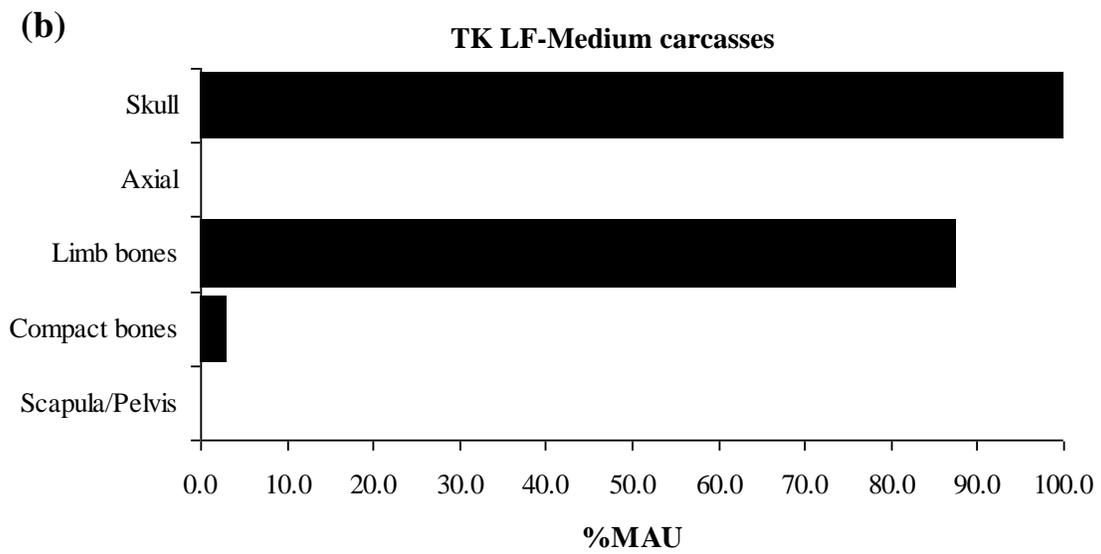
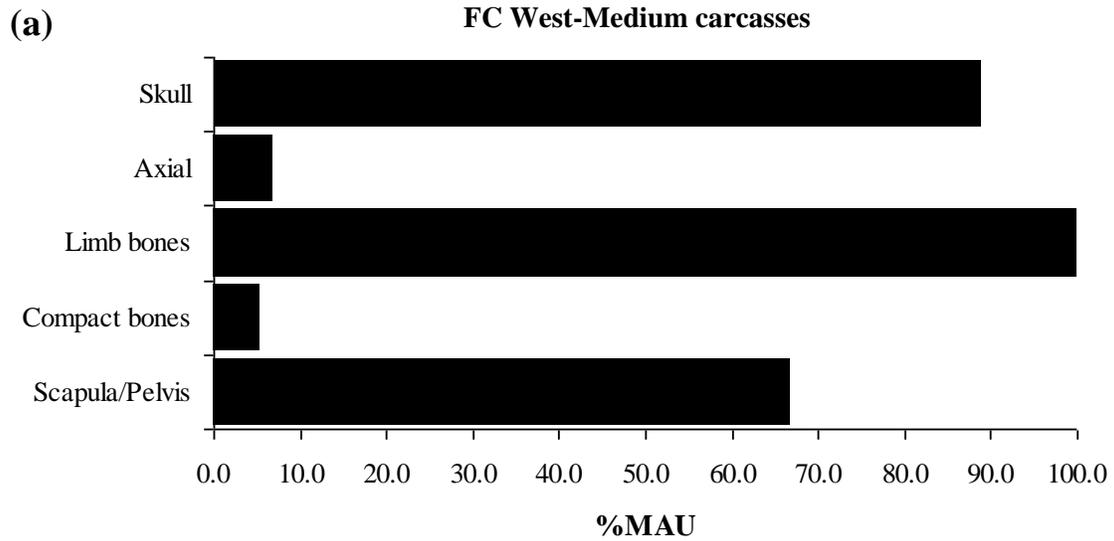
a lesser extent, intermediate limb bones, are well represented while metapodials are poorly represented. For large carcasses, high cranial representation is largely responsible for the low evenness value.

Assuming that axial bones were probably present on-site (attested to by the relatively high representation of crania) but subsequently removed via carnivore ravaging and perhaps water transport, several factors may have contributed to the uneven representation of skeletal elements at BK. Selective transport of small and medium carcasses could explain the differential representation of limb bones given the prevalence of meat- and marrow-rich elements. As mentioned in Chapter 4, however, this is unexpected in a hominid-transported assemblage, as small and medium animals are

Table 5.8. Regression and Spearman's statistics for the relationship between %MAU and %MI.

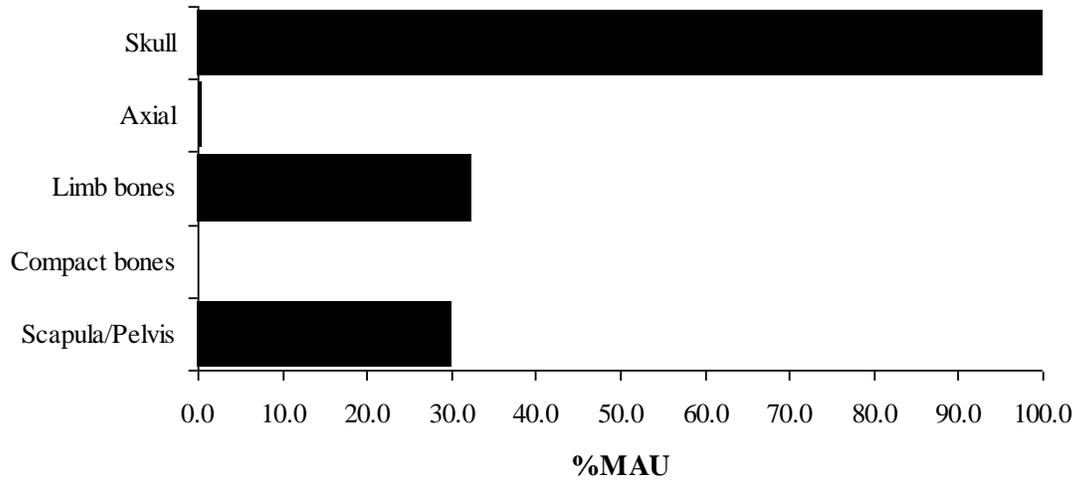
	FC West	TK LF	TK UF	BK		
	<u>Medium</u>	<u>Medium</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Large</u>
R <sup>2</sup>	0.17	0.45	<b>0.86</b>	<b>0.80</b>	0.30	0.49
F	0.12	1.02	<b>11.00</b>	<b>7.14</b>	0.39	1.24
P	0.749	0.369	<b>0.029</b>	<b>0.054</b>	0.565	0.328
r <sub>s</sub>	-0.37	0.28	0.81	0.71	0.58	0.77
P	>0.10	>0.10	>0.05	>0.05	>0.10	>0.05

Note: Significant values expressed in bold.



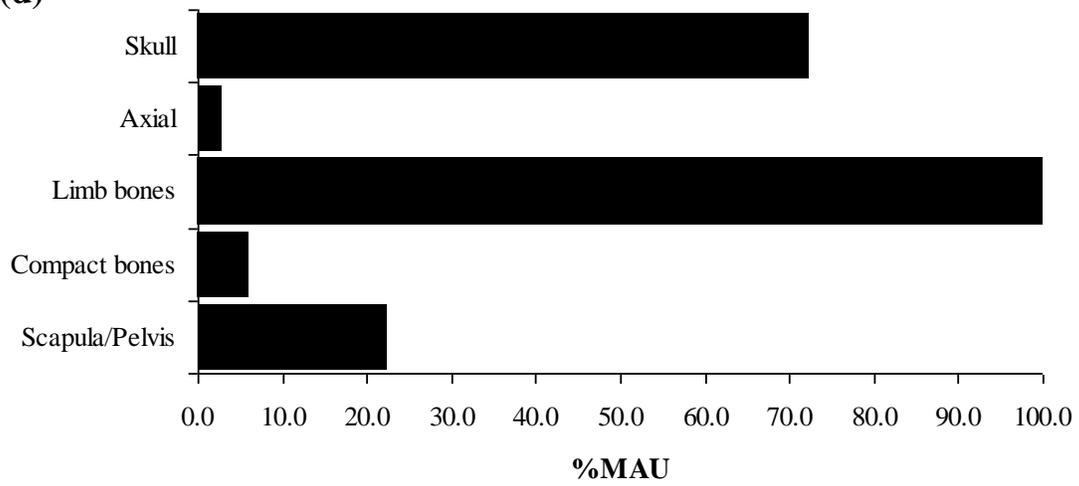
**(c)**

**TK UF-Medium carcasses**



**(d)**

**BK-Small carcasses**



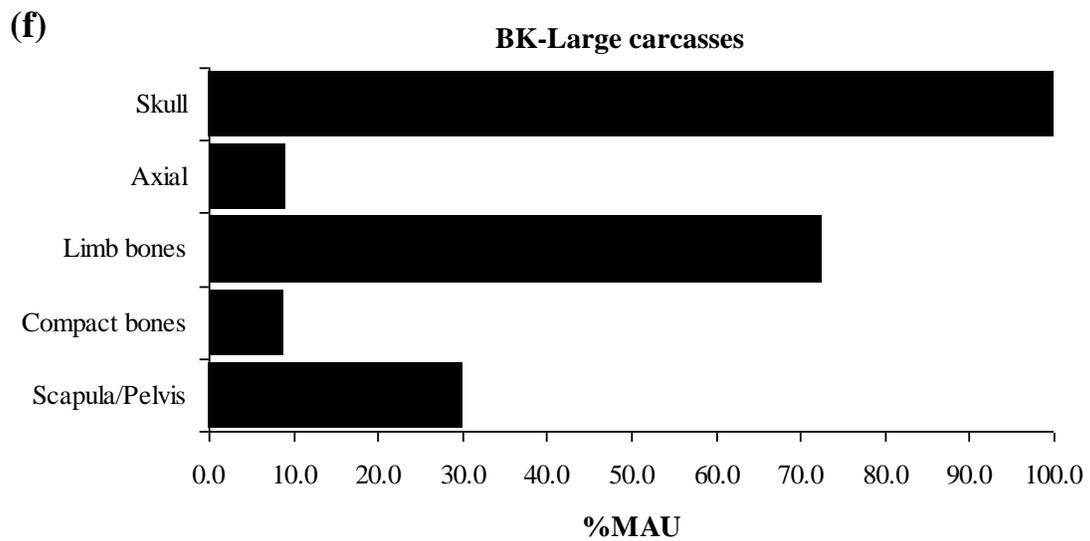
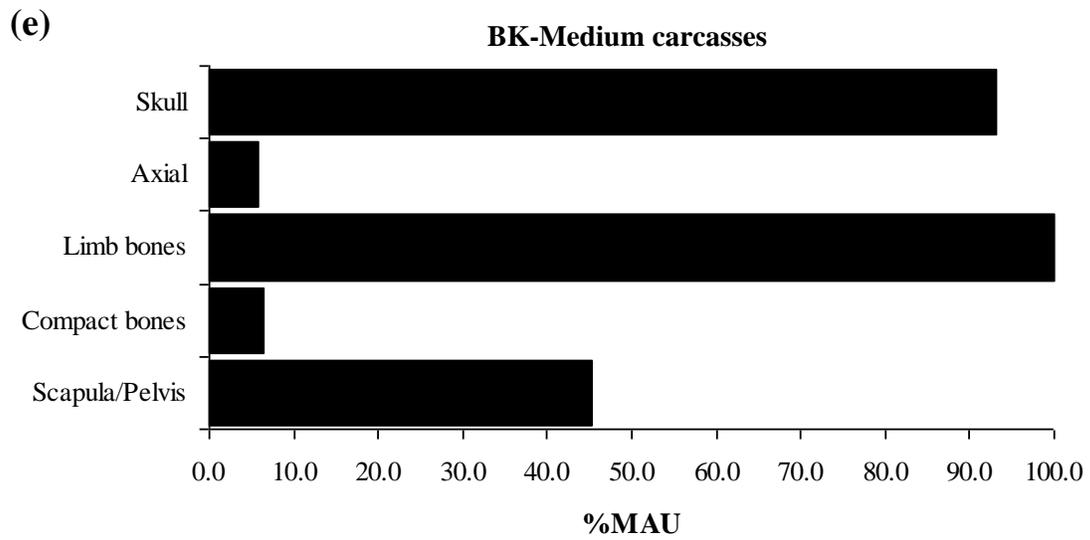


Figure 5.6. Relative representation of skeletal groups for (a) FC West medium carcasses, (b) TK LF medium carcasses, (c) TK UF medium carcasses, (d) DK small carcasses, (e) BK medium carcasses and (f) BK large carcasses.

Table 5.9. Shannon evenness index for element representation at the Bed II sites and several modern samples.

	<b>FC West</b>	<b>TK LF</b>	<b>TK UF</b>	<b>BK</b>		
	<u>Medium</u>	<u>Medium</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Large</u>
Sample size	10	9	18	92	159	69
Evenness	0.944	0.843	0.795	0.879	0.969	0.931

	<b>KFHD 1</b>	<b>Hadza transported assemblages</b>			<b>Hadza intercept blind</b>	
	<u>Small</u>	<u>Small</u>	<u>Medium</u>	<u>Large</u>	<u>Small</u>	<u>Medium</u>
Sample size	114	211	183	68	20	10
Evenness	0.957	0.997	0.998	0.953	0.902	0.188

Note: Evenness calculated using only “high survival” elements. KFHD 1 (= Koobi Fora Hyena Den) data from Lam (1992); hunting blind data from Lupo (2001), Hadza transport data from Monahan (1998).

typically transported complete by hunter-gatherers (Table 5.9 and Figure 5.5). The KFHD 1 den data show that hyenas can create low evenness values among assemblages of small carcasses. It is also possible that complete carcasses were deposited on-site and the primary agent of accumulation left most of the low utility elements unprocessed. Secondary agents may then have removed the remaining (low utility) elements off-site for consumption elsewhere. Some evidence for this is found in the fact that metacarpals are represented by the highest percentage of complete bones (see below). On the other hand, Monahan (1996b: 201) suggests that depressed metapodial representation may have resulted from intense processing by hominids, which rendered the resulting fragments less readily identifiable. However, it is difficult to see why the low-utility metapodials would have been processed more intensely than other limb bones (unless hominids only had access to metapodials). In addition, of the fragments that could be assigned to limb bone type only (i.e., upper, intermediate, metapodial), only 20% derived from metapodials. Therefore, it is unlikely that relative identifiability is responsible for low metapodial representation. The uneven values for large carcasses are not unexpected given how hunter-gatherers transport such animals. What is unexpected is the dominance of crania, which are transported least often by hunter-gatherers (Figure 5.6). It therefore seems likely

that most of the large animals died on-site (or very nearby) with subsequent scattering of skeletal parts.

### BONE SURFACE MODIFICATIONS

Tables 5.10 and 5.11 summarize surface mark frequencies for the Bed II sites. Very few surface marks were identified at FC West and TK. FC West and, especially, TK have extremely poor cortical surface preservation (see also Monahan, 1996b: 139). At FC West only 35.7% of specimens scored for surface preservation had well-preserved cortices while only 8.8% and 5.1% of specimens were scored as well-preserved at TK LF and TK UF, respectively. Therefore, cortical surface degradation is no doubt responsible for the virtual lack of surface modifications at these sites. In

contrast, preservation at BK is generally very good as about 60% of specimens scored had well-preserved cortices. Sediment abrasion is relatively common at BK, where 77 specimens exhibit such damage.

Figures 5.7–5.9 show examples of typical cutmarks, percussion marks and tooth marks in the BK assemblage. Although all types of surface damage occur in low frequencies, carnivore damage is more abundant than hominid damage overall (Table 5.11). One Size Class 2 humerus shows cutmarks, percussion marks, a percussion notch, carnivore gnawing and tooth pits (Figure 5.10), which probably indicates carnivore scavenging of the most marginal of hominid food refuse. The overall incidence of tooth-marking is 7.1% at FC West, 3.4% at TK LF, 0.0% at TK UF (Table 5.10) and 8.2% at BK (Table 5.11). One digested piece was found at FC West (1.1% of total NISP) while ten (0.4%) occur in the BK assemblage.

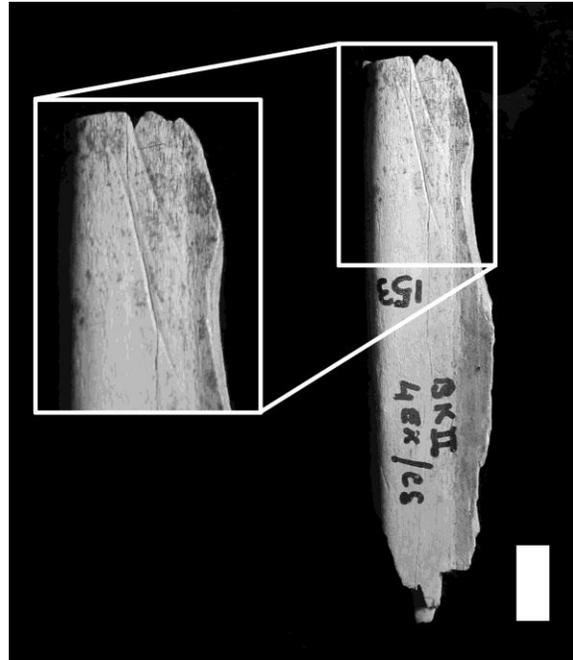


Figure 5.7. Bovid metatarsal fragment from BK with cutmarks. Scale bar = 2 cm.

Table 5.10. Tooth mark frequencies for medium carcasses at FC West and TK.

Element	FC West	TK LF	TK UF
Mandible	0/0 (0.0)	0/2 (0.0)	0/1 (0.0)
Vertebrae	0/2 (0.0)	0/1 (0.0)	0/0 (0.0)
Innominate	0/1 (0.0)	0/0 (0.0)	0/3 (0.0)
Ribs	0/1 (0.0)	0/0 (0.0)	0/1 (0.0)
Scapula	0/1 (0.0)	0/0 (0.0)	0/2 (0.0)
Humerus	0/3 (0.0)	0/1 (0.0)	0/3 (0.0)
Radius	0/1 (0.0)	0/3 (0.0)	0/3 (0.0)
Ulna	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Carpals	0/1 (0.0)	0/0 (0.0)	0/0 (0.0)
Metacarpal	0/3 (0.0)	0/1 (0.0)	0/0 (0.0)
Femur	0/1 (0.0)	0/0 (0.0)	0/4 (0.0)
Patella	0/0 (0.0)	0/1 (0.0)	0/0 (0.0)
Tibia	0/1 (0.0)	0/4 (0.0)	0/4 (0.0)
Tarsals	0/1 (0.0)	0/1 (0.0)	0/0 (0.0)
Metatarsal	1/2 (50.0)	0/2 (0.0)	0/1 (0.0)
Phalanges	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
Sesamoids	0/0 (0.0)	0/0 (0.0)	0/0 (0.0)
LBS	1/10 (10.0)	1/13 (7.7)	0/14 (0.0)
Total	2/28 (7.1)	1/29 (3.4)	0/36 (0.0)

Note: Numerator denotes number of marked specimens, denominator denotes total NISP for each skeletal element, percentage is in parentheses. Codes: LBS = unidentified limb bone fragment.

Table 5.11. Surface mark frequencies by element and carcass size at BK.

Element	NISP	TM	CM	PM
<b>Small carcasses</b>				
Mandible	16	0 (0.0)	0 (0.0)	0 (0.0)
Vertebrae	15	1 (6.7)	0 (0.0)	0 (0.0)
Innominate	6	1 (16.7)	0 (0.0)	0 (0.0)
Ribs	18	0 (0.0)	0 (0.0)	0 (0.0)
Scapula	3	0 (0.0)	0 (0.0)	0 (0.0)
Humerus	29	5 (17.2)	1 (3.4)	1 (3.4)
Radius	18	3 (16.7)	0 (0.0)	0 (0.0)
Ulna	5	0 (0.0)	0 (0.0)	0 (0.0)
Carpals	3	0 (0.0)	0 (0.0)	0 (0.0)
Metacarpal	18	2 (11.1)	0 (0.0)	2 (11.1)
Femur	38	4 (10.5)	1 (2.6)	1 (2.6)
Patella	3	0 (0.0)	0 (0.0)	0 (0.0)
Tibia	38	4 (10.5)	0 (0.0)	1 (2.6)
Tarsals	12	0 (0.0)	0 (0.0)	0 (0.0)
Metatarsal	23	3 (13.0)	1 (4.3)	0 (0.0)
Phalanges	8	0 (0.0)	0 (0.0)	0 (0.0)
Sesamoids	3	0 (0.0)	0 (0.0)	0 (0.0)
LBS	77	8 (10.4)	1 (1.3)	2 (2.6)
Total	333	31 (9.3)	4 (1.2)	7 (2.1)
<b>Medium carcasses</b>				
Mandible	41	1 (2.4)	0 (0.0)	0 (0.0)
Vertebrae	46	8 (17.4)	1 (2.2)	0 (0.0)
Innominate	21	3 (14.3)	1 (4.8)	0 (0.0)
Ribs	71	5 (7.0)	4 (5.6)	0 (0.0)
Scapula	20	0 (0.0)	0 (0.0)	0 (0.0)
Humerus	82	8 (9.8)	6 (7.3)	4 (4.9)
Radius	58	9 (15.5)	1 (1.7)	1 (1.7)
Ulna	12	3 (25.0)	0 (0.0)	0 (0.0)
Carpals	10	0 (0.0)	0 (0.0)	0 (0.0)
Metacarpal	35	2 (5.7)	1 (2.9)	1 (2.9)
Femur	61	6 (9.8)	2 (3.3)	2 (3.3)
Patella	2	0 (0.0)	0 (0.0)	0 (0.0)
Tibia	100	19 (19.0)	1 (1.0)	2 (2.0)
Tarsals	18	0 (0.0)	0 (0.0)	0 (0.0)
Metatarsal	53	6 (11.3)	3 (5.7)	2 (3.8)
Phalanges	12	0 (0.0)	0 (0.0)	0 (0.0)
Sesamoids	17	0 (0.0)	0 (0.0)	0 (0.0)
LBS	248	15 (6.0)	3 (1.2)	0 (0.0)
Total	907	85 (9.4)	23 (2.5)	12 (1.3)

Table 5.11. cont.

Element	NISP	TM	CM	PM
<b>Large carcasses</b>				
Mandible	20	1 (5.0)	0 (0.0)	0 (0.0)
Vertebrae	21	2 (9.5)	0 (0.0)	0 (0.0)
Innominate	6	0 (0.0)	1 (16.7)	0 (0.0)
Ribs	95	2 (2.1)	1 (1.1)	0 (0.0)
Scapula	10	1 (1.0)	1 (1.0)	0 (0.0)
Humerus	24	2 (8.3)	1 (4.2)	0 (0.0)
Radius	28	5 (17.9)	0 (0.0)	0 (0.0)
Ulna	4	2 (50.0)	0 (0.0)	0 (0.0)
Carpals	4	0 (0.0)	0 (0.0)	0 (0.0)
Metacarpal	8	0 (0.0)	1 (12.5)	0 (0.0)
Femur	27	1 (3.7)	0 (0.0)	0 (0.0)
Patella	2	0 (0.0)	0 (0.0)	0 (0.0)
Tibia	32	2 (6.3)	0 (0.0)	0 (0.0)
Tarsals	20	0 (0.0)	0 (0.0)	0 (0.0)
Metatarsal	11	1 (9.1)	0 (0.0)	0 (0.0)
Phalanges	7	0 (0.0)	0 (0.0)	0 (0.0)
Sesamoids	0	0 (0.0)	0 (0.0)	0 (0.0)
LBS	102	1 (0.9)	1 (0.9)	0 (0.0)
Total	421	20 (4.8)	6 (1.4)	0 (0.0)

Note: Numerator denotes number of marked specimens, denominator denotes total NISP for each skeletal element, percentage is in parentheses. Codes: LBS = unidentified limb bone fragment.

Table 5.12 summarizes tooth mark frequencies by limb bone segment. The poorly preserved faunas from FC West and TK show few or no tooth marks. Tooth mark frequencies are relatively low on all three carcass sizes at BK. Figure 5.11 displays midshaft tooth mark frequencies for BK relative to actualistic samples. Small, medium and large carcasses fall well within the range of the “hammerstone-to-carnivore” samples that model secondary access by carnivores. However, these frequencies also match well with the felid samples, which are also tooth-marked at low frequencies. Again, hominid-imparted surface mark data and bone breakage must be consulted to address the order of hominid access to carcasses.

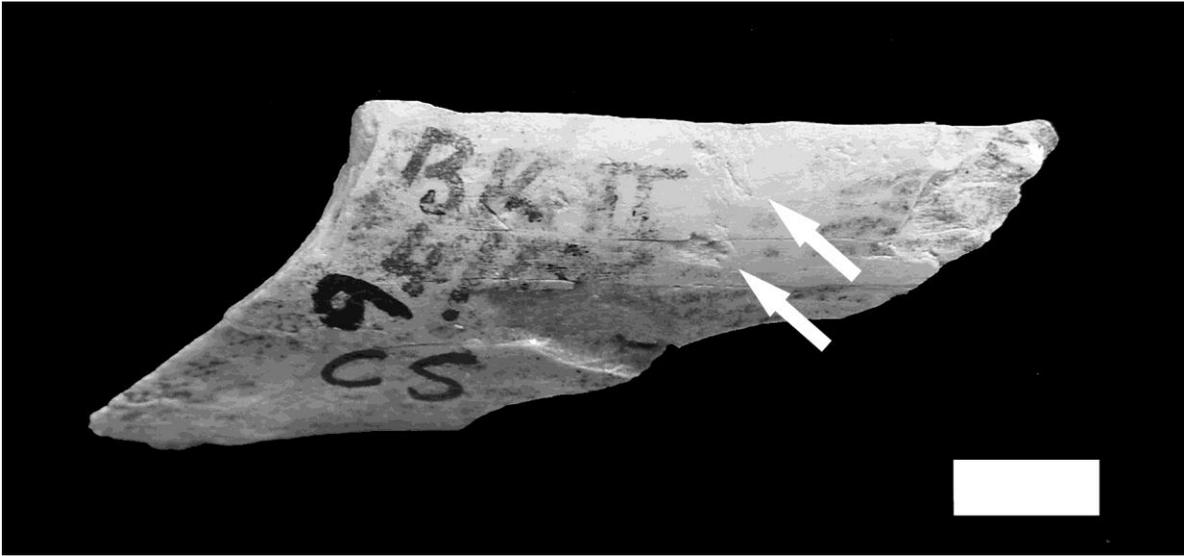


Figure 5.8. Bovid femur fragment from BK with percussion marks (arrows). Scale bar = 1 cm.



Figure 5.9. Bovid radio-ulna fragment from BK with tooth marks (arrows). Scale bar = 1 cm.

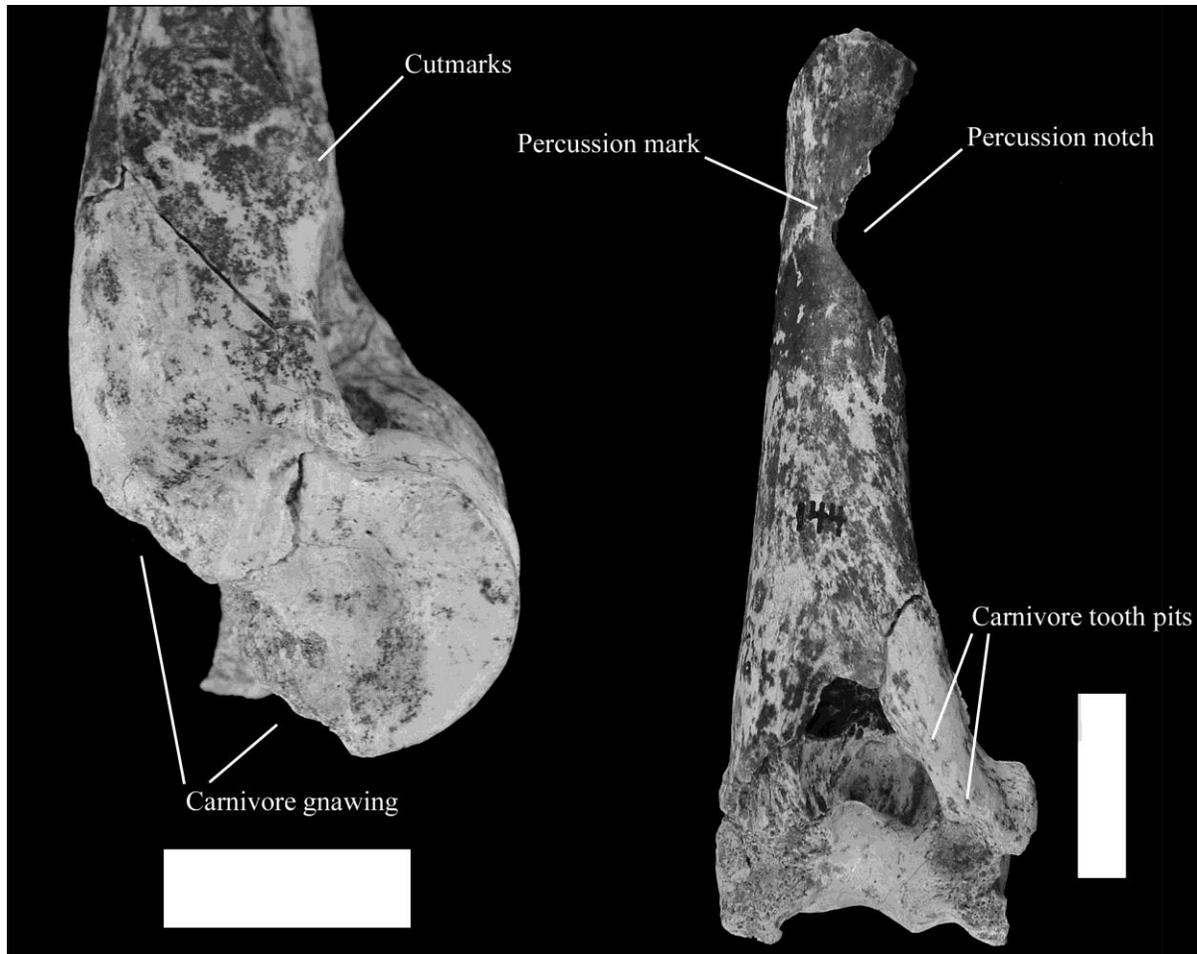


Figure 5.10. Lateral (left) and caudal (right) views of a Size Class 3a bovid humerus with co-occurring hominid and carnivore damage. Scale bars = 3 cm.

No hominid modifications were discovered in the FC West or TK assemblages.<sup>3</sup> Although cutmarks and percussion marks are present in significant frequencies especially among small and medium carcasses at BK, they still fall below those expected in an assemblage processed completely by hominids (Figure 5.12). This pattern would only be amplified by the inclusion of the very small fragments that are missing from the assemblage. Cutmarks on humeri and especially femora occur on what Domínguez-Rodrigo and Barba (in press) term “Hot Zones”; i.e., anatomical zones on limb bones where flesh scraps never survive after lion defleshing (Figure 5.13). Therefore, cutmarks on

<sup>3</sup> Two cutmarked specimens (a complete metatarsal and an intermediate limb bone fragment) were identified from an overlying level of FC West.

Table 5.12. Percentage of epiphyseal, near-epiphyseal, and midshaft specimens bearing tooth marks by carcass size at the Bed II sites.

	Small			Medium			Large		
	NISP	NISP TM	%	NISP	NISP TM	%	NISP	NISP TM	%
<b>FC West</b>									
EP	-	-	-	0	0	0.0	-	-	-
NEP	-	-	-	3	1	33.3	-	-	-
MSH	-	-	-	2	1	50.0	-	-	-
Total	-	-	-	5	2	40.0	-	-	-
<b>TK LF</b>									
EP	-	-	-	2	0	0.0	-	-	-
NEP	-	-	-	0	0	0.0	-	-	-
MSH	-	-	-	1	0	0.0	-	-	-
Total	-	-	-	3	0	0.0	-	-	-
<b>TK UF</b>									
EP	-	-	-	0	0	0.0	-	-	-
NEP	-	-	-	0	0	0.0	-	-	-
MSH	-	-	-	0	0	0.0	-	-	-
Total	-	-	-	0	0	0.0	-	-	-
<b>BK</b>									
EP	15	6	40.0	17	2	11.8	9	2	22.2
NEP	23	3	13.0	74	10	13.5	30	4	13.3
MSH	104	14	13.5	252	38	15.1	55	2	3.6
Total	142	23	16.2	343	50	14.6	94	8	8.5

Note: Only green-broken specimens with good surface preservation included. Codes: NISP = number of identified specimens, TM = tooth mark, EP = epiphyseal, NEP = near-epiphyseal, MSH = midshaft.

these locations unambiguously signal early access by hominids to carcasses. In addition, many cutmarks (including those on unidentified limb bone fragments that could not be anatomically oriented) on meat-bearing upper and intermediate limb bone fragments occur on midshaft sections in general (Table 5.13), which is also consistent with early access (Bunn, 2001; Bunn and Kroll, 1986; Domínguez-Rodrigo 1997, 1999a, b, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering and Domínguez-Rodrigo, 2007; Pickering et al., 2004c). However, the destruction of epiphyses has probably artificially depressed the frequency of cutmarked epiphyseal segments. Cutmarks and percussion marks are distributed equally among medium carcass limb bones (cutmarks:  $\chi^2 = 3.28$ ;  $p > 0.05$ ; percussion marks:  $\chi^2 = 1.33$ ;  $p > 0.05$ ), which suggests processing of complete limb units.

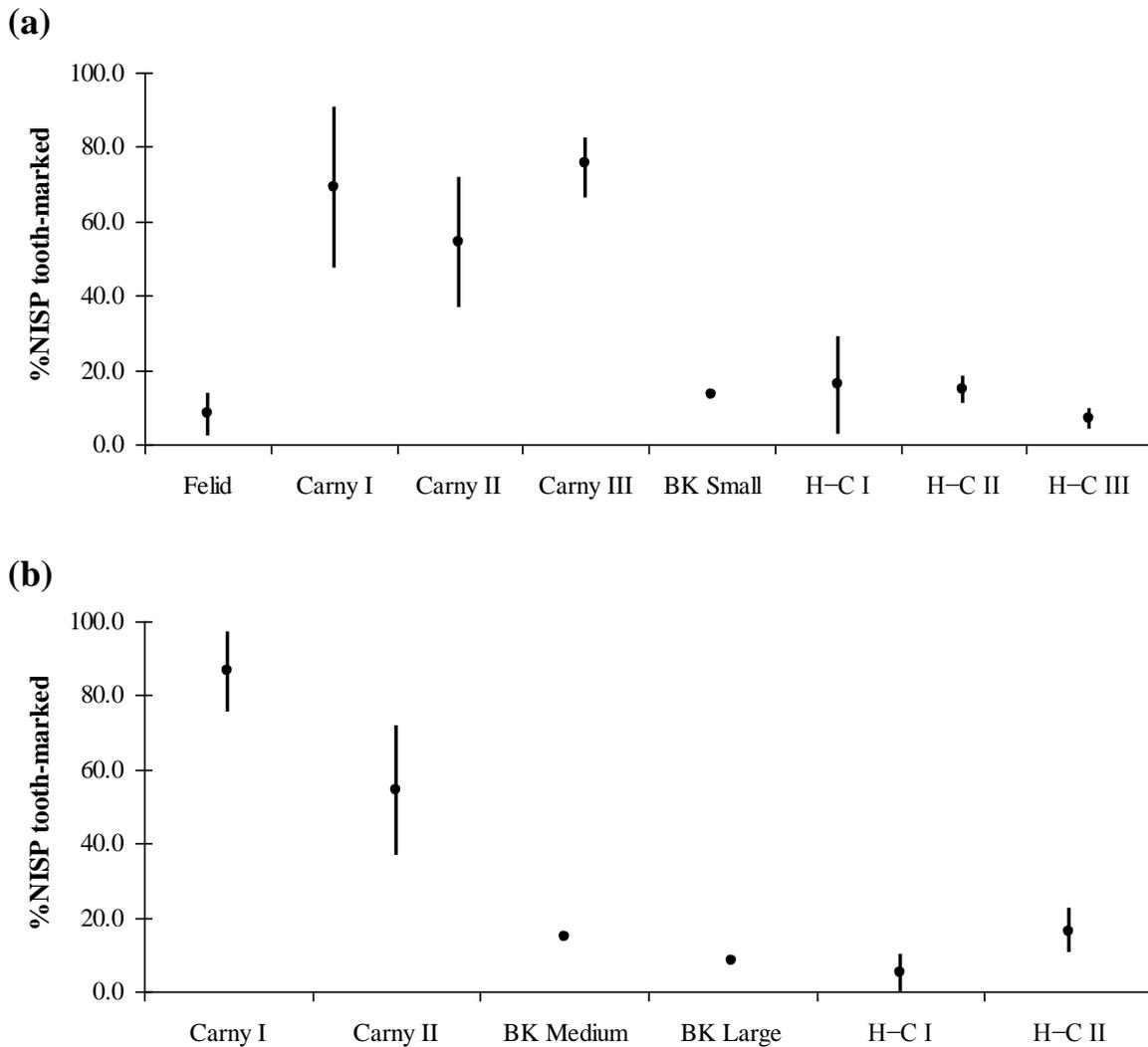


Figure 5.11. Percentage of tooth-marked midshaft specimens at BK for (a) small and (b) medium and large carcasses compared to the mean and 95% confidence intervals of several actualistic samples. Codes: Felid = felid-consumed carcass followed by hammerstone breakage, Carny = carnivore-only, H-C = hammerstone-to-carnivore. Note: Only fossil specimens with green breakage and good surface preservation are considered. Data from Blumenschine (1995), Capaldo (1997), Domínguez-Rodrigo et al. (in press b), Marean et al. (2000). The range of variation from Marean's experiments ("Carny III" and "H-C III") are somewhat smaller because confidence intervals were calculated by bootstrapping a single sample (Marean et al., 2000: Table 3).

Finally, the presence of cutmarked pelves and ribs (which are typically consumed early in the carnivore consumption sequence [Blumenschine, 1986a]) of medium and large carcasses also suggests early access.

Table 5.14 provides summary statistics for tooth pit dimensions on limb bone diaphyses at BK (no measurable tooth pits were found at FC West or TK). Only the sample of pits on medium

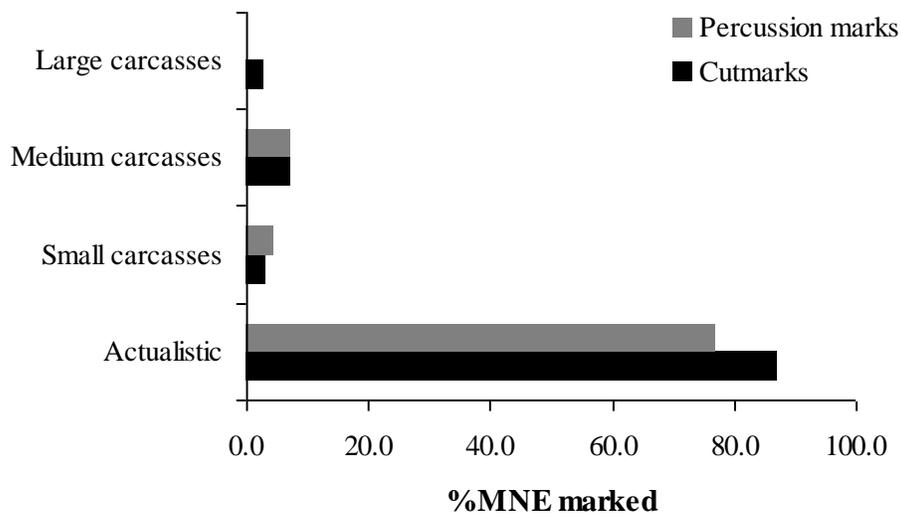
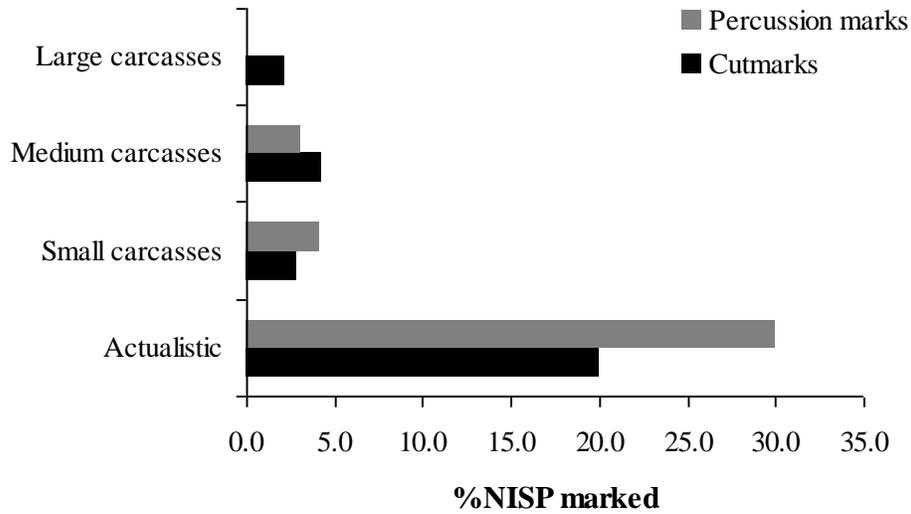


Figure 5.12. Butchery mark frequencies by (a) NISP and (b) MNE for BK and actualistic samples. Actualistic data from Blumenschine and Selvaggio (1988, 1991), Bunn (1982), Domínguez-Rodrigo (1997, 1999b), Domínguez-Rodrigo and Barba (2005), Lupo and O'Connell (2002), Pickering and Egeland (2006) and Pobiner and Braun (2005a).

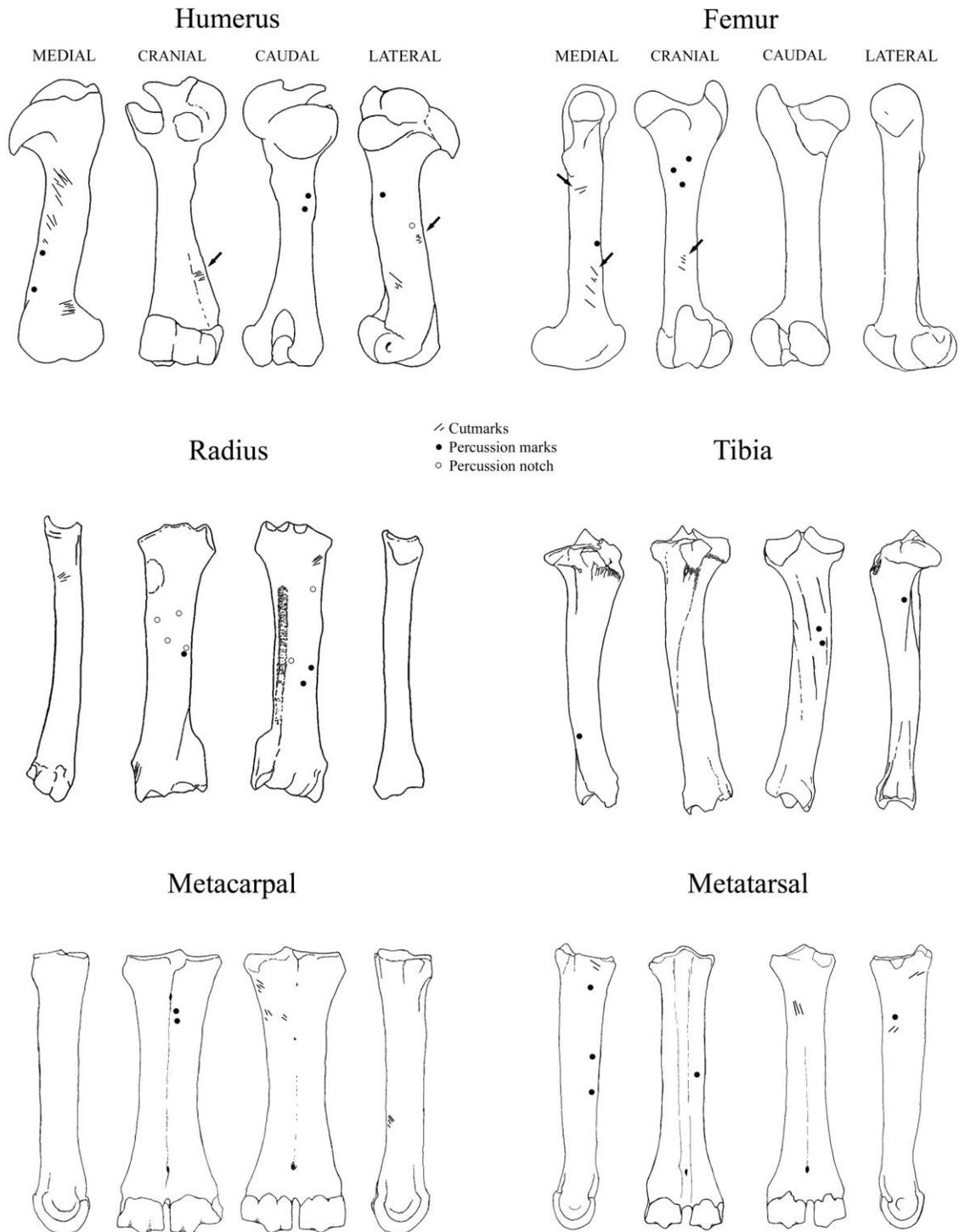


Figure 5.13. Composite diagram showing location of cutmarks and percussion marks and notches on limb bones from BK. Arrows indicate cutmarks on "Hot Zones".

carcasses is large enough to provide a reliable range of variation and therefore only these data are plotted in Figure 5.14. The BK data are similar to modern carnivores with robust dentitions like lions and hyenas. Although the sample size is small, the large carcass data are, unsurprisingly, consistent with larger carnivores as well.

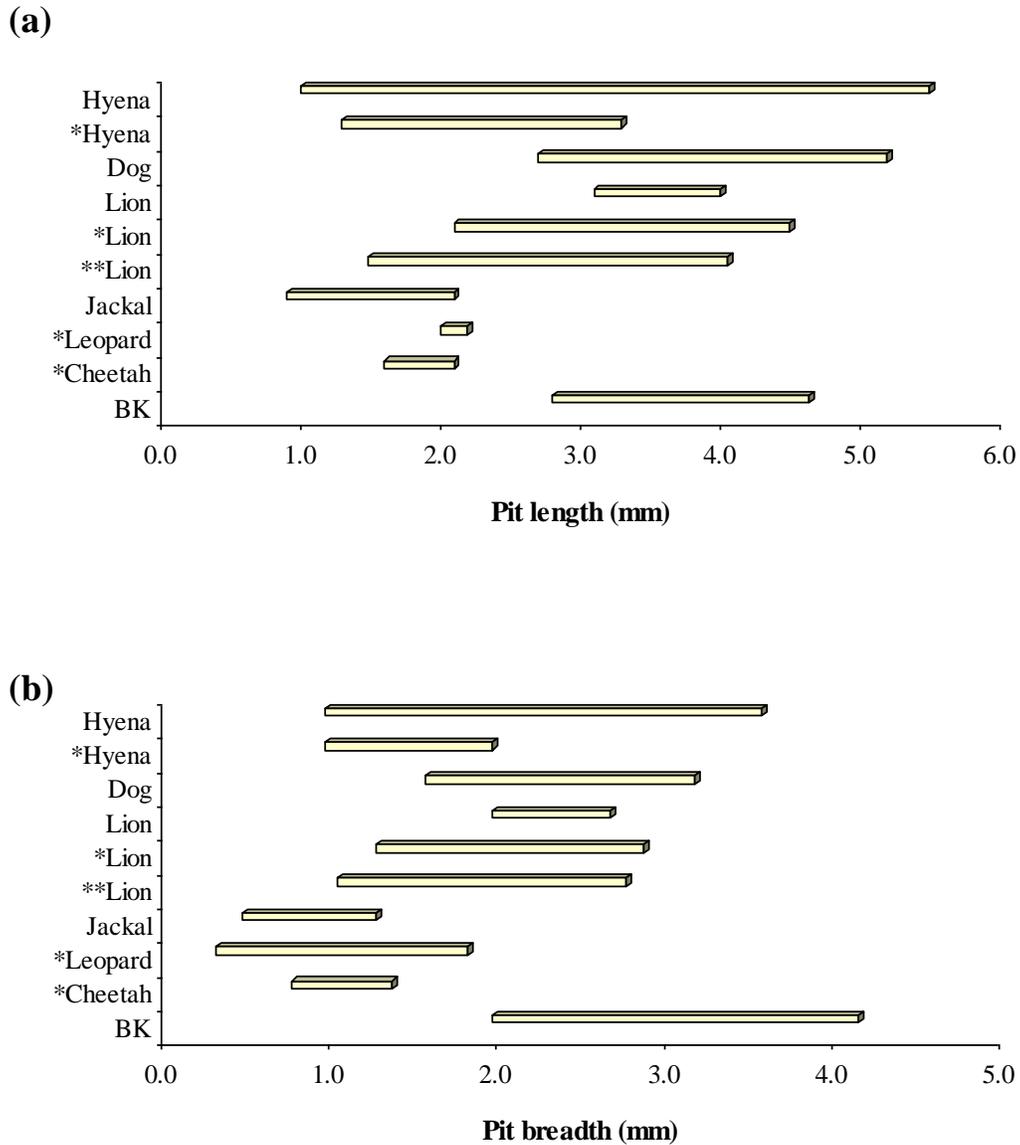


Figure 5.14. Range (95% confidence intervals) of tooth pit (a) lengths and (b) breadths from BK and several actualistic samples. Data marked with one asterisk (\*) are from Selvaggio (1994b), data marked with two asterisks (\*\*) from Pobiner (2007). All other actualistic data from Domínguez-Rodrigo and Piqueras (2003).

Table 4.13. Cutmark percentages (NISP) by bone section and carcass size on upper and intermediate limb bones fragments from BK.

	EP	NEP	MSH
<b>Small</b>			
NISP	0	2	2
%	0.0	50.0	50.0
<b>Medium</b>			
NISP	0	8	7
%	0.0	57.1	50.0
<b>Large</b>			
NISP	0	0	2
%	0.0	0.0	100.0

Note: Cells may add up to more than 100% because cutmarks can appear on more than one section. Codes: EP = epiphysis; NEP = near-epiphysis; MSH = midshaft.

Table 5.14. Summary statistics for tooth pits by carcass size at BK.

	Small	Medium	Large
<b>Length</b>			
N	3	17	5
Mean	2.0	3.1	4.7
S.D.	0.3	2.1	1.1
95% CI	1.3–2.7	2.0–4.2	3.3–6.1
<b>Breadth</b>			
N	3	17	5
Mean	1.4	2.2	3.4
S.D.	0.5	1.8	0.5
95% CI	0.2–2.6	1.3–3.1	2.8–4.1

### FRACTURE PATTERNS

With the exception of FC West, most breakage occurred during the nutritive phase at the Bed II sites (Figure 5.15). Complete limb bones are absent at FC West and TK and rare at BK (Table 5.15). All three Bed II sites show Type 3 circumference representation similar to experimental assemblages with intense hyena ravaging (Figure 5.3).

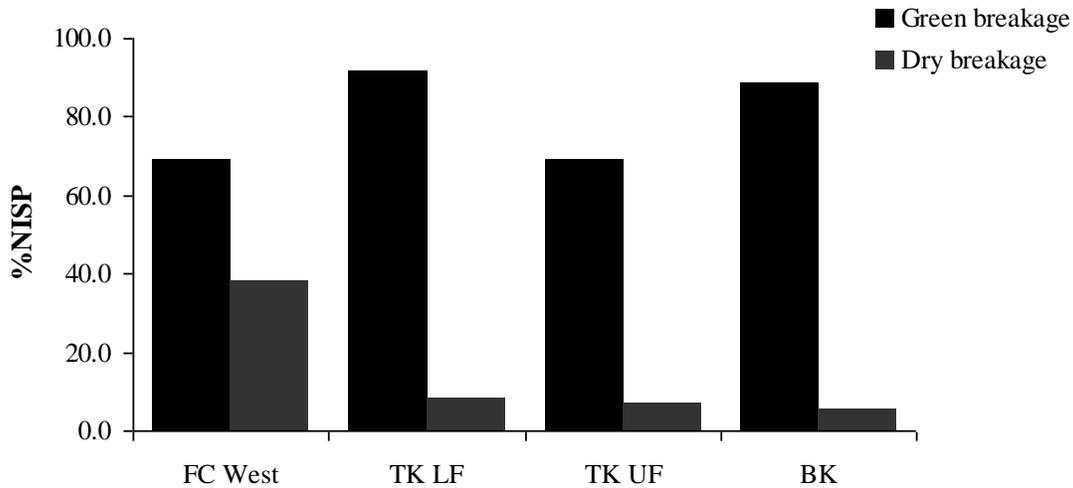


Figure 5.15. Percentage of green and dry breakage on medium carcass limb bones in the Bed II sites. Note: Specimens with recent breakage are not included, therefore values may not add to 100%.

Overall levels of fragmentation are listed in Table 5.16 and Table 5.17 provides limb bone fragmentation ratios (see Chapter 4 for actualistic data). Keeping in mind that all estimates of fragmentation are certainly underestimates given the removal of smaller fragments from the Bed II sites, medium carcasses are the most comminuted. Levels of limb bone fragmentation for TK LF and BK are similar to hyena- and human-processed assemblages and are far higher than those created by carnivores with less robust dentitions (leopards, dogs and jackals) (Figure 5.16). All of the Bed II sites show very high levels of epiphyseal destruction (Figure 5.16), which is comparable to assemblages that are heavily ravaged by hyenas in experimental and open-air naturalistic contexts.

Table 5.15. Incidence of complete limb bones by carcass size from the Bed II sites.

Element	Small	Medium	Large
Humerus	0/21 (0.0)	0/35 (0.0)	0/10 (0.0)
Radius	2/13 (15.4)	1/28 (3.6)	1/16 (6.3)
Metacarpal	2/8 (25.0)	1/13 (7.7)	1/6 (16.7)
Femur	0/22 (0.0)	1/23 (4.3)	1/11 (9.1)
Tibia	0/18 (0.0)	3/34 (8.8)	0/12 (0.0)
Metatarsal	0/12 (0.0)	0/13 (0.0)	0/3 (0.0)
Total	4/94 (4.3)	6/145 (4.1)	3/58 (5.2)

Table 5.16. Fragmentation indices by carcass size for the Bed II sites.

	Small		Medium		Large	
	<u>NISP:MNE</u>	<u>NISP:MNI</u>	<u>NISP:MNE</u>	<u>NISP:MNI</u>	<u>NISP:MNE</u>	<u>NISP:MNI</u>
FC West	-	-	1.19	10.75	-	-
TK LF	-	-	2.50	10.00	-	-
TK UF	-	-	1.96	11.00	-	-
BK	2.15	34.80	3.21	85.32	3.23	29.67

Table 5.17. Limb bone fragmentation indices by carcass size for the Bed II sites.

	Small		Medium		Large	
	<u>NISP:MNE</u>	<u>EP:SH</u>	<u>NISP:MNE</u>	<u>EP:SH</u>	<u>NISP:MNE</u>	<u>EP:SH</u>
FC West	-	-	1.78	0.23	-	-
TK LF	-	-	3.29	0.14	-	-
TK UF	-	-	2.08	0.13	-	-
BK	2.38	0.16	4.28	0.14	3.78	0.12

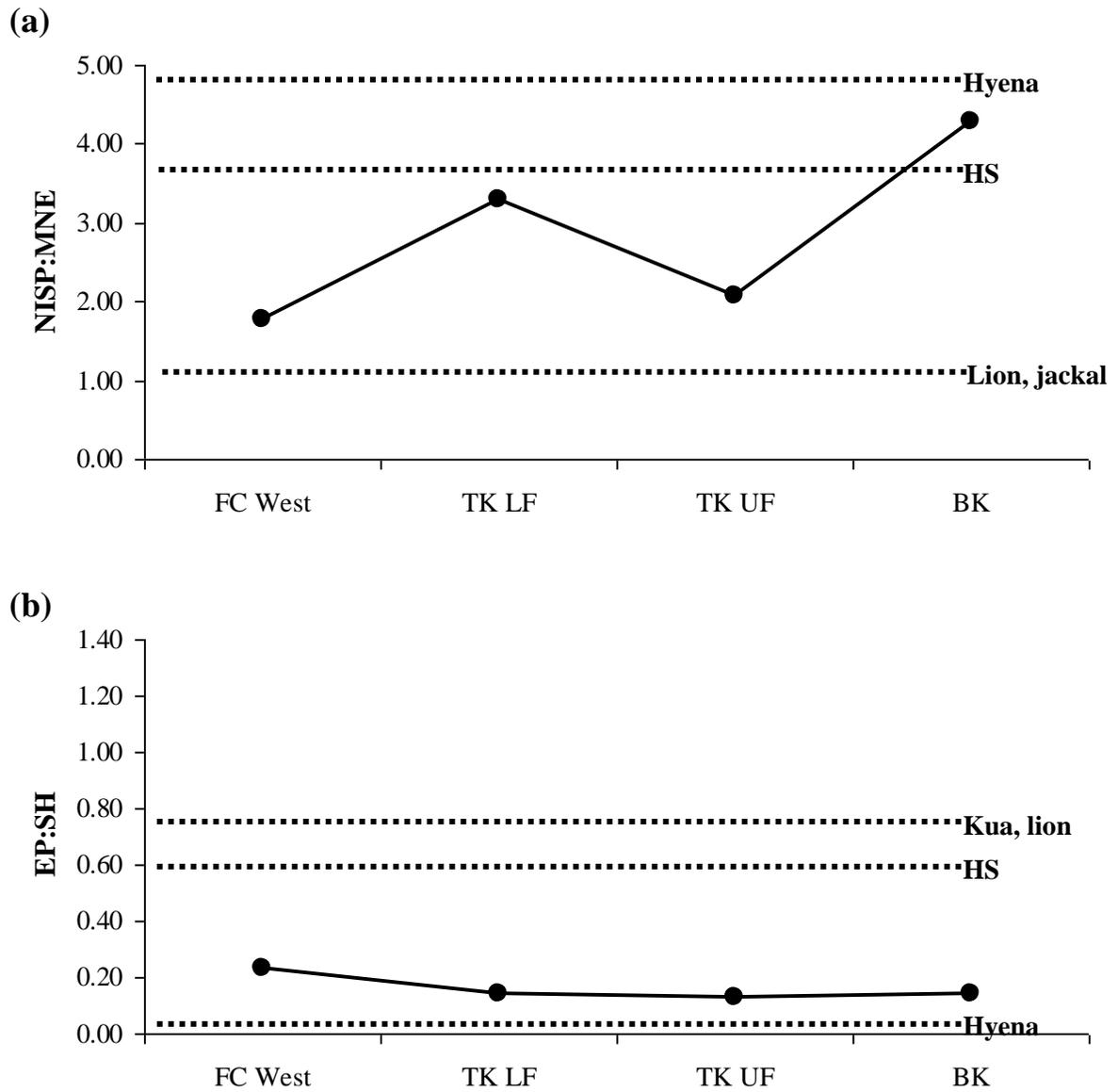


Figure 5.16. (a) Limb bone fragmentation and (b) epiphysis-to-shaft ratios for medium carcasses from the Bed II sites. Codes: HS = hammerstone-only.

Table 5.18 summarizes fracture plane data for the Bed II sites. As with the Bed I sites only the data from longitudinal and oblique planes are presented. Figures 5.17 and 5.18 show the distribution of angles in the Bed II sites relative to experimentally derived ranges for dynamic and static loading. All three sites have many angles completely outside the 95% confidence intervals of carnivore-broken assemblages. Notch analysis (limited to BK) shows a mixture of hominid and carnivore signals. Although most of the measurable notches fall within the range of carnivore-created notches (Figure 5.19), at least four can probably be linked to hominid marrow extraction. A higher frequency of notched specimens display tooth marks than percussion marks (Table 5.19). Carnivore breakage is also signaled by the presence of micronotches (Figure 5.20). Incomplete Type C (e.g., Figure 5.21) and Opposing Complete (e.g., Figure 5.22) notches are particularly common among medium and large carcasses, respectively, which is similar to the Masaai Mara hyena den assemblage. Several (likely) hominid-created Incipient notches (e.g., Figure 5.23) occur on medium carcasses.

Table 5.18. Summary statistics for fracture angles by carcass size from non-metapodial limb bone fragments in the Bed II assemblages.

	FC West	TK LF	TK UF	BK		
	<u>Medium</u>	<u>Medium</u>	<u>Medium</u>	<u>Small</u>	<u>Medium</u>	<u>Large</u>
<b>Long. &lt;90°</b>						
N	1	1	1	22	52	11
Mean	69.0	69.0	81.0	80.5	76.1	71.5
S.D.	-	-	-	8.5	13.4	17.9
95% CI	-	-	-	76.7-84.3	72.3-79.8	59.4-83.5
<b>Long. &gt;90°</b>						
N	2	2	-	2	31	10
Mean	121.5	101.5	-	97.0	101.3	101.9
S.D.	9.2	2.1	-	5.7	9.4	8.2
95% CI	38.9-180.0	82.4-120.6	-	46.2-147.8	97.8-104.7	96.0-107.8
<b>Obl. &lt;90°</b>						
N	3	3	4	27	115	45
Mean	63.3	72.0	54.8	71.7	65.5	65.6
S.D.	25.4	15.6	9.1	14.0	17.3	17.9
95% CI	0.2-126.5	33.2-110.8	40.3-69.2	66.2-77.3	62.3-68.7	60.2-71.0
<b>Obl. &gt;90°</b>						
N	4	3	6	15	70	39
Mean	107.0	109.3	107.50	111.6	107.4	110.1
S.D.	19.5	25.7	7.8	15.4	13.8	13.92
95% CI	76.0-138.0	45.4-173.3	99.3-115.7	103.1-120.1	104.1-110.7	105.6-114.6

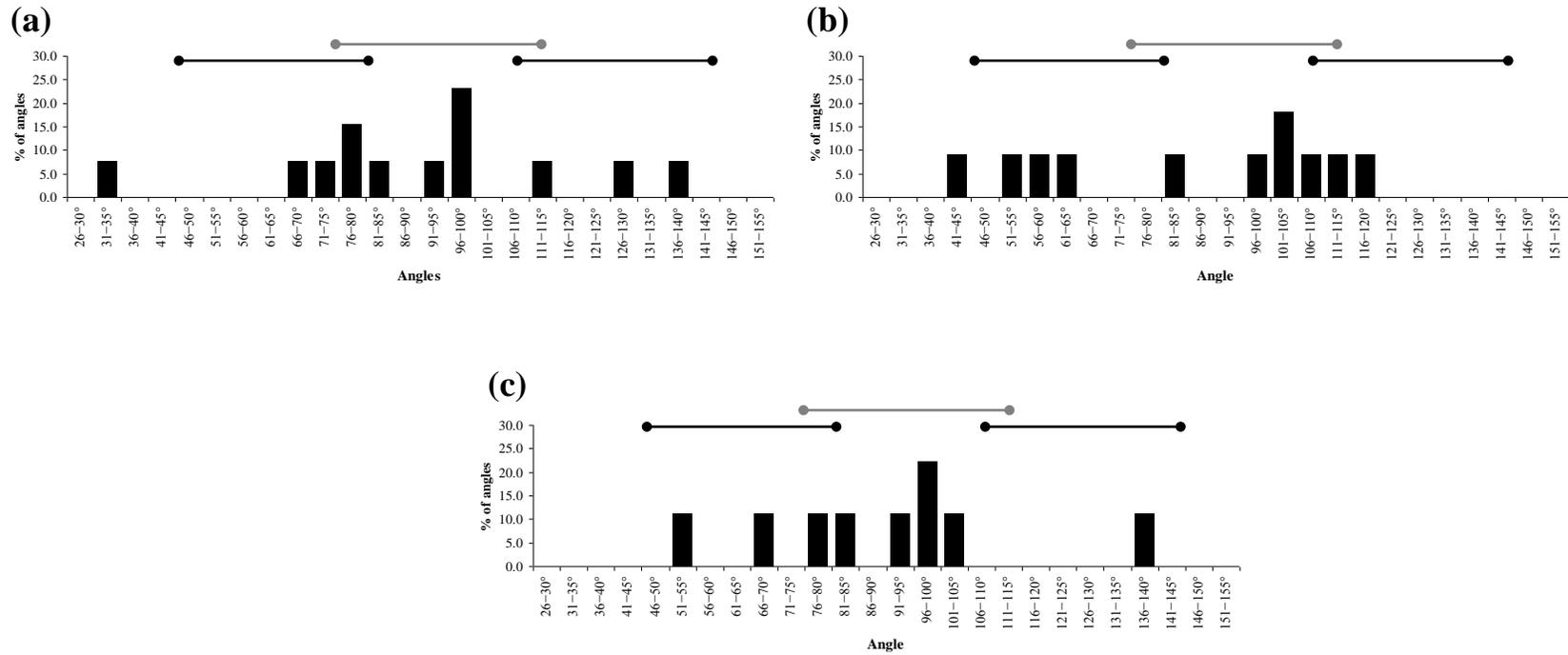


Figure 5.17. Distribution of longitudinal and oblique fracture angles on medium carcasses from (a) FC West, (b) TK LF and (c) TK UF. Note: Grey line denotes 95% confidence intervals of experimental static loading angles, black line denotes 95% confidence intervals of experimental dynamic loading angles.

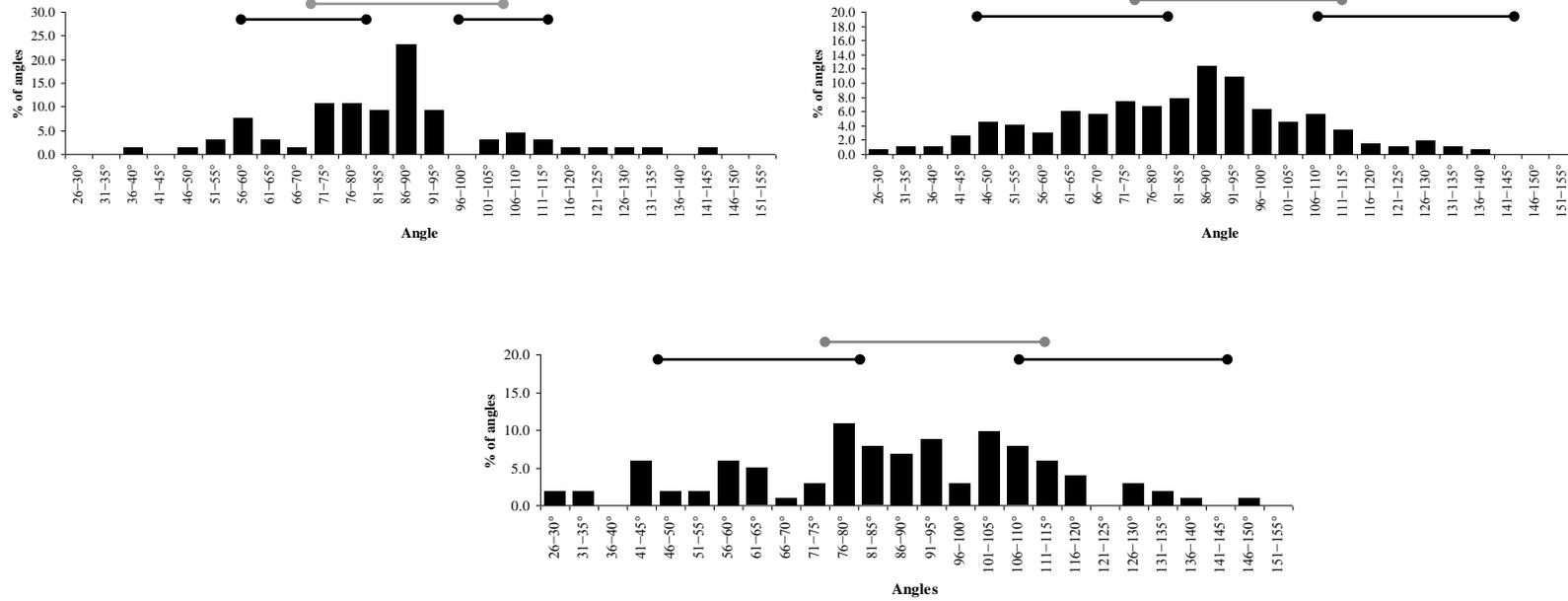


Figure 5.18. Distribution of longitudinal and oblique fracture angles from BK for (a) small carcasses, (b) medium carcasses and (c) large carcasses. Note: Grey line denotes 95% confidence intervals of experimental static loading angles, black line denotes 95% confidence intervals of experimental dynamic loading angles.

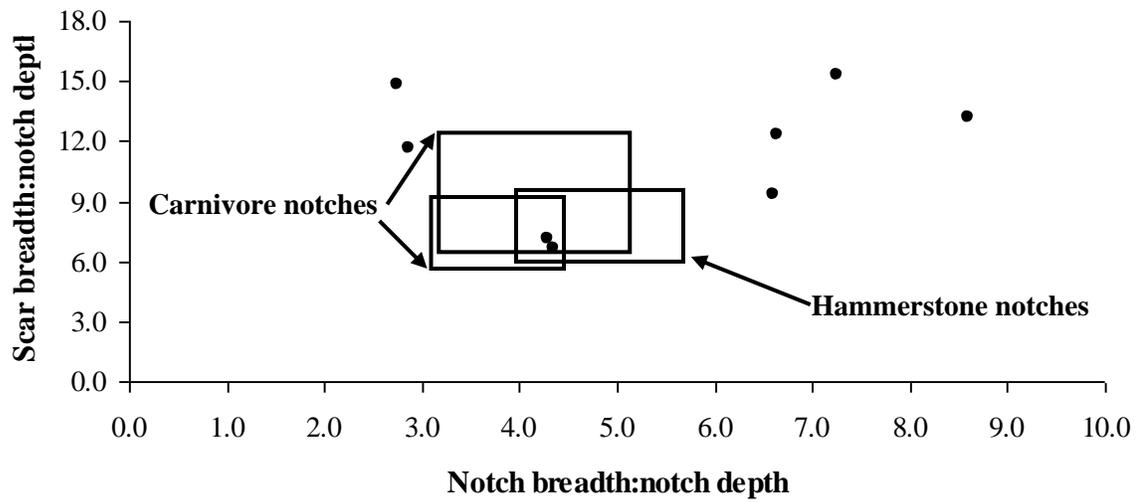
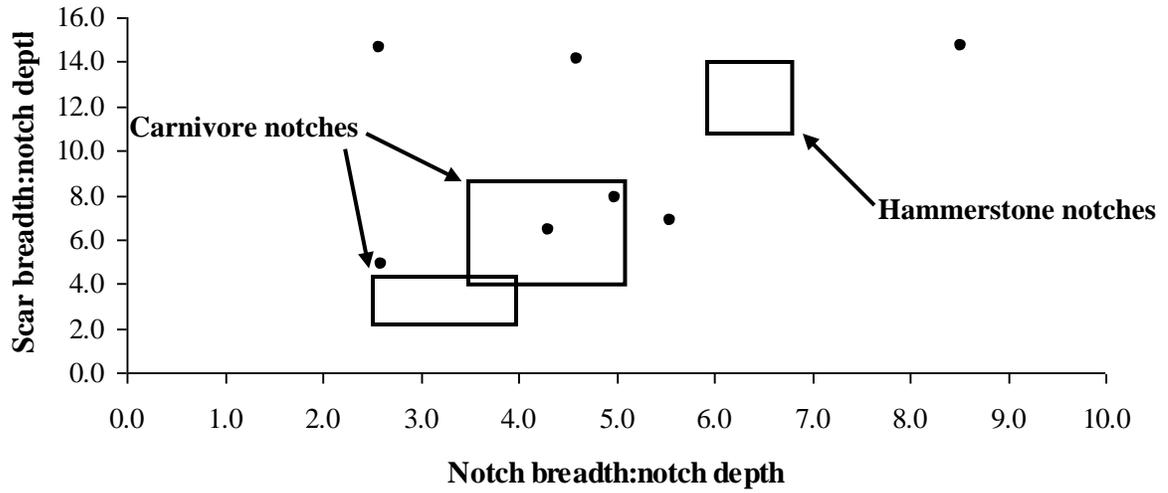
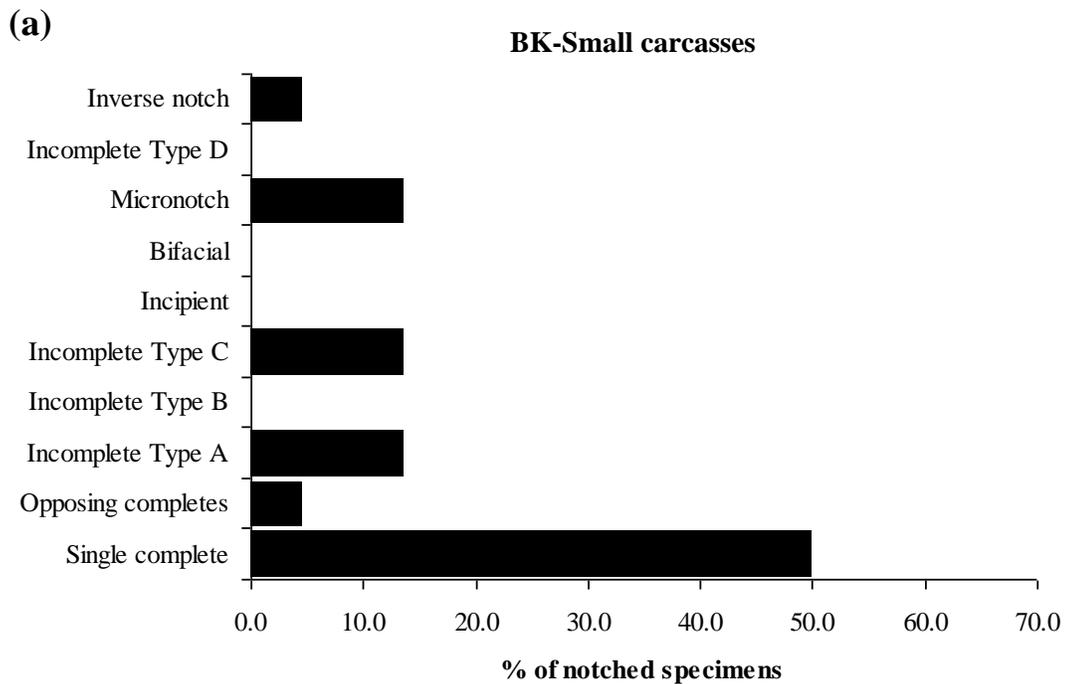


Figure 5.19. Notch dimensions on specimens from (a) small and (b) medium carcasses at BK. Boxes represent 95% confidence intervals of notch breadth:notch depth and scar breadth:notch depth ratios for experimental assemblages (Capaldo and Blumenchine, 1994) and a sample of notches from a hyena den in the Masaai Mara (Egeland et al., unpublished data).

Table 5.19. Surface mark frequencies on notched specimens from the Bed II sites and several actualistic samples.

	NISP notched	NISP TM	%	NISP PM	%
<b>BK</b>					
Small carcasses	14	4	28.6	3	21.4
Medium carcasses	18	5	27.8	1	5.6
Large carcasses	6	0	0.0	0	0.0
<b>Masaai Mara hyena den</b>					
Small carcasses	56	21	37.5	–	–
Medium carcasses	67	29	43.3	–	–
Total	123	50	40.7	–	–
<b>Experimental carnivore</b>					
Medium carcasses	45	35	77.8	–	–
<b>Experimental percussion I</b>					
Small carcasses	90	–	–	58	64.4
<b>Experimental percussion II</b>					
Small carcasses	27	–	–	13	48.1

Note: Only specimens with normal notches included. Data sources: Blumenschine and Selvaggio (1991: Tables 1a and 1b) and Pickering and Egeland (2006: Table 1).



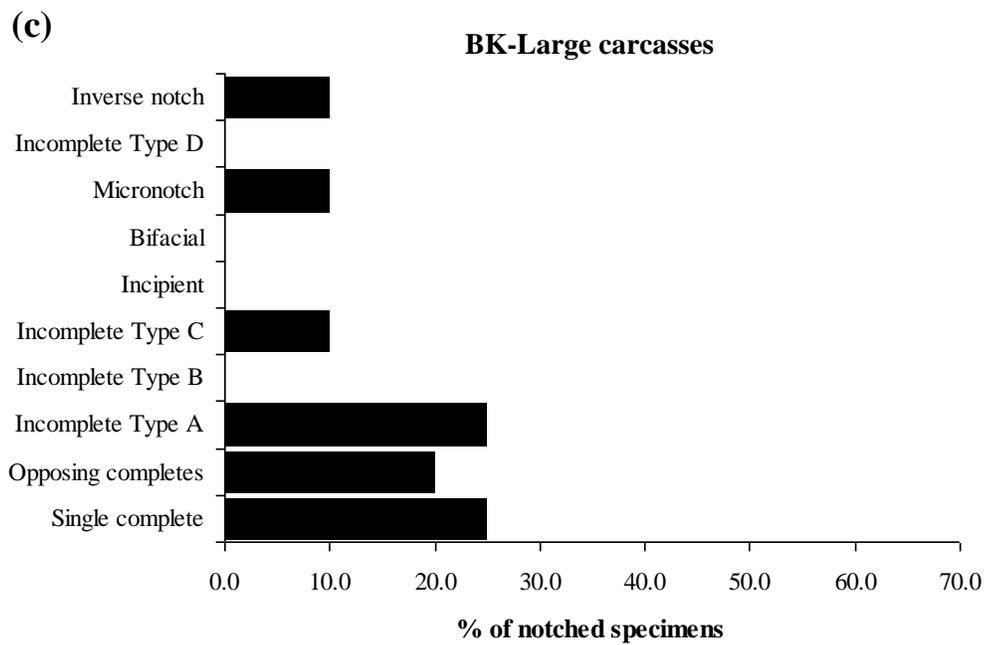
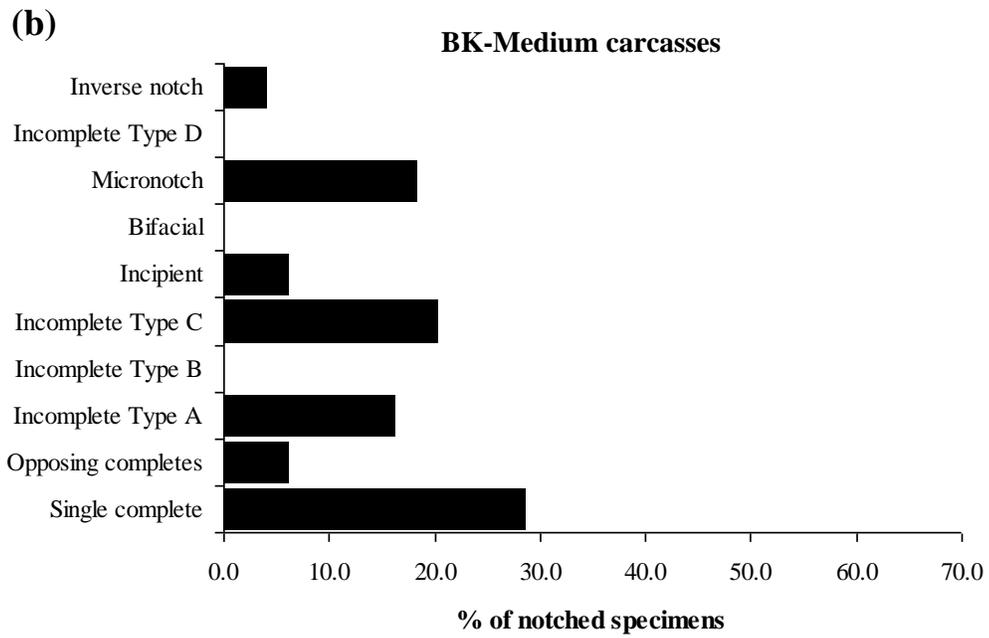


Figure 5.20. Frequency of notch types from BK for (a) small carcasses, (b) medium carcasses and (c) large carcasses.

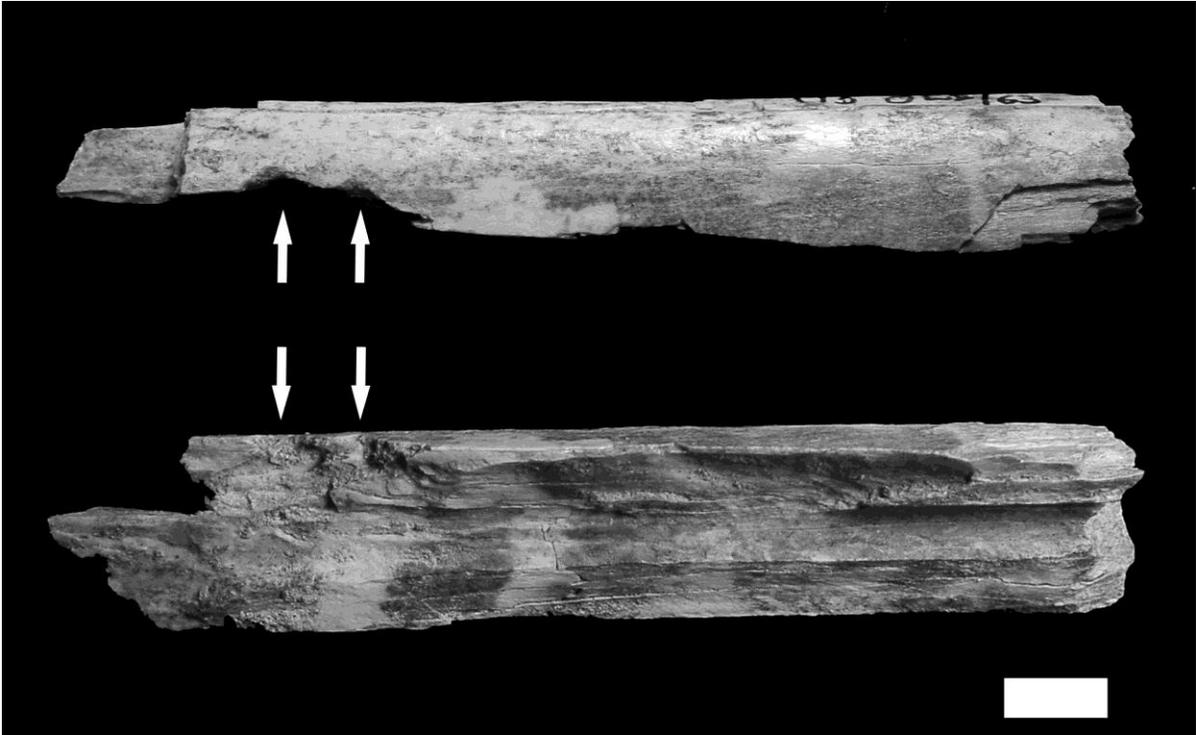


Figure 5.21. Incomplete Type C notch (arrows) on a bovid metatarsal from BK. Scale bar = 1 cm.

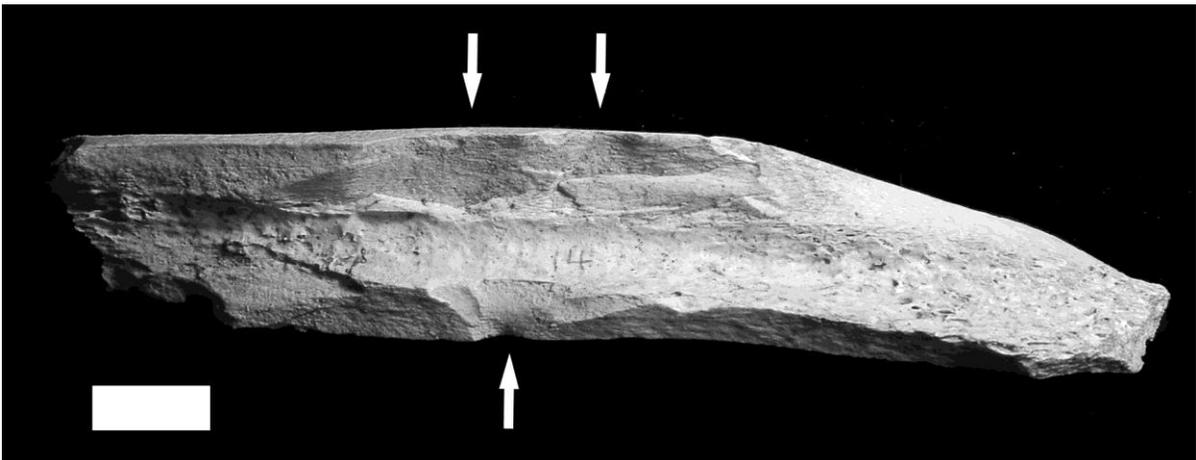


Figure 5.22. Opposing notches (arrows) on a bovid tibia fragment from BK. Scale bar = 1 cm.

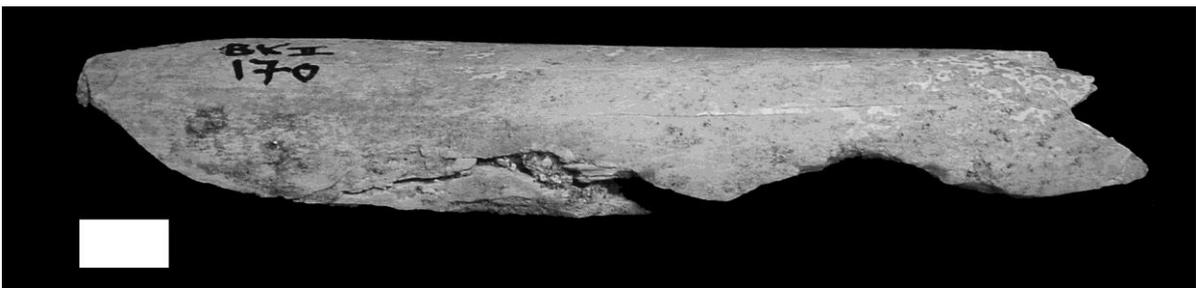


Figure 5.23. Incipient notch with incompletely detached flake on a bovid radius from BK. Scale bar = 1 cm.

## MORTALITY ANALYSIS

Table 5.20 provides the frequency occurrence (in terms of MNI) of each age class by bovid taxon at the Bed II sites. Only the taxon data are presented as the addition of unfused elements did not add to the juvenile MNIs. Adult individuals dominate at all three sites, although given the degree of attrition undergone by the assemblages it is dangerous to interpret this as a real pattern. Nevertheless, a ternary analysis shows that the mortality profile at BK shows a high frequency of adults for both small and medium carcasses (Figure 5.26).

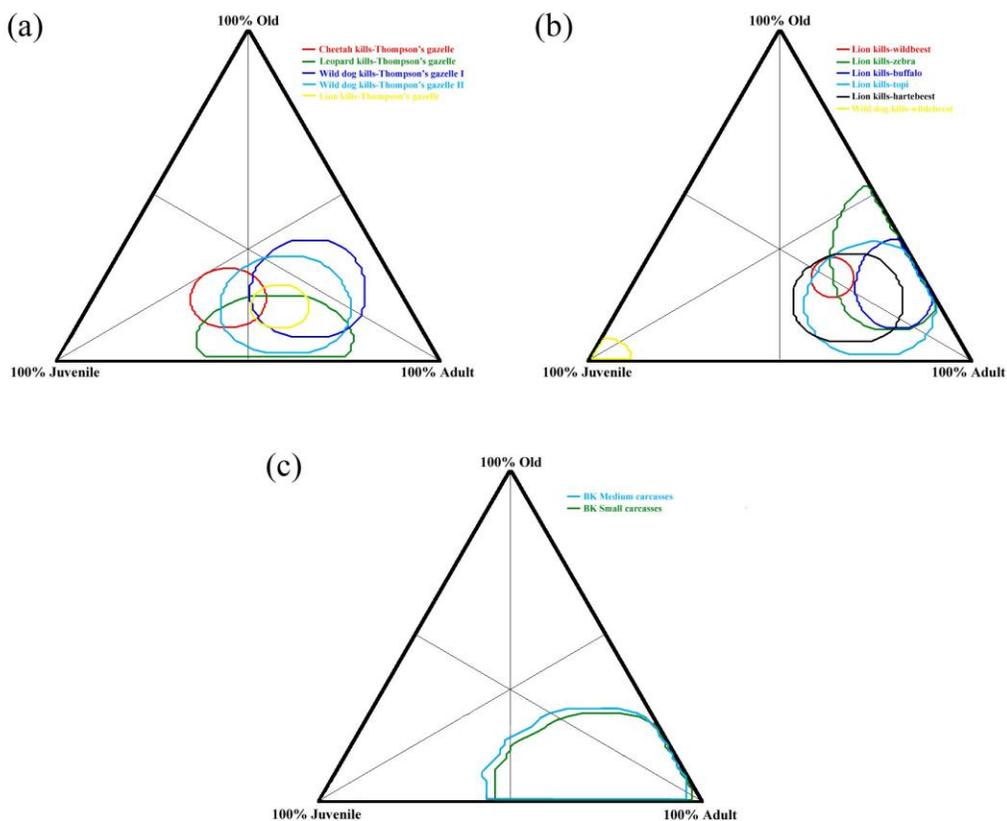


Figure 5.24. Triangular diagrams with 95% confidence intervals of mortality profiles for (a) modern carnivore kills of small animals, (b) modern carnivore kills of medium animals and (c) small and medium carcasses from BK.

Table 5.20. Frequency of juvenile, adult and old-aged individuals in the Bed II sites.

Taxon	FC West			TK LF		
	Juvenile (%)	Adult (%)	Old (%)	Juvenile (%)	Adult (%)	Old (%)
Antilopini	-	-	-	-	-	-
Size 2/3a Alcelaphini	1 (50.0)	1 (50.0)	0 (0.0)	1 (50.0)	1 (50.0)	0 (0.0)
Size 3b/4 Alcelaphini	-	-	-	-	-	-
Bovini	-	-	-	-	-	-
	TK UF			BK		
	Juvenile (%)	Adult (%)	Old (%)	Juvenile (%)	Adult (%)	Old (%)
Antilopini	-	-	-	0 (0.0)	1 (100.0)	0 (0.0)
Size 2/3a Alcelaphini	0 (0.0)	1 (100.0)	0 (0.0)	3 (25.0)	9 (75.0)	0 (0.0)
Size 3b/4 Alcelaphini	-	-	-	3 (25.0)	9 (75.0)	0 (0.0)
Bovini	-	-	-	2 (50.0)	2 (50.0)	0 (0.0)

## **CHAPTER 6**

### **SITE FORMATION AND HOMINID SITE USE**

This chapter summarizes the data presented in Chapters 4 and 5 to reconstruct the formational histories of the Bed I and II faunal assemblages. The formation of each assemblage is discussed at three inferential levels: (1) modification; (2) accumulation; and (3) acquisition. These data are then integrated with inferences of competition and the function of the lithic assemblages to examine hominid site use and hominid/carnivore interactions.

#### **BED I**

Past interpretations of DK (Potts, 1982, 1988) and FLKN 5 (Leakey, 1971) considered hominids as the primary agent in the formation of the large mammal assemblages. The analysis presented here calls into question this general conclusion. Although some hominid behavior is documented in these faunal accumulations, the preponderance of evidence implicates carnivores as the major biological agent in assemblage formation. On the other hand, results from FLKNN 2 agree with those of Leakey (1971), Bunn (1982) and Potts (1982, 1988), all of whom argued that the site represents a carnivore accumulation.

#### ***Carcass modification***

Surface mark frequencies alone indicate a near absence of hominid involvement with carcass modification at FLKNN 2 and FLKN 5 (both sites contain only a single hominid-modified specimen). Nearly every measurable notch from these assemblages is consistent with experimental carnivore samples. In every case over 25% of the notched specimens bear tooth marks while no percussion marks were documented on notched specimens. Micronotches are very common on both small and medium carcasses, while Incomplete Type C notches are common on especially medium carcasses from FLKN 5. This mirrors closely the results from the Masaai Mara hyena den. One Incipient notch was documented at FLKN 5. Fracture plane analysis also suggests that a majority of the nutritive breakage is attributable to the static loading characteristic of carnivore feeding. Although a handful of angles at FLKN 5 are well outside the 95% confidence intervals of the experimental carnivore

sample, the virtual lack of butchery damage in addition to the fact that carnivores are capable of creating very acute or very obtuse angles in low frequencies (Pickering et al., 2005) means that these data probably reflect carnivore bone breakage. FLKNN 2 displays the highest overall frequency of tooth marks among the Bed I sites and midshaft frequencies match most securely with “carnivore-only” controls. Although this pattern may simply reflect the fact that FLKNN 2 is dominated by larger fragments (which are more likely to preserve surface marks [Faith, in press]), the relatively poor preservation of the assemblage probably offsets any inflation in surface mark frequencies caused by the specimen size profile. The disjunction between the FLKN 5 samples and actualistic controls can probably be explained by a combination of the following factors: (1) felids played a significant role in modifying carcasses; (2) carnivore ravaging was less intense; and/or (3)



Figure 6.1. Bovid metapodials (top) and tibiae (bottom) from FLKN 5. Note that many are complete or nearly complete. Scale bar = 5 cm.

some of the assemblage is composed of background scatter that was not subjected to modification.



Figure 6.2. Bovid humeri (upper left) metacarpals (upper right) and radii (bottom) from FLKNN 2. Note that many are complete or nearly complete. Scale bar = 5 cm.

The lower tooth mark frequencies themselves are suggestive of at least some level of felid involvement in carcass modification at FLKN 5. Gross patterns of bone damage at both FLKNN 2 and FLKN 5, with the presence of so many complete, near complete and/or marginally gnawed limb bones (Figures 6.1 and 6.2), are also more consistent with a felid pattern of bone modification. The relatively high degree of dry breakage among the medium carcasses at FLKN 5

Table 6.1. Modal patterns of gross damage to limb bones of small- and medium-sized carcasses by large carnivores.

Element	Lion		Spotted hyena		Leopard		Cheetah	
	Small	Medium	Small	Medium	Small	Medium	Small	Medium
HM PR	destroyed	marginal gnawing	destroyed	destroyed	destroyed	-	no damage	-
HM SH	cylinder	TM only	destroyed	fragmented	TM only	-	no damage	-
HM DS	marginal gnawing	no damage	destroyed	marginal gnawing	no damage	-	TM only	-
RD PR	TM, marginal gnawing	no damage	destroyed	destroyed	no damage	-	-	-
RD SH	TM only	no damage	destroyed	fragmented	no damage	-	-	-
RD DS	destroyed	no damage	destroyed	destroyed	no damage	-	-	-
FM PR	destroyed	TM only	destroyed	marginal gnawing	TM only	-	no damage	-
FM SH	cylinder	TM only	destroyed	TM only	TM only	-	no damage	-
FM DS	destroyed	marginal gnawing	destroyed	partially destroyed	TM only	-	no damage	-
TA PR	destroyed	marginal gnawing	destroyed	marginal gnawing	marginal gnawing	-	-	-
TA SH	TM only	TM only	destroyed	destroyed	no damage	-	-	-
TA DS	no damage	no damage	destroyed	destroyed	no damage	-	-	-
MP PR	TM only	no damage	destroyed	TM only	no damage	-	no damage	-
MP SH	no damage	no damage	destroyed	fragmented	no damage	-	no damage	-
MP DS	destroyed	no damage	destroyed	destroyed	no damage	-	no damage	-

Note: Summarized and slightly modified from Pobiner (2007: 99-162) and supplemented with personal observations of captive lion, tiger, leopard and mountain lion feeding (Schnell and Egeland, unpublished data). Codes: TM = tooth marks, HM = humerus, RD = radius, FM = femur, TA = tibia, MP = metapodial, PR = proximal epiphysis, SH = midshaft, DS = distal epiphysis.

makes it likely that several more complete or nearly complete bones were once present in the assemblage. Table 6.1 presents modal levels of gross damage to limb bones caused by several large carnivore taxa. These data suggest that if intense hyena ravaging had taken place, most of the limb bones from small carcasses would have been destroyed and those from medium carcasses more heavily fragmented.

Tooth pit dimensions implicate large felids and/or hyenas as the primary carcass modifiers at FLKNN 2, a finding that is consistent with the fact that Size Class 3b prey predominate in the assemblage. Medium-sized felids and/or jackals are the most likely modifiers of small carcasses at FLKN 5 according to the tooth pit data. It is also possible that the small canid *Prototcyon*, which is represented by at least one individual at FLKN 5, also modified some of the small carcasses.

Despite the evidence for felid activity at FLKNN 2 and FLKN 5, it is clear that hyenas participated substantially in carcass modification at these sites. A scarcity of axial elements as seen in these assemblages is a well-documented outcome of hyena ravaging. Both Bunn (1982) and Potts (1982, 1988: 91-101) describe bone modifications at FLKNN 2 that are certainly attributable to hyenas (e.g., Figure 6.3). The intense fragmentation of small carcasses at FLKNN 2 is also probably a result of hyena ravaging. As argued above, the relatively low representation of limb bones among the small carcasses at FLKNN 2 and FLKN 5 is likely due to their deletion by hyenas. Overall, however, it appears that hyena ravaging was less intense at these sites, at least compared to current actualistic controls.

Hominids appear as more significant carcass modifiers at DK, as a total of nine specimens bear butchery marks in Level 2 while two were documented in Level 3. Although most notches fall

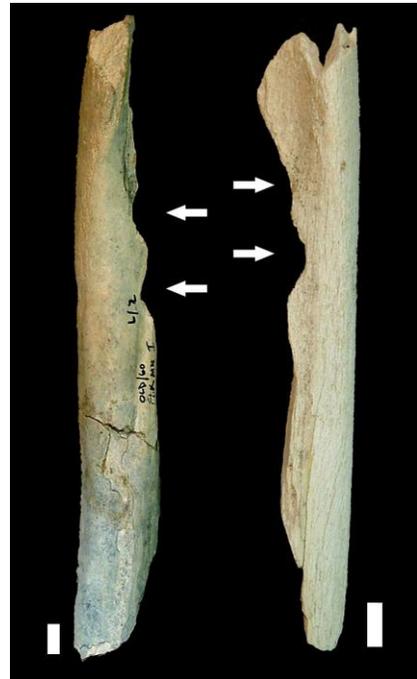


Figure 6.3. Cranial view of tibiae from FLKNN 2 (left) and the Masaai Mara den (right) showing similar patterns of notching (arrows). Scale bars = 1 cm.

within the carnivore range, the DK assemblages show the highest frequency of notches outside the carnivore and nearing the hammerstone range. In addition, one notched specimen (from Level 2) was found to preserve percussion marks and one of the two Incipient notches documented in the Bed I sites derives from Level 2 as well. The DK 2 and 3 medium carcass samples also show a number of fracture angles outside the carnivore range. Unlike FLKN 5, percussion marks are present in these assemblages (although in very low frequencies) and the frequency of hammerstone fracture angles is relatively high. In terms of tooth mark frequencies, the DK 2 small carcass sample is consistent with a “carnivore-only” scenario. Disregarding the DK 1 sample, which is very small and therefore difficult to interpret, the remaining DK samples show lower midshaft tooth mark frequencies. DK 3 in particular shows frequencies similar to “hammerstone-to-carnivore” experiments. Given the limited evidence for hominid bone-breaking, it is unlikely that this results solely, or even largely, from carnivore ravaging of hominid food refuse. Therefore, the low (Level 3) and intermediate (Level 2 medium carcasses) midshaft tooth mark frequencies at DK may also be the result of the above-mentioned factors, namely felid involvement, relatively low levels of ravaging and the possibility that some carcasses were simply not modified. According to tooth pit dimensions, large felids and/or hyenas were responsible for the modification of medium carcass (and perhaps small carcasses as well) in DK 2. Lower frequencies of complete or nearly complete bones at DK relative to FLKNN 2 and FLKN 5 suggest a greater degree of hominid and especially hyena involvement with carcass modification.

Among the Bed I sites, only DK 2 preserves specimens with co-occurring hominid and carnivore damage (Table 6.2). The small carcass sample falls within the 95% CI of actualistic assemblages with complete overlap in hominid and carnivore carcass modification (i.e., both hominids and carnivores processed all carcasses) while the medium carcass sample falls below the 95% CI. This suggests that some carcasses may have been processed sequentially by hominids and carnivores at DK 2; however, little or no overlap is documented in any of the other Bed I assemblages. A lack of overlap in carcass use could arise from three factors (see also Egeland et al.,

2004: 352): (1) hominids and/or carnivores processed carcasses intensely, leaving little or no nutritious tissue for subsequent consumers and thus providing no reason to further modify carcasses; (2) a temporal gap between hominid and carnivore site use resulted in a loss of carcass nutritive value through dessication; and/or (3) stone tool use and discard was not related to carcass processing. The presence of so many complete limb bones (reflecting untapped resources) in the Bed I assemblages makes intense carcass processing unlikely. The other two options are explored more fully below.

### ***Carcass accumulation***

Geological and taphonomic data demonstrate that water activity was not a significant factor in bone accumulation at the Bed I sites. Given this, both Bunn (1982, 1986) and Potts (1982, 1988) have used data on skeletal part abundance, levels of carcass mixing and the density and taxonomic diversity of faunal material to argue that these and other Bed I sites reflect transported assemblages rather than death sites. Although actualistic research shows that axial elements tend to remain at animal death sites while appendicular elements are transported away (e.g., Behrensmeyer, 1983; Behrensmeyer and Dechant Boaz, 1980; Blumenschine, 1986b), the limb-dominated pattern at the Bed I sites is at least as parsimoniously explained by selective deletion of axial bones through density mediated processes like carnivore ravaging (Marean et al., 1992).

More compelling arguments for carcass transport come from levels of carcass mixing and the density and diversity of faunal material. In modern savannas skeletons quickly become dispersed if they are not consumed or otherwise destroyed (Hill, 1979a, b, 1980; Hill and Behrensmeyer, 1984) and background scatters generally yield a maximum of about three to five individuals in areas many times larger than the excavated units of the Bed I sites (Behrensmeyer, 1983; Domínguez-Rodrigo, 1993), which have MNIs between 14 and 41. Table 6.3 presents the density of faunal remains at the Olduvai sites compared to several types of modern bone occurrences, most of which are based on Behrensmeyer's (1987) estimates from landscape scatters in Amboseli National Park. The Amboseli data are underestimates as ribs, sternae and limb bone shaft fragments were not counted

Table 6.2. Percentage of limb bone specimens from DK 2, BK and several actualistic samples bearing both hominid and carnivore damage.

	Size Class	NISP	TM + CM		TM + PM		TM + CM and/or PM	
			%	95% CI	%	95% CI	%	95% CI
<b>DK 2</b>	1-3	168	3.0	-	0.6	-	3.6	-
	1-2	29	10.3	-	0.0	-	10.3	-
	3	139	1.4	-	0.7	-	2.2	-
<b>BK</b>	1-3	485	1.2	-	0.2	-	1.4	-
	1-2	142	1.4	-	0.7	-	2.1	-
	3	343	1.2	-	0.0	-	1.2	-
<b>Selvaggio</b>								
C-H	1-4	549	-	-	-	-	42.4	33.1-52.0
C-H-C	1-4	202	-	-	-	-	30.0	18.0-42.1
<b>Capaldo</b>								
WB-C	1-3	212	14.0	5.5-22.5	-	-	-	-
	1-2	-	5.8	1.5-10.1	-	-	-	-
	3	-	36.8	14.7-58.9	-	-	-	-
HS-C	1-3	1698	4.8	3.5-6.1	4.9	-	-	-
	1-2	-	4.1	2.5-5.7	-	-	-	-
	3	-	6.4	4.3-8.5	-	-	-	-
<b>Marean</b>								
HS-C	1-2	701	-	-	5.7	-	-	-

Note: Only green-broken specimens with good surface preservation included. Codes: NISP = number of identified specimens, CM = cutmark, PM = percussion mark, TM = tooth mark, C-H = carnivore-to-hominid, C-H-C = carnivore-to-hominid-to-carnivore, WB-C = whole bone-to-carnivore, HS-C = hammerstone-to-carnivore. Data sources: Capaldo (1997, 1998), Marean (personal communication; Marean et al., 2000), Selvaggio (1994a, b, 1998).

Table 6.3. Density of faunal remains in the Bed I and II and modern surface assemblages.

Site/occurrence type	bones/m <sup>2</sup>	bones/m <sup>2</sup> : Time-averaged		
		5	10	100
DK 1	0.19	-	-	-
DK 2	0.60	-	-	-
DK 3	3.24	-	-	-
FLKNN 2	0.86	-	-	-
FLKN 5	9.71	-	-	-
FC West	4.52	-	-	-
TK LF	0.92	-	-	-
TK UF	1.55	-	-	-
BK	1.30	-	-	-
Background	≤0.005	0.002	0.003	0.03
Mass death	10.00–100.00	-	-	-
Individual death	1.00–20.00	-	-	-
Individual kill	1.00–20.00	-	-	-
Predation arena	0.01	0.003	0.005	0.05
Eating area	0.06	0.018	0.036	0.36
Den	75.00	-	-	-
Hadza intercept hunting blind	18.55	-	-	-

Note: Density is calculated by first dividing the depth of each deposit by 9 cm (the average thickness of the paleosols from Olduvai [Leakey, 1971]) to estimate the number of “surfaces” represented by each assemblage. Second, the number of bones is divided by the number of “surfaces”, which is then divided by the estimated area of excavation. For those assemblages deposited in a paleosol, the number of bones is simply divided by the estimated excavation area (see also Potts, 1988: 41). Time-averaged densities are estimated using a 6% burial rate (Behrensmeyer, 1983: 96). Density values for the modern assemblages are from Behrensmeyer (1987: 431) and data in Lupo (2001).

(Behrensmeyer, 1983: 95) and the sampling techniques employed (mostly vehicle survey) probably missed many small bones. Nevertheless, the Bed I sites appear to surpass the density of faunal remains seen in background scatters on modern landscapes. Although mass deaths via predation or other natural causes (drought, drowning) can concentrate faunal remains in high densities, the species diversity in such assemblages is very low (often a single species [Capaldo and Peters, 1995, 1996; Kruuk, 1972; Schaller, 1972; but see Haynes, 1988]). Although at both FLKNN 2 and FLKN 5 a single species makes up a significant proportion of the total MNI, a minimum of least eight large mammalian species are represented at each Bed I site. In addition, animals that inhabit several

different ecological contexts are present in the same assemblages (e.g., open plain alcelaphines and closed habitat reductines). It does seem, therefore, that a behavioral mechanism is required to explain the dense bone accumulations at Olduvai (cf. Bunn, 1982; Potts, 1982, 1988).

Identifying the agent of accumulation rests in large part on inferences of carcass modification, most of which, as argued above, can be linked to carnivores. Certainly the lack of stone tools at FLKNN 2 implicates large carnivores as the accumulating agent as hypothesized by Bunn (1982) and Potts (1982, 1988). Although both researchers correctly recognized the presence of hyena modifications, the data presented here suggest that it is more likely that felids played the dominant role in accumulating the carcasses. Clearly, it is difficult to associate any of the faunas with a particular carnivore taxon; however, the extremely closed habitat reconstructed for FLKNN 2 may have favored the solitary ambush predators *Megantereon* and *Dinofelis*. Regardless, if complete carcasses were being deposited on site, a prey profile dominated by Size Class 3b animals is more consistent with the prey preferences and carcass transport abilities of a larger-bodied felid. The presence of hyenas at FLKNN 2, even as secondary scavengers, is notable in such a closed habitat given their modern association with more open environments.

Despite the presence of stone tools, the FLKN 5 faunal assemblage is also largely the result of carnivore activity. As with FLKNN 2, carcasses were probably transported complete to FLKN 5. Hyena activity, though not intense, is documented at the site (which probably accounts for the depressed representation of small carcass limb bones), although again felids were probably the major accumulating agent. The tooth pit data suggest a small- or medium-sized carnivore was responsible for modifying many of the carcasses at FLKN 5, which is consistent with a prey profile dominated by Size Class 1 *Antidorcas recki* and Size Class 3a *Parmularius altidens* individuals. Although there are no unambiguous data indicating such behavior, the caching of carcasses in the trees of a densely woodland environment like FLKN 5 would have been a viable strategy for medium-sized felids such as leopards and *Megantereon*. The presence of medium-sized tragelaphine and hippotragine carcasses suggest that larger carnivores such as lions or *Homotherium* may also have been active in the area.

Hominids certainly played a larger (though still minimal) role in modifying carcasses at DK. It is therefore likely that they participated in accumulating and dispersing some of the carcasses at the site. Nevertheless, the preponderance of evidence points to carnivores as the major agent involved in bone accumulation and dispersal. The tooth pit data suggest larger carnivores were responsible for modifying most of the carcasses from at least DK 2, and the level of bone fragmentation indicates that hyenas were more active at DK than at the other Bed I sites. Although both hominids and carnivores were involved with carcasses at DK, there are several reasons to suspect that many of the animals represented at the site were not transported by either agent but rather died either at the DK locality or in close proximity to it. The high incidence of sediment abrasion, which, because of the generally fine-grained sedimentary matrix, is probably the result of trampling rather than water transport, suggests the site was a high traffic area for passing ungulates (though certainly open to interpretation, it is interesting to note that Leakey [1971: 23] recorded the presence of several narrow, steep-sided channels in Level 3 that she felt strongly resembled game trails). The presence of permanent shallow water and trees near DK probably served as magnets for many animals (including hominids and carnivores) just as they do in modern savannas, which may help account for the fact that DK shows the highest large mammal diversity among the Bed I sites. In addition, on modern landscapes such as wetland environments also contain the highest density of bones due to their preferential use by large herbivores (Behrensmeyer, 1983; Behrensmeyer and Dechant Boaz, 1980). The evidence from skeletal part frequencies for the transport of carcass parts off-site in Level 3 is also consistent with a death site interpretation. If such a scenario is correct for DK, then it is likely that the bone accumulation is due to animals being naturally attracted, rather than actively transported, to the site.

Studies in modern savannas provide several possibilities for the behavioral mechanisms involved in accumulating the Bed I faunas. One obvious candidate is carnivore (especially hyena) denning, which can produce dense clusters of bone in spatially restricted areas (Bunn, 1982, 1983a; Henschel et al., 1979; Hill, 1989; Lam, 1992; Mills and Mills, 1977). However, there is no stratigraphic evidence for burrows or other den structures at any of the Bed I sites. Therefore, the

closest modern analogue, at least for the bone accumulations at FLKNN 2 and FLKN 5, appears to be what are referred to as “eating areas” (Behrensmeyer, 1987: 430); i.e., locations to which carnivores repeatedly transport carcasses for consumption. This is a relatively common behavior among felids and typically involves transport distances of no more than about 300 m (Domínguez-Rodrigo, 1994). The removal and concentration of bones from nearby kills can produce relatively dense and spatially concentrated bone assemblages. For example, Tappen (1995: 235) documented an MNI of six, likely collected by lions, in the area surrounding an isolated tree in a wet savanna in Virunga National Park (Democratic Republic of the Congo). Such bone clusters are almost always associated with isolated trees or tree lines, probably due to the shade that they offer (Behrensmeyer, 1987; Haynes, 1985; Tappen, 1995). Leopards also commonly use trees to cache carcasses in order to protect these food items from competitors (Bailey, 1993; Brain, 1981; Cavallo and Blumenschine, 1989), a behavior that can lead to clusters of bone and other uneaten carcass parts at the bases of the trees (Bailey, 1993: 214; Cavallo and Blumenschine, 1989).

Eating areas are often associated with what are referred to as “predation foci” (Behrensmeyer, 1982: 42), “predation patches” (Behrensmeyer, 1983: 97), “predation arenas” (Behrensmeyer, 1987: 430) or “serial predation” areas (Haynes, 1988: 219). Such areas are particularly conducive to successful hunting and in modern savannas are typically found near cover and/or water sources (Behrensmeyer, 1982, 1983, 1987; Behrensmeyer and Dechant Boaz, 1980; Haynes, 1985, 1988). Because they are essentially dense conglomerations of individual kills, predation arenas tend to be more spatially diffuse than eating areas (Domínguez-Rodrigo, 1993). If DK does indeed represent a death site, then it is possible that the locality represents a particularly active predation arena. Although modern predation arenas tend to only contain species from a single ecological context (Domínguez-Rodrigo, 1993), which runs counter to the ecologically diverse DK fauna, the co-occurrence of open- and closed- or mixed-habitat species in predation arena assemblages has been documented (e.g., wildebeest [*Connochaetes taurinus*] and waterbuck [*Kobus ellipsiprymnus*]; Haynes, 1988). This particular predation arena, which surrounded a perennial pond in Hwange

National Park (Zimbabwe), was frequently utilized by lions and hyenas to procure prey (Haynes, 1988: 227). It is therefore possible that serial predation (supplemented by additional carcass input via natural deaths) over an extended period of time may be responsible for the dense accumulation of material at DK. Although the role of hominids in this process is difficult to characterize, the general paucity of on-site butchery damage may indicate, at least for DK 3, that hominids exploited this area by removing limb units from medium-sized animals for butchery elsewhere.

What is particularly intriguing about modern eating areas and predation arenas is that ungulates and humans (mostly poachers) in addition to large carnivores are repeatedly attracted to these locations (Behrensmeyer, 1987; Tappen, 1995). Such an overlap in the use of space matches well with Isaac's (1983: 9) "common amenity" conception of early site formation (see also Binford, 1983; Isaac and Crader, 1981: 84). As discussed above, it is likely the trees that were certainly common at all the Bed I sites played an important role as magnets for bone accumulations in the Plio-Pleistocene just as they do in modern savannas (Isaac, 1978b, 1983: 9, 15; Kroll, 1994: 133-134; Kroll and Isaac, 1984: 27-28; Potts, 1988: 262-264; Rose and Marshall, 1996).

Comparisons between the Bed I sites and typical modern eating areas or predation arenas clearly show that bone density is much higher for the fossil assemblages (Table 6.3). However, such a direct comparison fails to account for time averaging. Therefore, Table 6.3 also provides time-averaged bone density estimates for various types of assemblages based on a 6% burial rate (the maximum rate observed at Amboseli [Behrensmeyer, 1983: 96]). Estimating the time over which the Bed I sites formed is important for understanding the potential impact of time-averaging on the density of faunal material. Weathering stage profiles have commonly been used to make such estimates (e.g., Bunn, 1982; Potts, 1986), although not without controversy (Bunn and Kroll, 1987; Lyman and Fox, 1989). Here the weathering data presented in previous chapters are combined with deposit depth in order to provide approximate formation times. It is likely that weathering among the Olduvai assemblages progressed relatively slowly given the evidence for ample tree cover and undergrowth at most of the sites. Therefore, a specimen weathered to stage 2, for example, should be

assigned an exposure time towards the upper range of Behrensmeyer's (1978) time-since-death values; i.e., about five years. Based on this, the DK 3 paleosol appears to have been exposed for a decade or more. The general lack of refits at DK 3, which differs substantially from other Plio-Pleistocene paleosol assemblages such as FLK Level 22 (Bunn, 1982; Kroll, 1994) and FxJj 50 (Bunn et al., 1980; Kroll, 1994), supports this contention. For the other Bed I sites, a preponderance of weathering stages 0–2 and a lack of paleosol formation suggests more rapid sedimentation and thus shorter exposure times, perhaps on the order of five years or less for each depositional cycle. This is consistent with experiments showing that most simulated sites are buried in four years or less in modern fluvial and lacustrine settings (Schick, 1986: 62). If each depositional cycle is thus estimated at about five years and is represented by 9 cm of deposit (the average depth of the paleosols found at Olduvai [Leakey, 1971]), then the depth of the excavations at each site suggest a minimum of three cycles is sampled at DK 1 (= 15 years), seven at DK 2 (= 35 years), two at FLKNN 2 (= 10 years) and four at FLKN 5 (= 20 years). Although these estimates are not strictly equivalent to actual accumulation times, they do establish a minimum upper limit for how long a particular level could potentially receive bone input.

As Table 6.3 shows, even time-averaged eating areas and predation arenas would not approach the density seen at most of the Olduvai sites. However, it is very likely that over time unrelated background scatters of bones were incorporated into the behaviorally derived portions of the fossil assemblages. Most of the sporadically represented non-bovid carcasses may in fact reflect such natural background scatters, which would result in a higher than expected density of faunal remains at the Olduvai sites. It is also possible that burial rates at the Olduvai sites were higher, even substantially so, than the 6% observed by Behrensmeyer (1983) at Amboseli. This is especially likely for sites with taphonomic and geological evidence for rapid sedimentation. Relatively higher densities of bone could also be created if biological agents in the paleo-Olduvai Basin were accumulating carcasses at higher rates than those thus far observed in modern savannas. Finally, it is certainly possible that the time scales of site formation provided here, which are based on an assumption of

constant sedimentation rate, are gross underestimates. For example, 1,000 years of site use as an eating area would produce a density of 3.6 bones/m<sup>2</sup>, which is a value that begins to approach those of the higher density accumulations at Olduvai.

### ***Carcass acquisition***

This is the most remote of the inferential levels of assemblage formation. The first question is how often hominids were acquiring carcasses or carcass parts at the Bed I sites. A single cutmarked piece in addition to a general lack of other evidence for butchery at both FLKNN 2 and FLKN 5 link hominids to the acquisition (in some form or another) of only one carcass at each site. Given the time depth sampled at these sites, it appears that carcass acquisition rates were almost nil at these particular locations during the sampled time intervals. Butchery damage links hominids to the processing of parts from at least six carcass (three small, two medium, one large) at DK 2 and two carcasses (one small, one medium) at DK 3. Although each of the levels was exposed for many years and thus could have served as points of carcass deposition over a long period of time, nearly every butchered specimen shows a weathering stage of 0 or 1. Therefore, it is possible that these carcasses were acquired over a relatively short period of time (a season or a year?). Nevertheless, the small number of butchered carcasses still results in a very low rate of carcass acquisition at DK during the sampled time interval.

A general pattern of the timing of hominid acquisition of carcasses in terms of late or early access is difficult to identify given the small sample of butchered specimens. That is, although hominids enjoyed early access to fleshed carcasses in some cases, the issue of whether or not that access was systematic or regular is hard to address.

### ***Bed I summary***

The data presented above clearly indicate that all the Bed I sites represent palimpsests; that is, they are the result of the interdependent *and* independent actions of several agents, including hominids and carnivores. Although the presence of fossil specimens bearing both hominid and carnivore surface modifications suggests some interdependence in site formation at DK 2, the

remaining Bed I assemblages appear to reflect serial site use by hominids and carnivores in strictly unrelated depositional events. This is supported by taphonomic analyses of the other Bed I sites (Domínguez-Rodrigo, in press a). As palimpsests, each of the assemblages show differing degrees of integrity and resolution, where integrity refers to the “homogeneity of the agents responsible for materials in a deposit” and resolution to the “homogeneity of the events or situational conditions whose by-products are preserved in the deposit” (Binford, 1981: 19). Integrity and resolution at DK are very low, as both hominids and several types of large carnivores were responsible for the formation of the faunal assemblages. It seems that carcasses were accumulated and/or dispersed at DK through a combination of serial predation, natural deaths, off-site carcass part transport (some of it by hominids) and a mixing of natural background scatter. FLKNN 2 shows the highest integrity of the Bed I assemblages, as a lack of stone tools and butchery damage implicate carnivores as the only major biological agent involved in site formation. Moreover, it is possible that the accumulation of the FLKNN 2 assemblage can be linked largely to the activities of larger-bodied felids, as the slight levels of hyena ravaging occurred post-depositionally. Resolution at FLKNN 2 is also relatively high, as the incorporation of small amounts of natural background scatters appears to be the only other important source of bones, and, as seen above, hyenas the only other agent of carcass modification. FLKN 5 is intermediate in its integrity and resolution. Several different felid taxa in addition to hyenas and possible small canids were responsible for assemblage formation, although many of the carcasses were seemingly accumulated by felid transport with some additional input of natural background scatter.

## **BED II**

All of the Bed II faunas analyzed here were previously interpreted as resulting from hominid activities (Leakey, 1971; Monahan, 1996a, b; but see Binford, 1981). This analysis generally agrees with that conclusion, although several factors slightly complicate such an interpretation.

### *Carcass modification*

Poor surface preservation makes secure identifications of surface marks difficult for FC West and TK. However, 50% of the well-preserved limb bone midshafts from FC West preserve tooth marks, a value that falls at the lower range of “carnivore-only” experiments. Fracture plane analysis suggests that some nutritive breakage at all these sites might be attributable to hammerstone impact, although the sample sizes are very small. Levels of fragmentation suggest hominid and/or hyena bone breakage and the extent of epiphyseal loss indicates rather intense hyena ravaging.

Evidence for hominid modification is much more common at BK. Butchery mark frequencies are second only to FLK 22 among all the Olduvai Gorge assemblages (see below) and several notches fall within experimental hammerstone ranges. A similar number of notched limb bone specimens show tooth marks as show percussion marks for small carcasses while more notched medium carcass limb bone specimens show tooth marks than percussion marks at BK. Micronotches are present in lower frequencies at BK than in the Maasai Mara hyena den. Incomplete Type C notches are common on especially medium carcasses and Incipient notches are present only on medium carcasses. Many of the fracture planes fall within the hammerstone range while levels of fragmentation are consistent with hominid and/or hyena bone breakage. Epiphysis-to-shaft ratios suggest intensive ravaging by hyenas.

The midshaft tooth mark frequencies on all carcass sizes at BK fall within the range of “hammerstone-to-carnivore” samples. Although tooth mark frequencies also fall within the range of felid-modified samples, the low frequency of complete bones and high levels of fragmentation suggest that cats played little or no role in carcass modification. Tooth pit dimensions at BK implicate large felids and/or hyenas as the primary carcass modifiers, but, again, other evidence suggests that most carnivore damage can be attributed to hyenas. BK preserves several small and medium carcass specimens with co-occurring hominid and carnivore damage (Table 6.2), though the frequencies fall below the 95% CI of actualistic samples where both hominids and carnivores processed all carcasses. Although this suggests little overlap in carcass utilization by hominids and carnivores, it is possible

that hyena ravaging of hominid food refuse (i.e., overlap in carcass utilization) could have deleted bone portions that preserved co-occurring damage.

### *Carcass accumulation*

Water activity certainly played some role in accumulating and/or dispersing bones at the Bed II sites. The FC West material was probably not located in primary context, although transport distance appears to have been minimal (Petraglia and Potts, 1994). Given the presence of many lithic pieces <20 mm (de la Torre, 2005), the TK UF assemblage seems to have been in more-or-less primary context. However, the inclined nature of the paleosol makes it likely that overland waterflow winnowed out some of the smallest pieces (Petraglia and Potts, 1994). The TK LF assemblage also possesses high frequencies of lithic pieces <20 mm (de la Torre, 2005), again suggesting minor fluvial activity. As observed by Monahan (1996b: 219), the fresh condition of most BK bone specimens in addition to high frequencies of lithic debitage support Leakey's (1971: 199) original interpretation that the BK assemblage was originally deposited on or near the bank of a stream bed and subsequently washed and buried as channel fill with no long distance transport. The Bed II sites, while preserving many small lithic pieces, are severely deficient in similarly sized bone fragments, which probably reflects selective discard of smaller bone specimens during the excavations.<sup>4</sup>

As with the Bed I sites, the lack of axial remains cannot be used in isolation to distinguish the Bed II samples as transported assemblages. However, the Bed II sites show very high densities of faunal remains relative to modern landscape assemblages, and the removal of very small fragments means that the actual density of bone at the Bed II sites was much higher than that recorded in Table 6.3. A behavioral agent of accumulation is therefore strongly implied for the Bed II sites as well.

The proximity of FC West and TK to standing water points to a possibility that animals repeatedly visited these areas and died either naturally or via predation. This matches well with a predation arena/eating area model of site formation; i.e., the acquisition of carcasses followed by

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<sup>4</sup> New excavations conducted at BK in 2006 under the direction of M. Domínguez-Rodrigo have uncovered many very small bone specimens.

short distance transport to some preferred location for consumption. The incomplete and uneven skeletal part patterning of the four to ten individuals represented at these sites suggests that carcass parts were transported off-site or otherwise scattered subsequent to their active accumulation. Unfortunately, other than the presence of stone tools the only evidence that (tentatively) links hominids to the accumulation of the FC West and TK faunas are the fracture plane data. Although hyenas certainly played a role in carcass modification at these sites, no stratigraphic evidence for a den structure was found. That only tooth marks (a total of two specimens) occur in the very small subsample of well-preserved fragments at FC West suggests that the lithics and fauna at this site may be unrelated. Nevertheless, given the poor surface preservation it is currently impossible to determine with much certainty whether hominids or large carnivores were responsible for the accumulation of the FC West and TK faunas.

The parallels between FC West and TK and the Hadza hunting blind noted in Chapter 5 are not surprising given the general similarities between the inferred (fossil) and observed (Hadza) processes of bone accumulation; that is, the repeated, though intermittent, acquisition of animals near areas of standing (and often perennial) water sources, short distance carcass transport, subsequent processing and, finally, the dispersal of carcass parts off-site. Because the Hadza transport entire carcasses of small and medium-sized animals, either as intact carcasses or field-butchered units (Bunn, 1993, in press; Bunn et al., 1988, 1991; Monahan, 1998; O'Connell et al., 1988, 1990), skeletal representation at this particular hunting blind presumably resulted from the discard of a few "snack" items (often skulls, ribs and some limb bones). Even if hominids could be linked in some definitive way to these assemblages, it is important to stress that this does not make FC West and TK hunting blinds, nor does it mean that all the socio-ecological factors that condition the creation of Hadza intercept hunting assemblages and those of other African hunter-gatherer groups (e.g., Brooks and Yellen, 1987; Crowell and Hitchcock, 1978) apply to the Olduvai sites. The use of only one comparative assemblage also masks variability in what constitutes a "typical" Hadza hunting blind assemblage. For example, not all carcasses accumulated at these sites are the result of short distance

transport, as animals may run after being shot only to drop dead after several kilometers (Bunn et al., 1988). These carcasses may then be transported to the blind or directly back to the base camp. Regardless of the agent, the high density of faunal material suggests that carcasses were actively accumulated at FC West and TK while the incomplete and uneven skeletal part representation indicates that they were subsequently scattered from the sites.

There is no doubt that hominids played a major role in modifying carcasses at BK and therefore their participation in accumulating carcasses is strongly implied. However, only very general trends in hominid carcass transport strategies can be identified because the BK assemblage is a lumped sample of deeply stratified deposits and thus represents an amalgamation of many individual episodes of transport carried out (potentially) over many years. Among small and medium carcasses at BK, upper and intermediate limb bones are better represented than even crania, which suggests some selective transport of limb units (and perhaps non-cranial axial elements). The minimal representation of metapodials may indicate the abandonment of these low-utility bones at acquisition points or, perhaps, their removal from the site by scavengers subsequent to the transport of whole limb units. Uneven skeletal part representation among large carcasses is not surprising given the transport constraints they pose. However, the high representation of large carcass crania cannot be easily reconciled with an energy-maximizing transport strategy and thus remains difficult to explain. In terms of carnivore involvement in carcass accumulation, it is not known whether a den structure was present at BK given the secondary context of the site. However, the overall low tooth mark frequencies on limb bone midshafts in particular (3.6–15.1%) are inconsistent with modern hyena dens, where such frequencies range between 31.6–75.3% (Egeland et al., unpublished data; Faith, in press). Nevertheless, the presence of at least lions and hyenas (indicated by their fossil representation at the site and inferred from their known general occurrence in savanna ecosystems) means that large carnivores cannot be completely ruled out as accumulators of at least some of the BK fauna. It is also likely that natural background bones, including most conspicuously the highly rolled pieces that were

transported long distances and eventually deposited by nearby streams, became incorporated into the assemblage.

### ***Carcass acquisition***

No direct and completely unambiguous evidence can be brought to bear on issues of hominid carcass acquisition at FC West and TK. Surface modifications directly link hominids to the acquisition of at least eleven carcasses (three small, six medium, two large) at BK. Although the depth of the BK deposit and the likelihood of rapid sedimentation make it possible that carcass acquisition was spread out over a potentially long period of time, recent excavations at BK have revealed that lithic and faunal material are confined to several vertically constrained horizons (personal observations). This, and the fact that all but one butchered carcass is in weathering stage 0 or 1, opens the possibility for significant acquisition rates. However, assigning values awaits the analysis of the newly excavated material, which is currently in progress (Domínguez-Rodrigo, personal communication).

The timing of hominid carcass acquisition at FC West and TK, if indeed carcasses were acquired by hominids at these locales, is impossible to establish with confidence. Tooth mark frequencies at FC West simply show that bone-crushing carnivores accessed marrow cavities: they say nothing about the order of hominid access. At BK the frequency, and, more importantly, anatomical placement of cutmarks demonstrate convincingly that when hominids did acquire large mammals, they enjoyed early access to fully fleshed carcasses (see also Monahan, 1996a, b). When coupled with the cutmark data, skeletal part abundances show a pattern of access to high-utility upper and intermediate limb bones in addition to rib cages and meaty pelves.

### ***Bed II summary***

The Bed II Olduvai sites are, like the Bed I sites, best interpreted as palimpsest assemblages. Although a very small proportion of fossil specimens at BK preserve both hominid and carnivore surface modifications, overlap in carcass modification is suggested by the low midshaft tooth mark frequencies, which indicate bone-crushing carnivores (likely hyenas) gained secondary access to

*broken* limb bones. This is explained most parsimoniously if hyenas ravaged hammerstone-broken limb bones, a scenario that is supported by data on percussion marks, fracture angles and notch dimensions, all of which demonstrate that hominids participated significantly in bone breakage at BK. Therefore, hyenas would have been forced to concentrate on (1) the few remaining unbroken bones; (2) the nutritionally depleted limb bone shaft fragments; and, especially, (3) grease-laden axial elements and limb bone epiphyses. Low axial representation and low epiphysis-to-shaft ratios corroborate this inference. As Bunn (2007: 199-200) argues, this may indicate intermittent rather than continuous site use by hominids because axial elements and epiphyses only retain nutritionally attractive grease for a limited amount of time. Therefore, hyenas likely visited the site soon after (hours, days or perhaps weeks) hominid abandonment.

It is unfortunate that the FC West and TK fauna are so poorly preserved, as small, high resolution assemblages like these often provide the most precise information because they sample such a narrow range of behaviors (cf. Lupo, 2001). In other words, it is the small sample sizes that furnish these types of assemblages with potentially high resolution (see Isaac [1981b; Isaac et al., 1981] and Foley [1981] for discussions of the importance of smaller sites, “mini-sites” or “scatters”). The interpretation offered here for the formation of the FC West and TK faunal assemblages (i.e., carcass accumulation by hominids or carnivores, processing and/or consumption and, finally, subsequent carcass part dispersal) has important implications for O’Connell’s (1997; O’Connell et al., 2002; see also Blumenschine, 1987; Blumenschine et al., 1994) “near-kill” model of early site formation. This model is predicated on analogies with the occasional Hadza practice of dragging animals from a kill site to shaded areas near their hunting blinds (i.e., “near kill” locations). Such a comparison suggests to O’Connell (1997; O’Connell et al., 2002) that early sites (including those from Olduvai) were formed by hominids repeatedly transporting carcasses a short distance (several hundred meters or less) from nearby acquisition points. Although O’Connell (1997; O’Connell et al., 2002) feels that this adequately explains the formation of the *large* Plio-Pleistocene accumulations from sites like DK or BK, it is in fact the *smaller* sites such as FC West and TK that match more

closely with O'Connell's (1997; O'Connell et al., 2002) modern comparative sample. Importantly, it has been demonstrated here that many of the large Olduvai faunas (except FLK 22 and BK) are largely or exclusively the result of carnivore, and not hominid, behavior (see also Domínguez-Rodrigo et al., in press a). In addition, even though O'Connell (1997; O'Connell et al., 2002) is correct in stating that both Hadza near-kill accumulations and the large Plio-Pleistocene sites from Olduvai are dominated by crania and limb bones (as are many early sites), the latter are in most cases characterized by a *complete* and *even* representation of these skeletal elements while the former show the opposite pattern. In other words, most of the large Olduvai assemblages show skeletal abundances that indicate more-or-less complete carcass deposition while the Hadza accumulations are the result of butchery and subsequent transport, which results in incomplete and uneven skeletal representation. This pattern of skeletal representation is seen only in the smaller Olduvai assemblages like FC West and TK. Finally, most early sites are simply too large in terms of the number of animals represented to be comparable to even the atypically large Hadza blind assemblage analyzed by Lupo (2001), which shows an MNI of 11 and was used over the course of 10 or more years. Weathering and paleosol formation suggest an extended period of exposure (though not necessarily accumulation) for FC West and TK, both of which have low MNIs (between four and ten).

Again, the similarities between the Hadza assemblage and the small Bed II assemblages do not necessarily implicate hominids in the accumulation of the fauna, especially when unambiguous butchery damage is lacking. What these similarities do indicate, however, is that a "near-kill" model is not a plausible explanation for the formation of large Plio-Pleistocene bone assemblages. It is interesting to note here that Domínguez-Rodrigo et al. (2002) suggest that a "near-kill" interpretation may account for the formation of the early Pleistocene faunal assemblages from the ST Site Complex at Peninj (Tanzania), which *do* show substantial hominid input and are characterized by low MNIs and incomplete and uneven skeletal part representation.

BK samples dozens of instances of carcass transport and processing by multiple agents, including most prominently hominids. Unfortunately, this accumulative effect masks variability in the

situational contingencies that no doubt conditioned these decisions (Bartram and Marean, 1999: 18; Lupo, 2001). The integrity of the assemblage is also compromised to some extent given the participation of at least lions and hyenas in site formation. Regardless of the problems posed by BK in terms of resolution and integrity, it is important to reiterate that the carcasses that were accumulated and processed by hominids at the site were acquired in a fully fleshed state.

### COMPETITION AND SITE USE

As summarized in Chapter 1, competition generates predictions about how hominids and carnivores should exploit carcasses and utilize space. Figure 6.4 provides a theoretical model for competition based on two taphonomic measures: the ratio of axial (vertebrae + ribs) bones to limb bones (in terms of MNE) and the epiphysis-to-shaft ratio. This model is based on Domínguez-Rodrigo and Organista's (in press) "ravaging stages"

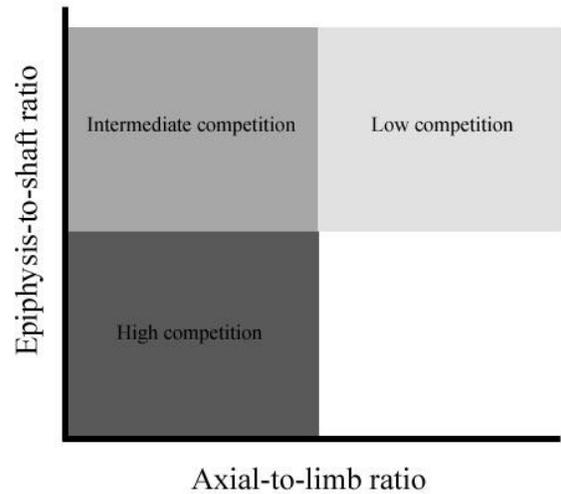


Figure 6.4. Theoretical model of competition based on axial-to-limb and epiphysis-to-shaft ratios. See text for explanation.

approach, which draws upon actualistic research on carnivore ravaging (see Binford [1981: 210-223, 256-280] for a similar approach). Sites in low competition areas (i.e., little or no carcass consumption) will show high axial-to-limb ratios and epiphysis-to-shaft ratios (upper right portion of graph). Once carcass consumption begins, carnivores choose to consume vertebrae first, as they have the lowest structural density and highest grease yield (Marean et al., 1992). Sites in intermediate competition areas, therefore, will show depressed axial-to-limb ratios but will retain high ratios of epiphyses to shafts (upper left portion of graph). As competition increases, carnivores that are still hungry then proceed to the limb bones, which they consume from the epiphyses. Therefore, high levels of competition will be reflected in both low axial-to-limb ratios and low epiphysis-to-shaft

ratios (lower left portion of graph). Table 6.4 provides these and other measures of competition for modern savannas, the sites in this study and several other Bed I and II sites.

Before proceeding, the appropriateness of comparisons between and among the modern and fossil datasets must be considered. Importantly, it is probably unwise to directly compare raw values from the modern samples to each other or to the Olduvai assemblages. No modern ecosystem provides a perfect analog for the Plio-Pleistocene Olduvai Basin and each of the modern and fossil assemblages is the result of unique combinations of ecological parameters including the dynamics of trophic interactions, carnivore and ungulate densities and rainfall. Consequently, “low competition” will differ by ecosystem and the accompanying taphonomic signatures will vary accordingly (cf. Tappen, 2001). A complete limb bone percentage of 68.8%, for example, may define low competition in the Serengeti, but may appear high relative to the Olduvai Basin ecosystem during Bed I and II times. Even comparisons between the fossil assemblages themselves, all of which derive from the same general area, may be slightly problematic given the depth of time sampled by the Bed I and II sites. Therefore, what is identified taphonomically from each assemblage as a single “level” of competition is in fact an aggregation of competitive interactions reflecting the continuous shift in microhabitats that certainly occurred over time at each site. However, if comparisons are made within the framework of these caveats, the general uniformitarian principles that govern the utilization of carcasses (Blumenshine et al., 1994) validate the use of taphonomic data for reconstructing competition. For example, whether discovered in the modern Amboseli Basin or at Plio-Pleistocene Olduvai, complete limb bones represent untapped within-bone resources and thus signal lower consumer-to-carcass ratios and a lack of carcass visibility; that is, lower competition. Thus, when used in combination with other lines of data, taphonomic variables can provide a proxy measure for the relative level of on-site competition for carcass resources and thus microhabitat.

With these issues in mind, Figure 6.5 plots the axial-to-limb and epiphysis-to-shaft ratios for the Olduvai sites. Although the Olduvai sites do appear to cluster in areas of the graph, the separation of competition levels is somewhat arbitrary and, thus, artificially sets boundaries on what is in fact a

continuum. Having said that, if habitat type predicts competition, then the FLKNN sites and FLK 22, which are reconstructed as densely forested habitats, should show the lowest levels of competition. These should be followed by the dense woodland habitats of the lower levels of FLKN (4–6) and riparian woodlands of HWK E, the mixed habitats of DK, the open bushlands of the upper levels of FLKN (1–3) and, finally, the open habitats of the remaining Bed II sites.

According to the taphonomic data, FLKN 6 and HWK E plot off the graph in the area of very low competition, followed by FLKN 3, which also reflects a relatively low competition setting. FLKNN 2 and FLKN 4 plot in the low to intermediate area, showing higher levels of axial bone destruction but high epiphysis-to-shaft ratios. These are followed by DK 2 and 3 and FLKN 1 and 2 and FLKN 5, which fall into the intermediate area. The remaining Bed II sites and FLK 15 all fall into the high competition area. FLK 22, FLKNN 3 and DK 1 appear as outliers at the bottom right portion of the graph.

Other taphonomic measures of competition can be used to further refine the results presented in Figure 6.5. For example, FLK 22 and FLKNN 3 should probably be considered as low competition assemblages given their high axial-to-limb ratios. Intensive fragmentation by hammerstone-wielding hominids probably accounts for the anomalously low epiphysis-to-shaft ratio at FLK 22 (Blumenshine, 1995; Domínguez-Rodrigo and Barba, 2006; Oliver, 1994), as hammerstone breakage produces disproportionately high frequencies of shaft fragments. A low competition setting for FLK 22 is also supported by the fact that almost 12% of the limb bones are complete. Although FLKNN 3 shows an anomalous combination of axial and epiphyseal survival, the fact that 40% of the limb bones at this site are complete suggests a low competition setting as well. The high competition environment inferred for BK probably helps explain the relatively low tooth mark frequencies at the site, as hyenas likely removed and thus tooth-marked limb bones off-site (cf. Blumenshine and Marean, 1993). Other inconsistencies are more difficult to explain. For instance, at FC West and TK LF (presumably high competition settings) the femur-to-tibia ratios are the highest of any of the Olduvai sites.

Table 6.4. Measures of competition for the Olduvai sites and several actualistic samples.

	EP:SH	% Complete	Axial:Limb	Femur:Tibia	HM PR + RD DS: HM DS + RD PR
<b>Olduvai Bed I</b>					
DK 1	0.31	0.0	1.00	0.25	3.00
DK 2	0.46	8.5	0.42	0.74	0.46
DK 3	0.50	8.7	0.35	0.76	0.23
FLKNN 2	0.88	23.3	0.24	0.55	0.23
FLKNN 3	0.37	40.0	1.00	1.25	0.54
FLKN 1-2	0.46	13.8	0.35	0.58	0.31
FLKN 3	0.58	14.9	0.63	0.60	0.13
FLKN 4	0.89	10.1	0.36	0.90	0.22
FLKN 5	0.60	16.3	0.36	0.67	0.24
FLKN 6	4.80	32.0	1.40	0.60	0.83
FLK 15	0.34	2.7	0.14	0.66	0.18
FLK 22	0.10	11.8	0.80	0.71	0.30
<b>Olduvai Bed II</b>					
HWKE 1-2	1.70	—	0.71	—	—
HWKE 3-5	1.60	—	0.73	—	—
MNK (Main)	0.21	—	0.33	—	—
FC West	0.23	0.0	0.33	2.00	0.00
TK LF	0.14	0.0	0.40	1.70	0.00
TK UF	0.13	0.0	0.36	0.50	—
BK	0.14	4.4	0.31	0.88	0.26
<b>Experimental</b>					
Solitary consumer (low competition)	0.70	—	—	—	—
Small consumer group (intermediate competition)	0.78	—	—	—	—
Large consumer group (high competition)	0.28	—	—	—	—
Heavily ravaged (high competition)	0.02	0.0	0.67	—	—

Table 6.4. cont.

	EP:SH	% Complete	Axial:Limb	Femur:Tibia	HM PR + RD DS: HM DS + RD PR
<b>Serengeti/Ngorongoro (Tanzania) landscape</b>					
Serengeti riparian woodlands (low competition)	–	68.8	5.90	0.33	–
Serengeti open woodlands/plains (intermediate competition)	–	41.3	1.70	0.76	–
Ngorongoro (high competition)	–	13.6	1.60	0.86	–
<b>Amboseli (Kenya) landscape</b>					
1970s (low competition)	–	56.9	3.08	0.97	39.28
2000s (high competition)	–	18.4	0.75	0.92	17.95
<b>Galana/Kulalu (Kenya) landscape</b>					
Riparian woodland (low competition)	–	60.9	2.65	1.41	–
Bushland (intermediate competition)	–	25.0	3.52	1.25	–
Open grassland (high competition)	–	27.5	2.55	1.20	–
<b>Carnivore dens</b>					
Spotted hyena den (low competition)	0.63	–	–	–	–

Note: “% Complete” denotes percent of limb bones that are complete. Data sources: Blumenschine (1989: Tables 5 and 6); Bunn (1982: Table 3.4), Capaldo (1998: Tables 7 and 8), Domínguez-Rodrigo (1996: Tables 3 and 6; Domínguez-Rodrigo et al., in press a), Faith and Behrensmeyer (2006: Tables 2 and 4, Figure 5), Monahan (1996a: Table 10) and Selvaggio (1994a: Table 1).

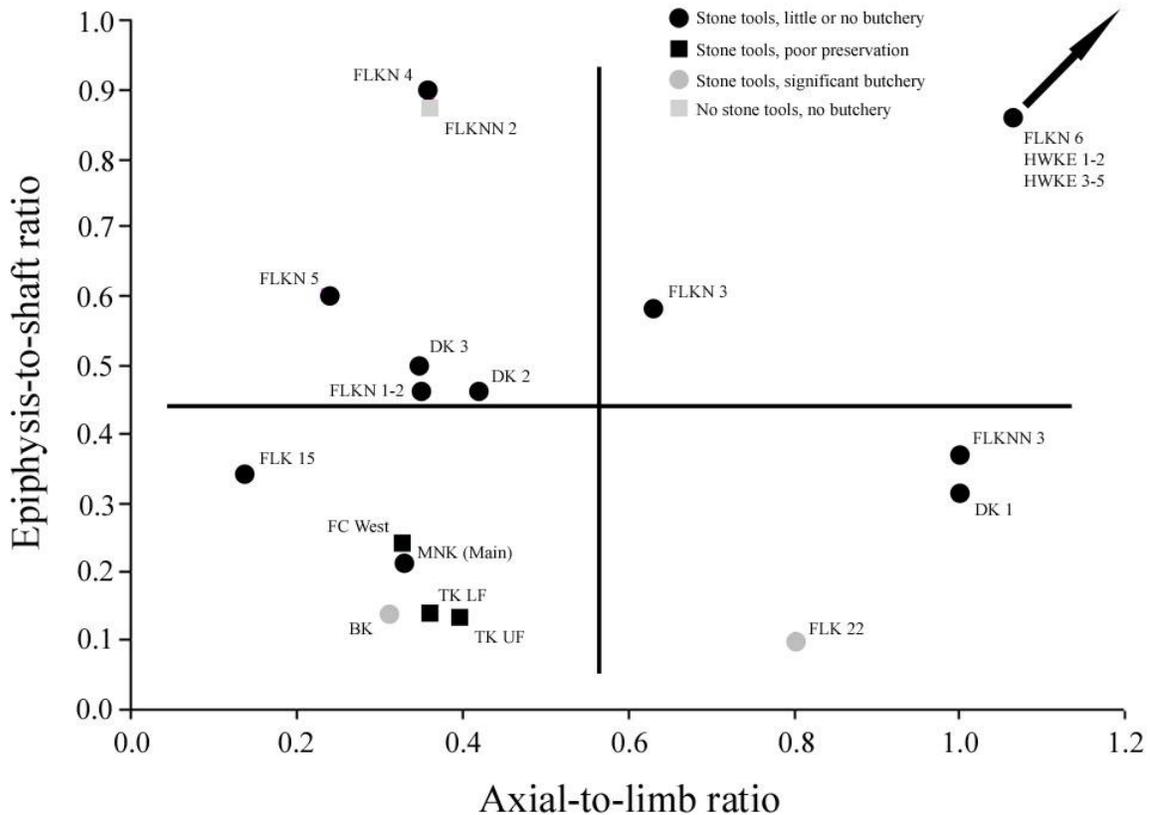


Figure 6.5. Measures of competition for the Olduvai sites. Note: “stone tools” = presence of stone artifacts; “no stone tools” = complete lack of stone artifacts; “little or no butchery” = assemblage with well-preserved cortices and a virtual (i.e., a few modified specimens) or complete lack of butchered bone; “poor preservation” = assemblage with poorly preserved cortices where butchery marks cannot be identified; “no butchery” = assemblage with well-preserved cortices and a complete lack of butchered bone; “significant butchery” = assemblage with well-preserved cortices and substantial evidence (i.e., dozens of fragments with hominid-induced surface modifications and other lines of evidence for hominid involvement in carcass modification) for butchery.

In general, the paleoecological and taphonomic data match fairly well. However, the slight mismatches do suggest that taphonomic variables can contribute to refined interpretations of paleohabitat. For example, although FLKN 3 is reconstructed as a broken woodland or bushland habitat (Fernández-Jalvo et al., 1998), the taphonomic data point to low levels of competition and perhaps a more closed environment (e.g., a dense clump of trees) directly on-site. Increased overall levels of competition in the paleo-Olduvai Basin may help explain several interesting characteristics of the Bed I and II bone assemblages. For example, the pressures imposed by a diverse and

presumably highly competitive Bed I large carnivore guild may have encouraged the repeated transport of carcasses by felids to competitive refugia like FLKNN 2 and FLKN 5 in frequencies higher than are observed in modern savannas. This is supported by taphonomic analyses of the other levels at FLKNN and FLKN, all of which implicate felids as the primary bone accumulator (Domínguez-Rodrigo et al., in press a). If this interpretation is correct, it suggests that these locations served as magnets for carcass transport over an extended period of time. That the lower competition sites from Olduvai appear more heavily ravaged than many modern landscape assemblages may be due to the exploitation by hyenas during Bed I and II times of densely forested habitats like FLKNN 2 or closed riparian woodlands like HWK East Levels 1–2 in lower Bed II (Monahan, 1996a, b) in higher frequencies than is observed today.

#### ***Hominid site use and the function of the Olduvai Gorge lithic assemblages***

Although many of the faunal assemblages from Olduvai cannot now be ascribed to hominid behavior, the presence of stone tools at nearly every site still signals their use of the areas (see Figure 6.5). The presence of complete bones and both hominid and carnivore surface modifications at the Olduvai Bed I artifact-bearing sites led Potts (1982, 1984a: 343-344; 1988: 253-255) to argue that hominids were forced to quickly butcher carcasses in areas of potentially intense competition in order to avoid interactions with large carnivores. Although Potts (1982, 1984a, 1988) was correct in his identification of both complete limb bones and the co-occurrence of hominid and carnivore damage, the former are more likely a reflection of low rather than high competition and the frequency of individual specimens with co-occurring damage is very low relative to actualistic assemblages (except for DK 2). This indicates that, although hominids and carnivores were attracted to the same areas, site usage was serial and was carried out by these agents in largely unrelated depositional events.

The taphonomic data suggest that, at least relative to the surrounding landscape, most of the Bed I sites were areas of low competition. Although a lack of stone tools at FLKNN 2 indicates that hominids were not active in this particular level, the presence of lithics in both the overlying and

underlying levels shows that this lower competition area was utilized by hominids. It is interesting to note that Long K, another non-artifact-bearing Bed I site that has only been partially analyzed, also appears to be a low competition assemblage (Potts, 1988). The single Bed I site with substantial evidence for hominid involvement with carcasses (FLK 22) also appears as a low competition assemblage (see also Blumenschine and Marean, 1993; Capaldo, 1997; Marean et al., 1992). Hominid utilization of high competition habitats during Bed I times is signaled by the presence of lithics at FLK 15, although the discovery of only nine artifacts (Leakey, 1971: 59) suggests that the use of this location was very short-lived. Overall, then, it appears that hominids concentrated their stone tool-using activities in lower competition environments during Bed I times.

Several of the Bed II artifact-bearing sites also cluster in areas of high competition, but stone tools appear in low competition areas at sites like HWK E as well (Monahan, 1996a, b). BK, which is the only Bed II site with good evidence for hominid carcass processing, is located in a high competition environment. This finding supports Monahan's (1996a: 118; see also Egeland et al., 2004) argument that hominids during upper Bed II times could control high competition locations to carry out carcass processing. Although there does appear to be a shift towards the utilization by hominids of higher competition areas during Bed II times, the major difference lies in an apparent ability to carry out *large-scale* carcass processing in high competition habitats. This is significant because carcass processing, as opposed to other subsistence activities, *invites* interactions with large carnivores.

The preceding discussion bears directly on interpretations of the function of the Olduvai stone tool assemblages and its relation to hominid site use. Toth (1985) demonstrated that sharp-edged flakes, and not the better-known "heavy duty" core forms, were often the desired goal of early stone knappers, and experimental work (Jones, 1981, 1994; Toth, 1985; Schick and Toth, 1993) and use-wear analysis (Keeley and Toth, 1981) revealed the effectiveness of flakes (along with that of other tool types) as carcass butchery tools. Although it was long assumed that the co-occurrence of stone tools with fossil bones linked early technology to carcass processing (e.g., Clark and Haynes, 1970;

Leakey, 1971), it was not until the discovery of cutmarks at Plio-Pleistocene sites that this relationship was confirmed (Bunn, 1981; Potts and Shipman, 1981). Percussion marks and other fracture features have demonstrated the use of artifacts as marrow-processing implements as well (Blumenschine, 1995; Bunn, 1981; Oliver, 1994). That butchered bones have been discovered at the earliest archaeological sites (de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005) in addition to many other Plio-Pleistocene localities leaves no doubt that from its inception early stone technology was used for processing carcasses.

Given this, it is surprising that butchery marks are virtually absent at DK and FLKN 5, and, indeed, at many of the well-preserved faunas at Olduvai (Domínguez-Rodrigo et al., in press a). A possible explanation for this pattern comes from Mora and de la Torre's (2005) recent examination of the function of stone technologies at Olduvai during Bed I and II times. Specifically, they revisit the idea that percussive activities unrelated to knapping sharp-edged flakes may have been an important component of the stone technology at Olduvai during Bed I and II times (see also Schick and Toth [1994] and Willoughby [1987] for important discussions of battered materials). In addition to hammerstones that show distinctive pitting related to flake production during hard-hammer percussion, they document the presence of "active hammerstones with fracture angles" (Mora and de la Torre, 2005: 181). These pieces are characterized by ridges with stepped and hinged fractures and, according to Mora and de la Torre (2005), the angularity of these pieces would have made them unsuitable for inducing predictable conchoidal fracture. Like Leakey (1971), they also distinguish anvils, which are cuboid blocks with battering along the edges. Finally, they suggest that many of the pieces originally described by Leakey (1971) as broken flakes and chips are in fact chunks detached from anvils during percussion. Many of these pieces show extensive battering and all lack most of the morphological features of flakes.

Figure 6.6 plots the technological classification of the lithic industries from DK, FLKN 5, FC West and TK following de la Torre (2004) and Mora and de la Torre (2005). The DK lithic assemblage is dominated by flakes, flake fragments and debitage. Although de la Torre (2004: 84)

identified 43 lithic pieces with evidence of battering (4.2% of the total assemblage), most of these are knapping hammerstones, suggesting that the production of flakes was a principle goal at DK. The FLKN 5 assemblage is fundamentally different in that only six flakes (one of which is retouched) are present. Both anvils and several hammerstones with fracture angles are present, and the fact that some smaller fragments show evidence of battering suggests that most of the angular fragments are the result of percussion activities not related to flake manufacture. This pattern is seen among all the levels of the FLKN locality, where in terms of weight almost 44% of the lithic material can be linked to non-knapping percussion (de la Torre, 2004; Mora and de la Torre, 2005). FC West and TK are even more pronounced in this regard. Although flakes and flake fragments are well-represented at both sites, about 60% of the total raw material weight at FC West and about 50% and at TK (UF and LF) is composed of various combinations of anvils, hammerstones, hammerstones with fracture angles and battered fragments (Mora and de la Torre, 2005). Although a complete technological reanalysis is not available for BK, flakes are extremely common at the site (de la Torre, 2004; Leakey, 1971).

Coupled with the faunal data, the characteristics of the lithic assemblages provide a more comprehensive look at hominid site use at Olduvai. The lack of butchery damage at DK is especially surprising given that flakes are fairly common in the lithic assemblage. As discussed above, it is possible that hominids, at least in Level 3, transported some carcass parts from medium animals off-site for butchery elsewhere. The early stages of core reduction appear to be missing at DK (de la Torre, 2004; Kimura, 2002), which suggests that hominids brought in partially knapped cores from another location (Toth, 1985). Although some of the non-knapping percussion activities at DK did involve marrow processing, the lack of extensive hominid bone-breakage indicates that other activities were carried out at least as often. Although no tools were discovered at FLKNN 2, the under- and overlying levels, both of which lack butchery damage, do have small lithic assemblages (less than 50 pieces) with only a handful of flakes (Domínguez-Rodrigo et al., in press a; Leakey, 1971). That the FLKN 5 lithic assemblage does not appear to be geared towards carcass butchery is

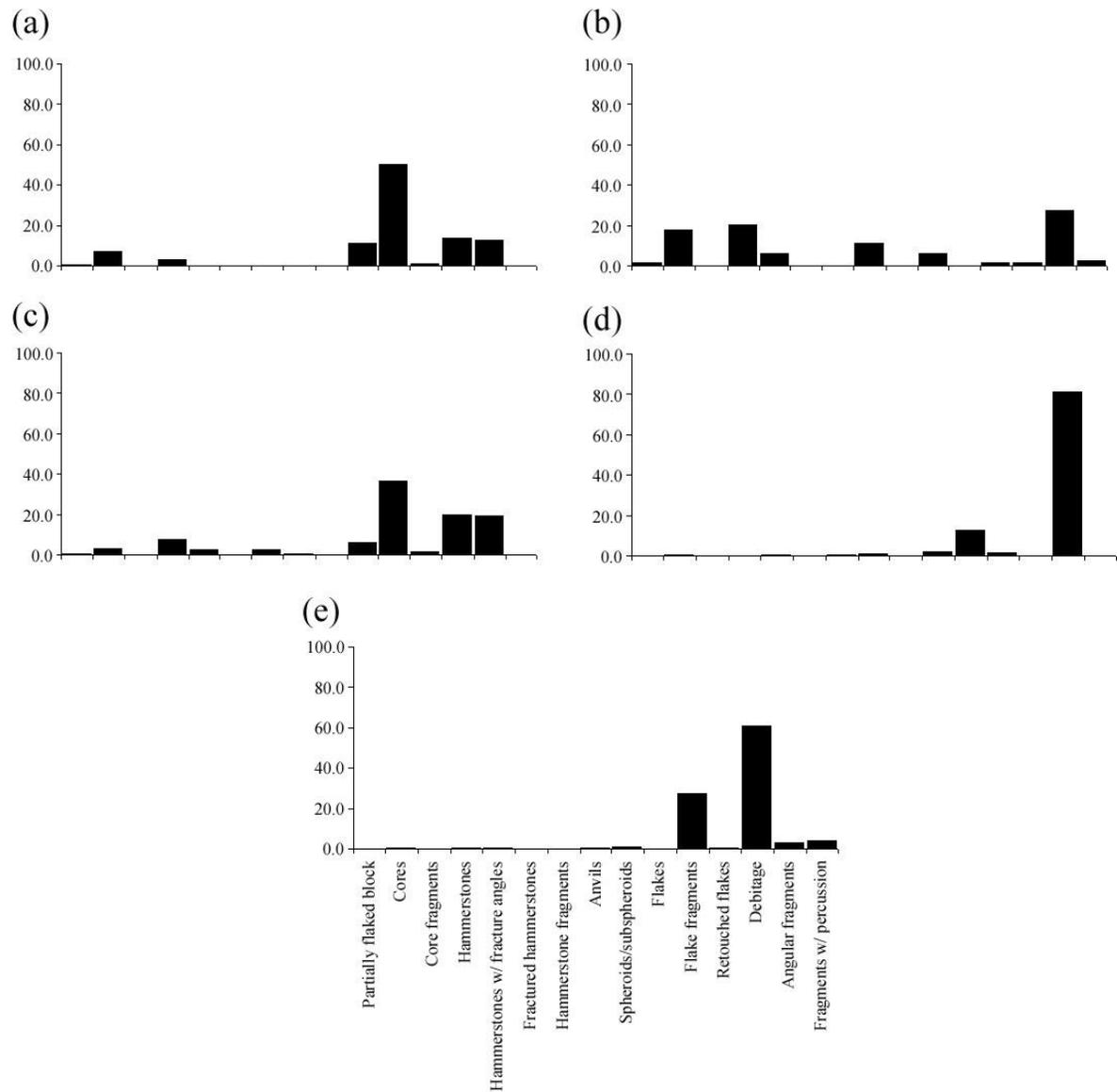


Figure 6.6. Distribution of lithic categories from (a) DK 1–3, (b) FLKN 5, (c) FC West, (d) TK LF and (e) TK UF.

consistent with the absence of butchery damage at the site. The documented battering activities cannot be associated with bone-breaking given that no percussion mark or other evidence for hominid marrow processing was identified. Surface preservation at FC West and TK makes it impossible to unambiguously link the fauna to the stone tools. However, the presence of many flakes signifies that the lithic assemblages at both sites would have been effective for carcass butchery. However,

battering activities unrelated to carcass butchery were also probably carried out at the sites. Cortical flakes are underrepresented in both assemblages (de la Torre, 2004), again suggesting that primary flaking occurred elsewhere. The many defleshing cutmarks at BK allows a functional link between the flakes and the fauna to be established (see also Monahan, 1996a, b). In addition, percussion marks, notches and fracture angles indicate that percussion activities at the site did involve marrow processing.

The fact that a significant proportion of the lithic pieces cannot be associated with carcass processing supports the idea of serial and unrelated site usage by hominids and carnivores. That is, hominids transported, used and discarded stone tools at sites that were subsequently utilized by carnivores to consume carcasses. Although many of the artifact-bearing Olduvai sites occurred in lower competition areas, especially during Bed I times, serial usage does not necessarily imply active avoidance of large carnivores by hominids. It may have been amenities like water, shade trees and probably food that drew hominids to these locations. This is supported by the battered components of the lithic assemblages, which, as suggested by Mora and de la Torre (2005), may have been used to process nuts in a manner much like chimpanzees (e.g., Boesch and Boesch-Achermann, 2000) or modern hunter-gatherers (e.g., Lee, 1979) do. Such activities are possibly documented at Melka Kunturé, Ethiopia (1.5 Ma; Chavaillon and Chavaillon, 1976), and almost certainly at the much younger site of Gesher Benot Ya'aqov, Israel (<1.0 Ma; Goren-Inbar et al., 2002). Whatever the exact resource, the undeniable importance of plant foods in the early hominid diet (Peters, 1987; Sept, 1992) and their seasonal availability (Peters et al., 1984) probably dictated to some extent when and where hominids chose to concentrate their tool-using activities at Olduvai (Peters and Blumenschine, 1995) and elsewhere (Sept, 2001). Renewed excavations, more use wear analysis and phytolith studies should help reveal what type of resources these tools were used to process. Nevertheless, systematic carcass processing is certainly documented at the flake-rich sites of FLK 22 and BK (this study; Bunn and Kroll, 1986; Monahan, 1996a, b). As suggested above, it is at these types of sites that carnivore interaction would have been potentially more direct.

## CHAPTER 7 CONCLUSIONS

This dissertation has attempted to generate data appropriate for tracking variability in hominid and carnivore behavior in the paleo-Olduvai Basin in relation to measurable behavioral ecological variables. Because of its ecological importance and taphonomic visibility, competition was chosen as a unifying concept for this exercise. Inferences of site formation and usage within the context of competitive interactions provide a framework for generating broad-scale models of hominid and carnivore behavior at Olduvai and beyond. In doing so, this concluding chapter focuses on three issues: (1) the implications of felid accumulations; (2) variability in hominid site use; and (3) the importance of meat in early hominid diets.

### FELID ACCUMULATIONS AT OLDUVAI

The FLKNN 2 and FLKN 5 faunal assemblages probably reflect the repeated transport of carcasses by felids to eating areas. Taphonomic analyses of the other levels at these sites confirm that felids utilized these areas over an extended period of time (Domínguez-Rodrigo et al., in press a). The density of carcasses at FLKNN and FLKN suggests that felids were transporting and concentrating carcasses at higher rates than has been thus far observed in modern savannas. Although most transport can probably be associated with solitary ambush predators like leopards, *Dinofelis* and *Megantereon*, the larger, social hunters like lions and *Homotherium* also may have practiced extensive carcass transport. This implies that competition among carnivores was very high in the Olduvai Basin during Bed I times. If true, this finding would help explain why even the faunas from lower competition settings at Olduvai appear more heavily ravaged than their modern counterparts, as hyenas appear as active carcass modifiers in very closed environments like FLKNN 2. Because observations of modern felids show that carcasses are typically transported no more than 300 m, it is likely that at least FLKN was very close to the higher competition, open habitats where a majority of the prey (i.e., alcelaphines and antilopines) was probably procured. Felid taphonomic signatures are conspicuously absent from the Bed II faunas. This is due in part to an increased hyena signal in the

Bed II faunas, which, due to greater bone-crushing, has probably obscured the signal of previous taphonomic agents. With the extinction of *Megantereon* and *Homotherium* after 1.5 Ma, this documented taphonomic shift appears to echo the changing configuration of the large carnivore guild between Bed I and Bed II times. A final point concerns the carcass foraging strategies of hominids. It has been suggested that tree-stored felid kills would have provided a relatively safe and potentially high-yielding scavenging opportunity for hominids (Blumenschine and Cavallo, 1992; Cavallo and Blumenschine, 1989). The fact that butchery damage is virtually absent in all the levels of both FLKN and FLKNN may mean that hominids did not regularly practice such a carcass foraging strategy, at least during Bed I times at Olduvai.

### **VARIABILITY IN HOMINID SITE USE**

One of the most important contributions of this study is the demonstration that hominids played little or no role in the formation of the faunal assemblages from DK and FLKN 5. This is true for most of the other Bed I sites as well (Domínguez-Rodrigo et al., in press a). As it stands, the fauna from only one Bed I site, FLK 22, can be considered as largely anthropogenic in origin. The high frequency of butchering tools and a myriad of taphonomic data indicate that hominids repeatedly transported fully fleshed carcasses to this location for systematic butchery (Bunn, 1982, 1986, 2007; Bunn and Kroll, 1986, 1988; Domínguez-Rodrigo, 1997, 1999a; Domínguez-Rodrigo and Barba, in press; Oliver, 1994). Among the other Bed I sites, DK appears to have been a predation arena that was only very occasionally exploited by hominids for carcass resources. Although some carcass processing occurred on-site, the fact that butchery tools, and not butchery marks, are relatively common suggests that (at least for Level 3) of the carcass parts obtained by hominids, most were transported off-site for further processing and/or consumption. It is also possible that much of the tool-using activity carried out at the site was not related to carcass butchery. The lithic and faunal data indicate that FLKN 5 (along with the other levels at the FLKN locality) was utilized by hominids for subsistence behaviors largely unrelated to carcass processing. Although FLKNN 2 lacks stone tools, the other levels contain small lithic assemblages that appear functionally unrelated to the fauna.

Among the Bed II faunas, only BK can be considered to have a significant hominid component, as a recent reanalysis of the MNK (Main) site contradicts Monahan's (1996a, b) interpretation of the site as a primarily hominid accumulation (Domínguez-Rodrigo and Egeland, unpublished data) and poor preservation does not permit accurate identifications of surface modifications at FC West and TK. Because of the low resolution and integrity of BK, it is difficult to tell if it was functionally similar in a socio-economic sense to FLK 22, although carcass butchery was certainly the major function of the BK lithic assemblage. On the other hand, non-carcass processing behavior may have been significant at FC West and TK.

Nearly all the artifact-bearing Bed I sites occurred in relatively low competition settings. Because carcass resources were procured rarely or not at all by hominids at DK, FLKNN or FLKN, it is unlikely that carnivore avoidance played a significant role in conditioning hominid tool use and discard at these locations. Because site use by hominids and carnivores appears unrelated in most cases, it was not necessarily lower levels of competition *per se* but rather the resources that such low competition settings provided, such as water, shade and especially vegetal foods, which drew hominids to these locations. The potential for ecological overlap between hominids and carnivores was much more pronounced at FLK 22. It is therefore possible that carnivore avoidance resulted in the use of a low competition habitat and promoted carcass part transport and site formation at FLK 22. The high carcass yields and the concomitant need for processing equipment would have encouraged transport to a central place like FLK 22 (Blumenschine et al., 1994), although whether social factors like food-sharing (e.g., Bunn, 2007a), offspring or mate provisioning (e.g., Oliver, 1994) or a sexual division of labor (e.g., Isaac, 1978b) further conditioned carcass transport behavior is currently impossible to test directly. However, the large food surpluses created by the transport of so many fully fleshed carcasses make it likely that at least food-sharing was practiced.

That the one Bed II site with substantial hominid input (BK) occurred in a high competition setting is potentially significant. The ability of hominids to monopolize carcasses under such circumstances may signal changes in body and/or group size or perhaps the control of fire, for which

there is (provisional) evidence at Koobi Fora, Kenya, by 1.6 Ma (Bellomo, 1994) and Swartkrans Member 3, South Africa, by ca. 1.0 Ma (Brain and Sillen, 1988) (see also Monahan, 1996a, b). Stone tools are also found in high competition settings at MNK (Main), FC West and TK. The stone tools and fauna are functionally unrelated at MNK (Main) (Domínguez-Rodrigo and Egeland, unpublished data) and may or may not be related at FC West and TK. Nevertheless, hominids were carrying out activities in these higher competition settings, a pattern that mirrors the shift towards more open habitats during Bed II times. Overall, these data provide compelling evidence for variability in site utilization by hominids within the paleo-Olduvai Basin over a period of about 600,000 years.

Variability in site use can also be documented at other early Pleistocene localities. For example, the presence of butchered bones, either in small scatters (Bunn, 1981, 1994) or dense accumulations (Pobiner, 2007), without associated lithics (Isaac's [Isaac and Crader, 1981] "Type D" sites) in the Okote Member (ca. 1.5 Ma) at Koobi Fora reflects the conservation and long distance transport of stone, as these sites are between 5–15 km from the nearest raw material source. Such occurrences are expected to be rare at Olduvai as most sites are located no more than about 2 km away from a suitable raw material source. Another Okote Member site, FxJj 50, appears to represent a central place similar to FLK 22 (Bunn et al., 1980, 1997). The Turkana Basin as a whole seems to record a general shift in site location over time. Hominid tool use and discard at sites dated to about 2.4 Ma and, less significantly, 1.9 Ma, appear more or less tethered to fixed resources on the landscape while later sites (ca. 1.6 Ma) occur in a variety of depositional environments and, as discussed above, are located many kilometers away from raw material sources (Rogers et al., 1994). At Peninj a complex of sites dated to 1.5 Ma probably reflects the butchery of carcasses near acquisition points and perhaps the subsequent transport of carcass parts to another location (Domínguez-Rodrigo et al., 2002). At Swartkrans there is some evidence to suggest that hominids were utilizing the cave during Member 3 times ca. 1.0 Ma (Brain, 1993; Pickering et al., 2004c). Due largely to small sample size and/or poor faunal preservation, hominid site use in the late Pliocene is less well documented. A possible exception to this is the large and well-preserved assemblage from

Kanjera South, Kenya, dated to 2.0 Ma (Plummer, 2004; Plummer et al., 1999). This site is potentially interesting in that if the fauna can be attributed to hominids it would demonstrate large-scale carcass processing in a relatively open grassland environment. However, little else can be said pending a full report on the excavations.

These data all confirm a rather basic behavioral ecological prediction: hominids varied their patterns of site use in relation to particular environmental variables. The data from Olduvai are especially enlightening in this regard, as it seems that hominids utilized sites for a variety of activities and therefore produced a variety of site “types”, from central places like FLK 22 to locations for possible vegetal processing like FLKN. The Olduvai data also highlight the almost singular standing of FLK 22 among other Plio-Pleistocene sites in terms of preservation, site integrity (i.e., primary position) and the extent of hominid butchery activity (see further discussion below).

### **MEAT AND THE EARLY HOMINID DIET**

Early carcass access by hominids at BK has now been established by two independent taphonomic analyses (see also Monahan, 1996a, b) and confirms an increasingly robust pattern documented at several Plio-Pleistocene sites in Africa, including Gona (Domínguez-Rodrigo et al., 2005), FxJj 50 and probably FwJj14A, FwJj14B and GaJi14 at Koobi Fora (Bunn et al., 1980, 1997; Domínguez-Rodrigo, 2002; Pobiner, 2007), the ST Site Complex at Peninj (Domínguez-Rodrigo et al., 2002), FLK 22 at Olduvai Gorge (Bunn, 2001, 2007; Bunn and Kroll, 1986; Domínguez-Rodrigo and Barba, in press) and Swartkrans Members 1–3, ca. 1.8–1.0 Ma (Pickering et al., 2004c, in press a, b). These data run counter to the hypothesis of a hominid strategy focused on passively scavenging from large carnivores (e.g., Binford, 1981; Blumenschine, 1995). Although early carcass access is strongly indicated by current data, it is impossible at this point to provide a clear taphonomic discrimination between confrontational or “power” scavenging (i.e., aggressively driving carnivores off kills; *sensu* Bunn, 1996: 322) and active hunting. Bunn (e.g., 2007: 198) favors hunting for the acquisition of small animals, as lions and hyenas can consume such carcasses in a short amount of time, and advocates power scavenging as the most likely acquisition strategy for medium animals.

Although no unambiguous hunting implements are preserved in the Plio-Pleistocene, Domínguez-Rodrigo et al. (2001: 298) have suggested that evidence for woodworking at 1.5 Ma may indicate the production of rudimentary spears. This is not to say that hominids would have ignored passive scavenging opportunities when they presented themselves; indeed it is likely, as Bunn and Ezzo (1993: 388) state, that hominids utilized a “flexible and sophisticated strategy of carcass acquisition that involved as the dominant methods active, confrontational scavenging to acquire large animals and both active scavenging and opportunistic hunting to acquire small animals. As part of this flexible, broadly based strategy, passive scavenging probably did occur, but not enough for it to be reflected as a significant, dominant factor in the known archaeological record” (see also Monahan, 1996a: 116-117).

Given the clear evidence for early carcass access, the question arises as to the frequency with which hominids acquired carcasses. Bunn (2007: 206-208) suggests that this question, and the evolution of hominid meat-eating, is best addressed in three stages. The first stage is represented by the oldest butchered bones, which occur at Bouri and OGS 6 and 7 from Gona, both in Ethiopia and dated to between 2.5–2.6 Ma. The assemblages at these sites contain a combined total of 15 butchered bones (de Heinzelin et al., 1999; Domínguez-Rodrigo et al., 2005; Semaw et al., 2003), which signify the first unambiguous evidence for hominids utilizing stone tools to process animals larger than those commonly taken by non-human primates. However, the extremely small sample sizes suggest that carcass acquisition was sporadic and there is currently no evidence for large-scale carcass transport. The second stage, which spans the interval between 2.3–1.9 Ma, contains several sites with relatively large bone accumulations. Although there is some evidence for carcass processing during the 2.3–1.9 Ma interval at Koobi Fora (Isaac, 1997), no confirmed functional relationship (in the form of cutmarks and/or percussion marks) has yet been demonstrated between the lithics and fauna discovered at most of the Pliocene sites: A.L. 666, Hadar, Ethiopia (2.3 Ma; Kimbel et al., 1994), FtJi 2 and Omo 123, Omo, Ethiopia (2.3 Ma; Howell et al., 1987), Lokalalei, West Turkana, Kenya (2.3 Ma; Kibunjia, 1994), Senga 5A, Upper Semliki Area, Democratic

Republic of the Congo (2.2 Ma; Harris et al., 1987). In most cases this is due not necessarily to a lack of carcass butchery but to poor surface preservation. Again, possible exceptions to this are Kanjera South and the recently reported 1.9 Ma site of FwJj 20 from the Upper Burgi Member at Il Dura, Kenya (Braun et al., 2007). Evidence for meat-eating increases dramatically during the third interval after 1.9 Ma, as butchered bones are common at Koobi Fora, Olduvai Gorge, Peninj and Swartkrans. There seems to be good evidence for large-scale carcass transport and butchery, especially at FLK 22. However, this “leap” is much less pronounced given the data presented in this study, which demote several Bed I Olduvai sites from central places to (largely) carnivore accumulations (for revisions of the other Bed I sites see Domínguez-Rodrigo et al. [in press a]). Therefore, FLK 22 appears as a rather isolated occurrence at 1.8 Ma, which is then followed at ca. 1.5 Ma by the ST Site Complex (Domínguez-Rodrigo et al., 2002) and the Okote sites at Koobi Fora, including FxJj 50 (Bunn et al., 1980, 1997; Domínguez-Rodrigo, 2002) and the recently reported sites of FwJj14A, FwJj14B and GaJi14 (Pobiner, 2007). The latter three sites contain between 70 and almost 150 butchered fragments and all preserve the remains of over a dozen large mammals (Pobiner, 2007).

The issue of the frequency of meat-eating and its importance to the early hominid diet creates a predicament very similar to that for Americanists engaged in the “Pleistocene Overkill” debate. For example, the presence of at least 14 megafaunal kill/butchery sites in North America can either be seen as a virtual lack of Clovis hunting pressure (Grayson and Melzter, 2003: 588) or, considering the vagaries of the taphonomic record, a “phenomenally rich record” (Fiedel and Haynes, 2004: 126). Ancillary data supports the latter position for the Plio-Pleistocene, at least for the record around 1.5–1.6 Ma. Significant increases in the body and brain size (McHenry, 1992, 1994) and energy requirements (Stuedel-Numbers, 2006) of *Homo erectus*, which date from 1.5 Ma at Olduvai (Manega, 1993) and 1.65 Ma at Koobi Fora (except for one isolated occipital [KMN-ER 2598]; Gathogo and Brown [2006]), probably required a higher quality diet focused on easily digested animal protein (Aiello and Wheeler, 1995). However, even the expected lag between the commencement of large mammal butchery at 2.5–2.6 Ma and the appearance of the full collection of

its consequent adaptations in *H. erectus* about 1.6 Ma still leaves FLK 22, the most extreme example of hominid carcass transport and meat-eating, as an anomaly at 1.8 Ma. This is especially evident considering the data presented in this study (see also Domínguez-Rodrigo et al., in press a) and the fact that butchered bones are very rare in the landscape samples from the ca. 1.7 Ma lowermost Bed II deposits (Pobiner, 2007). Hominid associations during this time period at Olduvai include *Australopithecus boisei* and perhaps two different species of early *Homo* (Blumenschine et al., 2003): one more primitive taxon represented most completely by OH 62 (Johanson et al., 1987) and another by the recently discovered OH 65, which appears more similar to the larger-brained KNM-ER 1470 specimen from Koobi Fora (Blumenschine et al., 2003). What is needed are full taphonomic analyses of other late Pliocene and early Pleistocene faunal assemblages like those from Dmanisi (Republic of Georgia), which is nearly 1.8 Ma and contains both cutmarks (Lordkipanidze et al., 2005) and hominids intermediate to early *Homo* and *H. erectus* in body and brain size (Rightmire et al., 2006), Kanjera South and the Il Dura sites, all of which should help place FLK 22 and thus early hominid meat-eating into context.

In preserving one of world's richest records of early hominid behavior, Olduvai Gorge provides a tremendous opportunity to examine spatio-temporal variability in hominid behavior. A lack of hominid involvement in the formation of many of the faunal assemblages from the artifact-bearing sediments in Bed I means that large-scale carcass transport and butchery were not being carried out at these localities. Rather than marginalizing these assemblages in discussions of hominid behavior, however, this study has attempted to utilize taphonomic data to (1) illuminate the dynamics of a large carnivore guild within which hominids at least occasionally competed; (2) inform usefully on hominid habitat preferences; and (3) add a new dimension to our understanding of hominid site use in the paleo-Olduvai Basin and, potentially, beyond. The use of competition as a taphonomically identifiable and ecologically relevant variable suggests that large carnivore interactions were likely very different during the Plio-Pleistocene. The extent to which this affected hominid foraging strategies would have varied both with hominid competitive abilities and the scale of meat-eating.

Reconstructing competition levels also suggest that hominid tool-using was concentrated in lower competition settings during Bed I times, while during Bed II times more artifact-bearing sites occur in higher competition, and presumably more open, habitats. Especially significant is the evidence for large-scale carcass transport and processing at what appears to be a highly competitive setting at BK. Finally, the absence of butchery evidence, particularly at the Bed I sites, indicates that hominid tool-using at Olduvai cannot be exclusively linked to carcass processing. Integrating the results of this study with ongoing work at other important Plio-Pleistocene sites, all of which was stimulated by and is based ultimately on the seminal work of previous researchers, will hopefully contribute to a greater appreciation of early hominid variability during this important time period.

## APPENDIX I SKELETAL PART CODES

Table I.1. Element codes.

Code	Element
CRN	Cranium
MR	Mandible
HY	Hyoid
AT	Atlas
AX	Axis
CE	Cervical
TH	Thoracic
LM	Lumar
VT	Vertebra
SAC	Sacrum
IM	Innominate
RB	Rib
ST	Sternum
SC	Scapula
HM	Humerus
RD	Radius
UL	Ulna
MC	Metacarpal
CPR	Radial carpal
CPI	Intermediate carpal
CPU	Ulnar carpal
CPS	Fused second and third carpal
CPF	Fourth carpal
CPA	Accessory carpal
MCF	Fifth metacarpal
FM	Femur
PT	Patella
TA	Tibia
CL	Calcaneous
AS	Astragalus
LTM	Lateral malleolus
MT	Metatarsal
TRC	Fused central and fourth tarsal
TRS	Second tarsal
TRF	First tarsal
MTS	Second metatarsal
PHF	First phalanx
PHS	Second phalanx

Table I.1. cont.

Code	Element
PHT	Third phalanx
SEP	Proximal sesamoid
SED	Distal sesamoid
TFR	Tooth fragment
UPP	Upper limb bone
INT	Intermediate limb bone
MP	Metapodial
NMP	Non-metapodial limb bone
NUPP	Non-upper limb bone
LBS	Unidentified limb bone
US	Unidentified fragment

**APPENDIX II**  
**DK SKELETAL PART FREQUENCIES**

Table II.1. Size Class 1 skeletal element frequencies for DK 1.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	4	2	2.0	100.0	1
MR	1	1	0.5	25.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	1	1	0.0	1.8	1
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	0	0	0.0	0.0	0
RD	2	1	0.5	25.0	1
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	2	2	1.0	50.0	1
CPU	0	0	0.0	0.0	0
CPS	1	1	0.5	25.0	1
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	2	2	1.0	50.0	2
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	1	1	0.5	25.0	1
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	1	1	0.1	6.3	1
PHS	0	0	0.0	0.0	0

Table II.1. cont.

Element	NISP	MNE	MAU	%MAU	MNI
PHT	2	2	0.3	12.5	1
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	1	–	–	–	–
TFR	4	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

Table II.2. Size Class 2 skeletal element frequencies for DK 1.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	1	1	1.0	100.0	1
MR	3	1	0.5	50.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	2	2	0.1	14.3	1
LM	1	1	0.2	20.0	1
SAC	0	0	0.0	0.0	0
IM	1	1	0.5	50.0	1
RB	3	1	0.0	3.6	1
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0

Table II.2. cont.

Element	NISP	MNE	MAU	%MAU	MNI
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	1	1	0.5	50.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	1	1	0.1	12.5	1
PHS	1	1	0.1	12.5	1
PHT	1	1	0.1	12.5	1
SEP	0	0	0.0	0.0	0
SED	1	1	0.1	12.5	1
VT	0	–	–	–	–
TFR	3	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	1	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

Table II.3. Size Class 3 skeletal element frequencies for DK 1.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	15	7	7.0	100.0	7
MR	16	7	3.5	50.0	7
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	2	2	0.4	5.7	1
TH	0	0	0.0	0.0	0
LM	5	5	1.0	14.3	2
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	11	6	0.2	3.1	1

Table II.3 cont.

Element	NISP	MNE	MAU	%MAU	MNI
ST	0	0	0.0	0.0	0
SC	4	2	1.0	14.3	2
HM	1	1	0.5	7.1	1
RD	3	2	1.0	14.3	1
UL	1	1	0.5	7.1	1
MC	6	3	1.5	21.4	2
CPR	1	1	0.5	7.1	1
CPI	1	1	0.5	7.1	1
CPU	0	0	0.0	0.0	0
CPS	1	1	0.5	7.1	1
CPF	2	2	1.0	14.3	2
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	4	2	1.0	14.3	2
PT	0	0	0.0	0.0	0
TA	7	5	2.5	35.7	3
CL	2	2	1.0	14.3	2
AS	1	1	0.5	7.1	1
LTM	1	1	0.5	7.1	1
MT	4	4	2.0	28.6	4
TRC	1	1	0.5	7.1	1
TRS	1	1	0.5	7.1	1
TRF	2	2	1.0	14.3	2
MTS	0	0	0.0	0.0	0
PHF	3	3	0.4	5.4	1
PHS	2	2	0.3	3.6	1
PHT	1	1	0.1	1.8	1
SEP	4	4	0.3	3.6	1
SED	1	1	0.1	1.8	1
VT	1	-	-	-	-
TFR	8	-	-	-	-
UPP	2	-	-	-	-
INT	0	-	-	-	-
MP	2	-	-	-	-
NMP	3	-	-	-	-
NUPP	0	-	-	-	-
LBS	2	-	-	-	-
US	1	-	-	-	-

Table II.4. Size Class 4 skeletal element frequencies for DK 1.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0	0.0	0
MR	0	0	0	0.0	0
HY	0	0	0	0.0	0
AT	0	0	0	0.0	0
AX	0	0	0	0.0	0
CE	0	0	0	0.0	0
TH	0	0	0	0.0	0
LM	0	0	0	0.0	0
SAC	0	0	0	0.0	0
IM	1	1	0.5	100.0	1
RB	1	1	0.0	7.1	1
ST	0	0	0.0	0.0	0
SC	1	1	0.5	100.0	1
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0

Table II.4. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	0	-	-	-	-
TFR	0	-	-	-	-
UPP	0	-	-	-	-
INT	0	-	-	-	-
MP	0	-	-	-	-
NMP	0	-	-	-	-
NUPP	0	-	-	-	-
LBS	0	-	-	-	-
US	0	-	-	-	-

Table II.5. Size Class 1 skeletal element frequencies for DK 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	16	4	4.0	100.0	4
MR	18	6	3.0	75.0	5
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	3	3	0.6	15.0	1
TH	2	2	0.1	3.6	2
LM	1	1	0.2	5.0	1
SAC	1	1	1.0	25.0	1
IM	3	3	1.5	37.5	1
RB	7	3	0.1	2.7	1
ST	0	0	0.0	0.0	0
SC	2	2	1.0	25.0	2
HM	1	1	0.5	12.5	1
RD	2	2	1.0	25.0	1
UL	0	0	0.0	0.0	0
MC	7	5	2.5	62.5	5
CPR	1	1	0.5	12.5	1
CPI	1	1	0.5	12.5	1
CPU	1	1	0.5	12.5	1
CPS	0	0	0.0	0.0	0
CPF	1	1	0.5	12.5	1
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	8	4	2.0	50.0	4
PT	3	3	1.5	37.5	3
TA	5	5	2.5	62.5	5

Table II.5. cont.

Element	NISP	MNE	MAU	%MAU	MNI
CL	0	0	0.0	0.0	0
AS	3	3	1.5	37.5	2
LTM	2	2	1.0	25.0	2
MT	2	2	1.0	25.0	2
TRC	3	3	1.5	37.5	2
TRS	1	1	0.5	12.5	1
TRF	1	1	0.5	12.5	1
MTS	0	0	0.0	0.0	0
PHF	8	8	1.0	25.0	1
PHS	4	4	0.5	12.5	1
PHT	5	5	0.6	15.6	1
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	—	—	—	—
TFR	8	—	—	—	—
UPP	0	—	—	—	—
INT	0	—	—	—	—
MP	1	—	—	—	—
NMP	0	—	—	—	—
NUPP	0	—	—	—	—
LBS	4	—	—	—	—
US	1	—	—	—	—

Table II.6. Size Class 2 skeletal element frequencies for DK 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	6	3	3.0	100.0	3
MR	18	3	1.5	50.0	3
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	1	1	1.0	33.3	1
CE	1	1	0.2	6.7	1
TH	0	0	0.0	0.0	0
LM	4	3	0.6	20.0	2
SAC	0	0	0.0	0.0	0
IM	3	3	1.5	50.0	3
RB	12	4	0.1	4.8	1
ST	0	0	0.0	0.0	0
SC	4	1	0.5	16.7	1
HM	5	3	1.5	50.0	3

Table II.6. cont.

Element	NISP	MNE	MAU	%MAU	MNI
RD	8	6	3.0	100.0	4
UL	3	3	1.5	50.0	3
MC	7	6	3.0	100.0	5
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	1	1	0.5	16.7	1
CPS	1	1	0.5	16.7	1
CPF	3	3	1.5	50.0	3
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	6	4	2.0	66.7	3
PT	1	1	0.5	16.7	1
TA	12	5	2.5	83.3	4
CL	1	1	0.5	16.7	1
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	8	4	2.0	66.7	3
TRC	0	0	0.0	0.0	0
TRS	1	1	0.5	16.7	1
TRF	2	2	1.0	33.3	1
MTS	2	2	1.0	33.3	1
PHF	7	6	0.8	25.0	1
PHS	4	3	0.4	12.5	1
PHT	2	2	0.3	8.3	1
SEP	8	8	0.5	16.7	1
SED	1	1	0.1	4.2	1
VT	2	–	–	–	–
TFR	9	–	–	–	–
UPP	1	–	–	–	–
INT	1	–	–	–	–
MP	3	–	–	–	–
NMP	5	–	–	–	–
NUPP	0	–	–	–	–
LBS	8	–	–	–	–
US	0	–	–	–	–

Table II.7. Size Class 3 skeletal element frequencies for DK 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	58	15	15.0	100.0	15
MR	88	24	12.0	80.0	21
HY	0	0	0.0	0.0	0
AT	4	4	4.0	26.7	4
AX	3	3	3.0	20.0	3
CE	17	8	1.6	10.7	3
TH	9	7	0.5	3.3	3
LM	12	11	2.2	14.7	4
SAC	2	2	2.0	13.3	2
IM	25	15	7.5	50.0	10
RB	32	7	0.3	1.7	2
ST	0	0	0.0	0.0	0
SC	21	13	6.5	43.3	9
HM	44	25	12.5	83.3	16
RD	43	21	10.5	70.0	13
UL	16	10	5.0	33.3	9
MC	37	20	10.0	66.7	12
CPR	1	1	0.5	3.3	1
CPI	2	2	1.0	6.7	2
CPU	5	5	2.5	16.7	3
CPS	6	6	3.0	20.0	4
CPF	2	2	1.0	6.7	1
CPA	1	1	0.5	3.3	1
MCF	0	0	0.0	0.0	0
FM	44	23	11.5	76.7	16
PT	1	1	0.5	3.3	1
TA	73	30	15.0	100.0	18
CL	6	5	2.5	16.7	3
AS	2	2	1.0	6.7	1
LTM	4	4	2.0	13.3	3
MT	41	23	11.5	76.7	13
TRC	4	4	2.0	13.3	2
TRS	5	5	2.5	16.7	4
TRF	2	2	1.0	6.7	1
MTS	1	1	0.5	3.3	1
PHF	14	13	1.6	10.8	2
PHS	10	8	1.0	6.7	1
PHT	10	10	1.3	8.3	2
SEP	18	18	1.1	7.5	3
SED	2	2	0.3	1.7	1

Table II.7. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	4	–	–	–	–
TFR	35	–	–	–	–
UPP	13	–	–	–	–
INT	16	–	–	–	–
MP	17	–	–	–	–
NMP	9	–	–	–	–
NUPP	12	–	–	–	–
LBS	42	–	–	–	–
US	3	–	–	–	–

Table II.8. Size Class 4 skeletal element frequencies for DK 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	2	1	1.0	100.0	1
MR	3	1	0.5	50.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	13	4	0.1	14.3	1
ST	0	0	0.0	0.0	0
SC	2	1	0.5	50.0	1
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	2	1	0.5	50.0	1
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0

Table II.8. cont.

Element	NISP	MNE	MAU	%MAU	MNI
CL	1	1	0.5	50.0	1
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	1	1	0.5	50.0	1
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	—	—	—	—
TFR	0	—	—	—	—
UPP	0	—	—	—	—
INT	0	—	—	—	—
MP	0	—	—	—	—
NMP	1	—	—	—	—
NUPP	1	—	—	—	—
LBS	4	—	—	—	—
US	0	—	—	—	—

Table II.9. Size Class 5/6 skeletal element frequencies for DK 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	3	1	1.0	100.0	1
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	2	2	0.4	40.0	1
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	1	1	0.5	50.0	1
RB	53	3	0.1	10.7	2
ST	0	0	0.0	0.0	0
SC	3	1	0.5	50.0	1

Table II.9. cont.

Element	NISP	MNE	MAU	%MAU	MNI
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	3	2	1.0	100.0	1
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	50.0	1
PT	0	0	0.0	0.0	0
TA	1	1	0.5	50.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	5	—	—	—	—
TFR	11	—	—	—	—
UPP	2	—	—	—	—
INT	1	—	—	—	—
MP	0	—	—	—	—
NMP	0	—	—	—	—
NUPP	0	—	—	—	—
LBS	15	—	—	—	—
US	13	—	—	—	—

Table II.10. Size Class 1 skeletal element frequencies for DK 3.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	9	3	3.0	100.0	3
MR	12	6	3.0	100.0	4
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	2	2	0.4	13.3	1
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	1	1	0.5	16.7	1
RB	4	1	0.0	1.2	1
ST	0	0	0.0	0.0	0
SC	2	1	0.5	16.7	1
HM	3	3	1.5	50.0	2
RD	4	2	1.0	33.3	2
UL	0	0	0.0	0.0	0
MC	6	4	2.0	66.7	3
CPR	1	1	0.5	16.7	1
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	1	1	0.5	16.7	1
MCF	0	0	0.0	0.0	0
FM	7	5	2.5	83.3	4
PT	0	0	0.0	0.0	0
TA	9	4	2.0	66.7	3
CL	2	2	1.0	33.3	2
AS	4	4	2.0	66.7	4
LTM	1	1	0.5	16.7	1
MT	7	5	2.5	83.3	4
TRC	1	1	0.5	16.7	1
TRS	2	2	1.0	33.3	1
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	5	5	0.6	20.8	2
PHS	4	4	0.5	16.7	1
PHT	2	2	0.3	8.3	1
SEP	1	1	0.1	2.1	1
SED	0	0	0.0	0.0	0

Table II.10. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	0	–	–	–	–
TFR	1	–	–	–	–
UPP	1	–	–	–	–
INT	0	–	–	–	–
MP	7	–	–	–	–
NMP	3	–	–	–	–
NUPP	0	–	–	–	–
LBS	5	–	–	–	–
US	0	–	–	–	–

Table II.11. Size Class 2 skeletal element frequencies for DK 3.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	5	1	0.5	50.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	2	1	0.2	20.0	1
TH	3	2	0.1	14.3	1
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	1	1	0.5	50.0	1
RB	12	2	0.1	7.1	1
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	2	2	1.0	100.0	2
RD	0	0	0.0	0.0	0
UL	1	1	0.5	50.0	1
MC	2	2	1.0	100.0	1
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	50.0	1
PT	0	0	0.0	0.0	0

Table II.11. cont.

Element	NISP	MNE	MAU	%MAU	MNI
TA	2	2	1.0	100.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	4	2	1.0	100.0	2
TRC	1	1	0.5	50.0	1
TRS	1	1	0.5	50.0	1
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	1	1	0.1	12.5	1
PHS	2	2	0.3	25.0	1
PHT	3	3	0.4	37.5	1
SEP	3	3	0.2	18.8	1
SED	0	0	0.0	0.0	0
VT	1	—	—	—	—
TFR	1	—	—	—	—
UPP	2	—	—	—	—
INT	1	—	—	—	—
MP	0	—	—	—	—
NMP	5	—	—	—	—
NUPP	3	—	—	—	—
LBS	5	—	—	—	—
US	0	—	—	—	—

Table II.12. Size Class 3 skeletal element frequencies for DK 3.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	38	19	19.0	100.0	19
MR	54	13	6.5	34.2	13
HY	2	2	1.0	5.3	1
AT	4	3	3.0	15.8	3
AX	2	2	2.0	10.5	2
CE	5	2	0.4	2.1	1
TH	5	3	0.2	1.1	1
LM	6	5	1.0	5.3	2
SAC	0	0	0.0	0.0	0
IM	12	7	3.5	18.4	6
RB	26	8	0.3	1.5	2
ST	0	0	0.0	0.0	0

Table II.12. cont.

Element	NISP	MNE	MAU	%MAU	MNI
SC	15	6	3.0	15.8	4
HM	33	18	9.0	47.4	13
RD	26	13	6.5	34.2	9
UL	9	5	2.5	13.2	4
MC	20	9	4.5	23.7	7
CPR	5	5	2.5	13.2	3
CPI	1	1	0.5	2.6	1
CPU	1	1	0.5	2.6	1
CPS	2	2	1.0	5.3	2
CPF	2	2	1.0	5.3	1
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	35	17	8.5	44.7	10
PT	0	0	0.0	0.0	0
TA	48	22	11.0	57.9	14
CL	5	5	2.5	13.2	3
AS	4	4	2.0	10.5	3
LTM	1	1	0.5	2.6	1
MT	35	16	8.0	42.1	11
TRC	4	4	2.0	10.5	2
TRS	5	5	2.5	13.2	3
TRF	1	1	0.5	2.6	1
MTS	1	1	0.5	2.6	1
PHF	6	5	0.6	3.3	1
PHS	2	2	0.3	1.3	1
PHT	0	0	0.0	0.0	0
SEP	8	8	0.5	2.6	1
SED	1	1	0.1	0.7	1
VT	3	–	–	–	–
TFR	30	–	–	–	–
UPP	11	–	–	–	–
INT	6	–	–	–	–
MP	17	–	–	–	–
NMP	10	–	–	–	–
NUPP	8	–	–	–	–
LBS	74	–	–	–	–
US	1	–	–	–	–

Table II.13. Size Class 4 skeletal element frequencies for DK 3.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	7	3	0.1	5.4	1
ST	0	0	0.0	0.0	0
SC	3	1	0.5	25.0	1
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	5	4	2.0	100.0	2
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0

Table II.13. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

Table II.14. Size Class 5/6 skeletal element frequencies for DK 3.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	2	2	1.0	100.0	2
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	1	1	0.2	20.0	1
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	2	2	1.0	100.0	1
RB	19	6	0.2	21.4	2
ST	0	0	0.0	0.0	0
SC	1	1	0.5	50.0	1
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	1	1	0.5	50.0	1
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	50.0	1
PT	0	0	0.0	0.0	0

Table II.14. cont.

Element	NISP	MNE	MAU	%MAU	MNI
TA	2	1	0.5	50.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	4	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

**APPENDIX III**  
**FLKNN2 SKELETAL PART FREQUENCIES**

Table III.1. Size Class 1 skeletal element frequencies for FLKNN 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	1	1	0.0	2.4	1
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	1	1	0.5	33.3	1
RD	1	1	0.5	33.3	1
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	4	3	1.5	100.0	2
PT	0	0	0.0	0.0	0
TA	2	2	1.0	66.7	2
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	1	1	0.5	33.3	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0

Table III.1. cont.

Element	NISP	MNE	MAU	%MAU	MNI
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	2	–	–	–	–
TFR	0	–	–	–	–
UPP	1	–	–	–	–
INT	0	–	–	–	–
MP	1	–	–	–	–
NMP	1	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

Table III.2. Size Class 2 skeletal element frequencies for FLKNN 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	2	2	2.0	100.0	2
MR	2	2	1.0	50.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	1	1	0.2	10.0	1
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	2	1	0.0	1.8	1
ST	0	0	0.0	0.0	0
SC	3	3	1.5	75.0	2
HM	1	1	0.5	25.0	1
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	1	1	0.5	25.0	1
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0

Table III.2. cont.

Element	NISP	MNE	MAU	%MAU	MNI
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	1	1	0.5	25.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	3	3	1.5	75.0	2
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	1	1	0.1	6.3	1
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	1	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	1	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

Table III.3. Size Class 3 skeletal element frequencies for FLKNN 2.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	19	6	6.0	92.3	6
MR	17	6	3.0	46.2	5
HY	0	0	0.0	0.0	0
AT	1	1	1.0	15.4	1
AX	0	0	0.0	0.0	0
CE	3	2	0.4	6.2	1
TH	10	7	0.5	7.7	3
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	2	1	0.5	7.7	1
RB	39	13	0.5	7.1	1
ST	0	0	0.0	0.0	0
SC	8	8	4.0	61.5	4
HM	14	13	6.5	100.0	10
RD	12	12	6.0	92.3	11
UL	8	6	3.0	46.2	5
MC	15	13	6.5	100.0	12
CPR	0	0	0.0	0.0	0
CPI	2	2	1.0	15.4	1
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	11	5	2.5	38.5	5
PT	1	1	0.5	7.7	1
TA	19	9	4.5	69.2	7
CL	1	1	0.5	7.7	1
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	14	8	4.0	61.5	7
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	3	3	0.4	5.8	2
PHS	2	2	0.3	3.8	1
PHT	1	1	0.1	1.9	1
SEP	2	2	0.1	1.9	1
SED	1	1	0.1	1.9	1

Table III.3. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	0	-	-	-	-
TFR	0	-	-	-	-
UPP	0	-	-	-	-
INT	0	-	-	-	-
MP	0	-	-	-	-
NMP	0	-	-	-	-
NUPP	0	-	-	-	-
LBS	1	-	-	-	-
US	0	-	-	-	-

**APPENDIX IV**  
**FLKN 5 SKELETAL PART FREQUENCIES**

Table IV.1. Size Class 1 skeletal element frequencies for FLKN 5.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	87	18	18.0	100.0	18
MR	53	14	7.0	38.9	11
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	1	1	0.2	1.1	1
TH	5	5	0.4	2.0	2
LM	4	3	0.6	3.3	1
SAC	0	0	0.0	0.0	0
IM	22	14	7.0	38.9	7
RB	12	3	0.1	0.6	1
ST	1	1	1.0	5.6	1
SC	12	11	5.5	30.6	6
HM	15	12	6.0	33.3	9
RD	20	14	7.0	38.9	10
UL	9	8	4.0	22.2	6
MC	21	15	7.5	41.7	9
CPR	8	8	4.0	22.2	6
CPI	3	3	1.5	8.3	3
CPU	5	5	2.5	13.9	4
CPS	5	5	2.5	13.9	4
CPF	6	6	3.0	16.7	3
CPA	2	2	1.0	5.6	1
MCF	0	0	0.0	0.0	0
FM	17	8	4.0	22.2	5
PT	4	4	2.0	11.1	3
TA	27	18	9.0	50.0	11
CL	8	8	4.0	22.2	4
AS	9	9	4.5	25.0	6
LTM	7	7	3.5	19.4	4
MT	31	18	9.0	50.0	11
TRC	8	8	4.0	22.2	5
TRS	7	7	3.5	19.4	4
TRF	3	3	1.5	8.3	2
MTS	0	0	0.0	0.0	0
PHF	37	31	3.9	21.5	3
PHS	35	34	4.3	23.6	4

Table IV.1. cont.

Element	NISP	MNE	MAU	%MAU	MNI
PHT	35	34	4.3	23.6	4
SEP	20	20	1.3	6.9	2
SED	5	5	0.6	3.5	1
VT	1	–	–	–	–
TFR	9	–	–	–	–
UPP	2	–	–	–	–
INT	1	–	–	–	–
MP	5	–	–	–	–
NMP	1	–	–	–	–
NUPP	2	–	–	–	–
LBS	21	–	–	–	–
US	4	–	–	–	–

Table IV.2. Size Class 2 skeletal element frequencies for FLKN 5.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	2	1	1.0	40.0	1
MR	4	2	1.0	40.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	1	1	0.2	8.0	1
TH	2	1	0.1	2.9	1
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	3	3	1.5	60.0	2
RB	11	2	0.1	2.9	1
ST	0	0	0.0	0.0	0
SC	2	2	1.0	40.0	2
HM	1	1	0.5	20.0	1
RD	6	5	2.5	100.0	4
UL	1	1	0.5	20.0	1
MC	3	2	1.0	40.0	1
CPR	1	1	0.5	20.0	1
CPI	0	0	0.0	0.0	0
CPU	1	1	0.5	20.0	1
CPS	1	1	0.5	20.0	1
CPF	1	1	0.5	20.0	1

Table IV.2. cont.

Element	NISP	MNE	MAU	%MAU	MNI
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	6	2	1.0	40.0	2
PT	2	2	1.0	40.0	1
TA	9	5	2.5	100.0	3
CL	0	0	0.0	0.0	0
AS	1	1	0.5	20.0	1
LTM	0	0	0.0	0.0	0
MT	7	2	1.0	40.0	2
TRC	1	1	0.5	20.0	1
TRS	3	3	1.5	60.0	3
TRF	0	0	0.0	0.0	0
MTS	2	2	1.0	40.0	1
PHF	7	7	0.9	35.0	1
PHS	6	6	0.8	30.0	1
PHT	7	7	0.9	35.0	1
SEP	10	10	0.6	25.0	1
SED	0	0	0.0	0.0	0
VT	2	–	–	–	–
TFR	0	–	–	–	–
UPP	5	–	–	–	–
INT	0	–	–	–	–
MP	3	–	–	–	–
NMP	1	–	–	–	–
NUPP	2	–	–	–	–
LBS	25	–	–	–	–
US	0	–	–	–	–

Table IV.3. Size Class 3 skeletal element frequencies for FLKN 5.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	30	7	7.0	82.4	7
MR	27	7	3.5	41.2	5
HY	1	1	0.5	5.9	1
AT	3	3	3.0	35.3	3
AX	2	2	2.0	23.5	2
CE	12	5	1.0	11.8	2
TH	5	4	0.3	3.4	1
LM	3	2	0.4	4.7	1
SAC	0	0	0.0	0.0	0
IM	7	4	2.0	23.5	2
RB	22	8	0.3	3.4	2
ST	0	0	0.0	0.0	0
SC	12	3	1.5	17.6	2
HM	28	14	7.0	82.4	9
RD	21	10	5.0	58.8	7
UL	13	9	4.5	52.9	7
MC	19	13	6.5	76.5	11
CPR	5	5	2.5	29.4	3
CPI	3	3	1.5	17.6	2
CPU	3	3	1.5	17.6	2
CPS	2	2	1.0	11.8	1
CPF	2	2	1.0	11.8	2
CPA	2	2	1.0	11.8	1
MCF	0	0	0.0	0.0	0
FM	30	12	6.0	70.6	8
PT	2	2	1.0	11.8	1
TA	57	17	8.5	100.0	10
CL	4	4	2.0	23.5	3
AS	6	6	3.0	35.3	3
LTM	6	6	3.0	35.3	3
MT	22	16	8.0	94.1	10
TRC	3	3	1.5	17.6	2
TRS	6	6	3.0	35.3	4
TRF	1	1	0.5	5.9	1
MTS	2	2	1.0	11.8	1
PHF	10	8	1.0	11.8	1
PHS	4	4	0.5	5.9	1
PHT	7	6	0.8	8.8	1
SEP	13	13	0.8	9.6	1
SED	7	7	0.9	10.3	1

Table IV.3. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	2	–	–	–	–
TFR	1	–	–	–	–
UPP	10	–	–	–	–
INT	5	–	–	–	–
MP	12	–	–	–	–
NMP	8	–	–	–	–
NUPP	6	–	–	–	–
LBS	40	–	–	–	–
US	5	–	–	–	–

Table IV.4. Size Class 4 skeletal element frequencies for FLKN 5.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	1	1	1.0	100.0	1
MR	2	1	0.5	50.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	1	1	0.1	7.1	1
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	4	1	0.0	3.6	1
ST	0	0	0.0	0.0	0
SC	1	1	0.5	50.0	1
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0

Table IV.4. cont.

Element	NISP	MNE	MAU	%MAU	MNI
TA	1	1	0.5	50.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	1	1	0.5	50.0	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	—	—	—	—
TFR	0	—	—	—	—
UPP	0	—	—	—	—
INT	0	—	—	—	—
MP	0	—	—	—	—
NMP	0	—	—	—	—
NUPP	0	—	—	—	—
LBS	0	—	—	—	—
US	0	—	—	—	—

Table IV.5. Size Class 5/6 skeletal element frequencies for FLKN 5.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	5	3	0.1	100.0	1
ST	0	0	0.0	0.0	0

Table IV.5. cont.

Element	NISP	MNE	MAU	%MAU	MNI
SC	0	0	0.0	0.0	0
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	1	–	–	–	–

**APPENDIX V**  
**FC WEST SKELETAL PART FREQUENCIES**

Table V.1. Size Class 2 skeletal element frequencies for FC West.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	1	1	0.5	100.0	1
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0

Table V.1. cont.

Element	NISP	MNE	MAU	%MAU	MNI
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	1	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

Table V.2. Size Class 3 skeletal element frequencies for FC West.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	2	1	1.0	66.7	1
MR	2	1	0.5	33.3	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	1	1	0.1	4.8	1
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	1	1	0.5	33.3	1
RB	1	1	0.0	2.4	1
ST	0	0	0.0	0.0	0
SC	1	1	0.5	33.3	1
HM	3	3	1.5	100.0	2
RD	1	1	0.5	33.3	1
UL	0	0	0.0	0.0	0
MC	3	1	0.5	33.3	2
CPR	0	0	0.0	0.0	0
CPI	1	1	0.5	33.3	1
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0

Table V.2. cont.

Element	NISP	MNE	MAU	%MAU	MNI
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	33.3	1
PT	0	0	0.0	0.0	0
TA	1	1	0.5	33.3	1
CL	1	1	0.5	33.3	1
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	2	2	1.0	66.7	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	1	–	–	–	–
TFR	1	–	–	–	–
UPP	1	–	–	–	–
INT	0	–	–	–	–
MP	2	–	–	–	–
NMP	1	–	–	–	–
NUPP	1	–	–	–	–
LBS	5	–	–	–	–
US	0	–	–	–	–

Table V.3. Size Class 4 skeletal element frequencies for FC West.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	1	1	1.0	100.0	1
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0

Table V.3. cont.

Element	NISP	MNE	MAU	%MAU	MNI
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	1	1	0.5	50.0	1
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	50.0	1
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	1	1	0.5	50.0	1
MT	2	1	0.5	50.0	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	1	–	–	–	–
LBS	1	–	–	–	–
US	0	–	–	–	–

Table V.4. Size Class 5/6 skeletal element frequencies for FC West.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	1	1	1.0	100.0	1
MR	2	1	0.5	50.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	2	1	0.5	50.0	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	1	1	0.1	12.5	1
PHT	0	0	0.0	0.0	0
SEP	1	1	0.1	6.3	1
SED	0	0	0.0	0.0	0

Table V.4. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	0	-	-	-	-
TFR	3	-	-	-	-
UPP	0	-	-	-	-
INT	0	-	-	-	-
MP	0	-	-	-	-
NMP	0	-	-	-	-
NUPP	0	-	-	-	-
LBS	0	-	-	-	-
US	0	-	-	-	-

**APPENDIX VI**  
**TK SKELETAL PART FREQUENCIES**

Table VI.1. Size Class 1/2 skeletal element  
frequencies for TK LF.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	1	1	0.5	100.0	1
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	100.0	1
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0

Table VI.1. cont.

Element	NISP	MNE	MAU	%MAU	MNI
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	0	–	–	–	–
US	0	–	–	–	–

Table VI.2. Size Class 3 skeletal element frequencies for TK LF.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	4	2	1.0	100.0	2
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	1	1	0.1	7.1	1
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	1	1	0.5	50.0	1
RD	3	2	1.0	100.0	2
UL	0	0	0.0	0.0	0
MC	1	1	0.5	50.0	1
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	2	2	1.0	100.0	1

Table VI.2. cont.

Element	NISP	MNE	MAU	%MAU	MNI
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	1	1	0.5	50.0	1
TA	4	2	1.0	100.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	2	1	0.5	50.0	1
TRC	0	0	0.0	0.0	0
TRS	1	1	0.5	50.0	1
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	1	1	0.1	6.3	1
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	2	–	–	–	–
INT	2	–	–	–	–
MP	0	–	–	–	–
NMP	1	–	–	–	–
NUPP	0	–	–	–	–
LBS	8	–	–	–	–
US	2	–	–	–	–

Table VI.3. Size Class 4 skeletal element frequencies for TK LF.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	2	2	0.4	40.0	1
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0

Table VI.3. cont.

Element	NISP	MNE	MAU	%MAU	MNI
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	1	1	0.5	50.0	1
HM	0	0	0.0	0.0	0
RD	1	1	0.5	50.0	1
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	50.0	1
PT	0	0	0.0	0.0	0
TA	3	2	1.0	100.0	1
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	1	–	–	–	–
NMP	1	–	–	–	–
NUPP	0	–	–	–	–
LBS	2	–	–	–	–
US	0	–	–	–	–

Table VI.4. Size Class 5/6 skeletal element frequencies for TK LF.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	0	0	0.0	0.0	0
MR	1	1	0.5	100.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	0	0	0.0	0.0	0
RD	0	0	0.0	0.0	0
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	1	1	0.5	100.0	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0

Table VI.4. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	1	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	3	–	–	–	–
US	1	–	–	–	–

Table VI.5. Size Class 3 skeletal element frequencies for TK UF.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	14	5	5.0	100.0	5
MR	8	5	2.5	50.0	5
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	3	3	1.5	30.0	3
RB	1	1	0.0	0.7	1
ST	0	0	0.0	0.0	0
SC	2	1	0.5	10.0	1
HM	3	3	1.5	30.0	3
RD	3	2	1.0	20.0	2
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	4	4	2.0	40.0	3
PT	0	0	0.0	0.0	0

Table VI.5. cont.

Element	NISP	MNE	MAU	%MAU	MNI
TA	4	3	1.5	30.0	2
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	1	1	0.5	10.0	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	1	–	–	–	–
UPP	2	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	12	–	–	–	–
US	0	–	–	–	–

Table VI.6. Size Class 4 skeletal element frequencies for TK UF.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	1	1	1.0	100.0	1
MR	0	0	0.0	0.0	0
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	0	0	0.0	0.0	0
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	4	1	0.5	50.0	1
RB	2	1	0.0	3.6	1
ST	0	0	0.0	0.0	0

Table VI.6. cont.

Element	NISP	MNE	MAU	%MAU	MNI
SC	1	1	0.5	50.0	1
HM	1	1	0.5	50.0	1
RD	3	2	1.0	100.0	2
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	0	0	0.0	0.0	0
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	0	–	–	–	–
UPP	0	–	–	–	–
INT	0	–	–	–	–
MP	0	–	–	–	–
NMP	0	–	–	–	–
NUPP	0	–	–	–	–
LBS	2	–	–	–	–
US	0	–	–	–	–

Table VI.7. Size Class 5/6 skeletal element frequencies for TK UF.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	2	1	1.0	100.0	1
MR	1	1	0.5	50.0	1
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	1	1	0.2	20.0	1
TH	0	0	0.0	0.0	0
LM	1	1	0.2	20.0	1
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	2	2	0.1	7.1	1
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	0	0	0.0	0.0	0
RD	1	1	0.5	50.0	1
UL	0	0	0.0	0.0	0
MC	2	2	1.0	100.0	1
CPR	1	1	0.5	50.0	1
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	50.0	1
PT	0	0	0.0	0.0	0
TA	0	0	0.0	0.0	0
CL	0	0	0.0	0.0	0
AS	1	1	0.5	50.0	1
LTM	0	0	0.0	0.0	0
MT	1	1	0.5	50.0	1
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0

Table VI.7. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	0	-	-	-	-
TFR	2	-	-	-	-
UPP	1	-	-	-	-
INT	0	-	-	-	-
MP	0	-	-	-	-
NMP	0	-	-	-	-
NUPP	0	-	-	-	-
LBS	0	-	-	-	-
US	0	-	-	-	-

**APPENDIX VII**  
**BK SKELETAL PART FREQUENCIES**

Table VII.1. Size Class 1 skeletal element frequencies for BK.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	4	2	2.0	80.0	2
MR	6	2	1.0	40.0	2
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	1	1	0.1	2.9	1
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	4	4	2.0	80.0	3
RB	0	0	0.0	0.0	0
ST	0	0	0.0	0.0	0
SC	0	0	0.0	0.0	0
HM	3	3	1.5	60.0	3
RD	7	5	2.5	100.0	4
UL	0	0	0.0	0.0	0
MC	0	0	0.0	0.0	0
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	1	1	0.5	20.0	1
PT	0	0	0.0	0.0	0
TA	4	3	1.5	60.0	3
CL	0	0	0.0	0.0	0
AS	0	0	0.0	0.0	0
LTM	0	0	0.0	0.0	0
MT	2	2	1.0	40.0	2
TRC	0	0	0.0	0.0	0
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	0	0	0.0	0.0	0

Table VII.1. cont.

Element	NISP	MNE	MAU	%MAU	MNI
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	-	-	-	-
TFR	0	-	-	-	-
UPP	0	-	-	-	-
INT	0	-	-	-	-
MP	1	-	-	-	-
NMP	1	-	-	-	-
NUPP	3	-	-	-	-
LBS	3	-	-	-	-
US	2	-	-	-	-

Table VII.2. Size Class 2 skeletal element frequencies for BK.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	22	6	6.0	57.1	6
MR	26	7	3.5	33.3	7
HY	0	0	0.0	0.0	0
AT	1	1	1.0	9.5	1
AX	1	1	1.0	9.5	1
CE	3	2	0.4	3.8	1
TH	0	0	0.0	0.0	0
LM	6	2	0.4	3.8	2
SAC	2	2	2.0	19.0	2
IM	2	2	1.0	9.5	2
RB	21	4	0.1	1.4	1
ST	0	0	0.0	0.0	0
SC	3	1	0.5	4.8	1
HM	26	18	9.0	85.7	12
RD	11	8	4.0	38.1	5
UL	4	4	2.0	19.0	3
MC	18	8	4.0	38.1	5
CPR	1	1	0.5	4.8	1
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	1	1	0.5	4.8	1
CPF	0	0	0.0	0.0	0

Table VII.2. cont.

Element	NISP	MNE	MAU	%MAU	MNI
CPA	1	1	0.5	4.8	1
MCF	0	0	0.0	0.0	0
FM	36	21	10.5	100.0	13
PT	3	3	1.5	14.3	2
TA	34	15	7.5	71.4	10
CL	6	6	3.0	28.6	3
AS	1	1	0.5	4.8	1
LTM	3	3	1.5	14.3	2
MT	22	10	5.0	47.6	7
TRC	1	1	0.5	4.8	1
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	2	2	0.3	2.4	1
PHS	1	1	0.1	1.2	1
PHT	3	3	0.4	3.6	1
SEP	3	3	0.2	1.8	1
SED	0	0	0.0	0.0	0
VT	2	–	–	–	–
TFR	2	–	–	–	–
UPP	9	–	–	–	–
INT	2	–	–	–	–
MP	2	–	–	–	–
NMP	11	–	–	–	–
NUPP	7	–	–	–	–
LBS	39	–	–	–	–
US	2	–	–	–	–

Table VII.3. Size Class 3 skeletal element frequencies for BK.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	63	13	13.0	74.3	13
MR	84	21	10.5	60.0	20
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	7	7	7.0	40.0	7
CE	9	7	1.4	8.0	2
TH	10	9	0.6	3.7	3
LM	15	11	2.2	12.6	2
SAC	1	1	1.0	5.7	1
IM	21	11	5.5	31.4	7
RB	70	13	0.5	2.7	1
ST	0	0	0.0	0.0	0
SC	20	11	5.5	31.4	6
HM	82	35	17.5	100.0	17
RD	58	28	14.0	80.0	19
UL	12	7	3.5	20.0	4
MC	35	13	6.5	37.1	7
CPR	2	2	1.0	5.7	2
CPI	2	2	1.0	5.7	2
CPU	1	1	0.5	2.9	1
CPS	3	3	1.5	8.6	2
CPF	2	2	1.0	5.7	2
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	61	23	11.5	65.7	14
PT	2	2	1.0	5.7	2
TA	100	34	17.0	97.1	19
CL	4	4	2.0	11.4	4
AS	4	4	2.0	11.4	3
LTM	2	2	1.0	5.7	1
MT	53	13	6.5	37.1	8
TRC	4	4	2.0	11.4	3
TRS	2	2	1.0	5.7	2
TRF	1	1	0.5	2.9	1
MTS	1	1	0.5	2.9	1
PHF	7	6	0.8	4.3	2
PHS	3	3	0.4	2.1	2
PHT	2	2	0.3	1.4	1
SEP	3	3	0.2	1.1	1
SED	19	19	2.4	13.6	2

Table VII.3. cont.

Element	NISP	MNE	MAU	%MAU	MNI
VT	4	–	–	–	–
TFR	9	–	–	–	–
UPP	25	–	–	–	–
INT	20	–	–	–	–
MP	11	–	–	–	–
NMP	35	–	–	–	–
NUPP	21	–	–	–	–
LBS	137	–	–	–	–
US	28	–	–	–	–

Table VII.4. Size Class 4 skeletal element frequencies for BK.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	37	10	10.0	100.0	10
MR	28	8	4.0	40.0	8
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	8	6	1.2	12.0	1
TH	4	3	0.2	2.1	1
LM	1	1	0.2	2.0	1
SAC	1	1	1.0	10.0	1
IM	6	3	1.5	15.0	2
RB	62	9	0.3	3.2	1
ST	0	0	0.0	0.0	0
SC	4	2	0.5	5.0	1
HM	17	8	4.0	40.0	4
RD	22	11	5.5	55.0	7
UL	3	2	1.0	10.0	1
MC	6	4	2.0	20.0	2
CPR	1	1	0.5	5.0	1
CPI	1	1	0.5	5.0	1
CPU	1	1	0.5	5.0	1
CPS	1	1	0.5	5.0	1
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	24	9	4.5	45.0	8
PT	2	2	1.0	10.0	2

Table VII.4. cont.

Element	NISP	MNE	MAU	%MAU	MNI
TA	30	10	5.0	50.0	5
CL	3	3	1.5	15.0	3
AS	6	6	3.0	30.0	4
LTM	2	2	1.0	10.0	2
MT	11	3	1.5	15.0	2
TRC	2	2	1.0	10.0	2
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	3	3	0.4	3.8	1
PHS	1	1	0.1	1.3	1
PHT	1	1	0.1	1.3	1
SEP	2	2	0.1	1.3	1
SED	0	0	0.0	0.0	0
VT	1	—	—	—	—
TFR	0	—	—	—	—
UPP	9	—	—	—	—
INT	4	—	—	—	—
MP	10	—	—	—	—
NMP	4	—	—	—	—
NUPP	3	—	—	—	—
LBS	37	—	—	—	—
US	3	—	—	—	—

Table VII.5. Size Class 5 skeletal element frequencies for BK.

Element	NISP	MNE	MAU	%MAU	MNI
CRN	6	1	1.0	40.0	1
MR	5	2	1.0	40.0	2
HY	0	0	0.0	0.0	0
AT	0	0	0.0	0.0	0
AX	0	0	0.0	0.0	0
CE	0	0	0.0	0.0	0
TH	2	1	0.1	2.9	1
LM	0	0	0.0	0.0	0
SAC	0	0	0.0	0.0	0
IM	0	0	0.0	0.0	0
RB	34	11	0.4	15.7	1
ST	0	0	0.0	0.0	0

Table VII.5. cont.

Element	NISP	MNE	MAU	%MAU	MNI
SC	4	3	1.5	60.0	2
HM	3	2	1.0	40.0	1
RD	6	5	2.5	100.0	4
UL	1	1	0.5	20.0	1
MC	2	2	1.0	40.0	2
CPR	0	0	0.0	0.0	0
CPI	0	0	0.0	0.0	0
CPU	0	0	0.0	0.0	0
CPS	0	0	0.0	0.0	0
CPF	0	0	0.0	0.0	0
CPA	0	0	0.0	0.0	0
MCF	0	0	0.0	0.0	0
FM	3	2	1.0	40.0	2
PT	0	0	0.0	0.0	0
TA	3	2	1.0	40.0	2
CL	0	0	0.0	0.0	0
AS	1	1	0.5	20.0	1
LTM	0	0	0.0	0.0	0
MT	0	0	0.0	0.0	0
TRC	1	1	0.5	20.0	1
TRS	0	0	0.0	0.0	0
TRF	0	0	0.0	0.0	0
MTS	0	0	0.0	0.0	0
PHF	0	0	0.0	0.0	0
PHS	1	1	0.1	5.0	1
PHT	0	0	0.0	0.0	0
SEP	0	0	0.0	0.0	0
SED	0	0	0.0	0.0	0
VT	0	–	–	–	–
TFR	5	–	–	–	–
UPP	0	–	–	–	–
INT	1	–	–	–	–
MP	0	–	–	–	–
NMP	8	–	–	–	–
NUPP	0	–	–	–	–
LBS	25	–	–	–	–
US	29	–	–	–	–

**APPENDIX VIII**  
**SURFACE MARK CATALOG INFORMATION**

Table VIII.1. Surface mark catalog information for the Olduvai sites.

Site/Level	Catnum	Element	Size Class	Mark
DK 1	6	MP	3b	TM
DK 1	22	MT	3	TM
DK 1	31	CRN	US	TM
DK 1	40	MT	3	TM
DK 1	286	HM	3a	TM
DK 1	299	MC	3b	PM
DK 1	666	CE	3	TM
DK 1	4001	LM	3b	TM
DK 1	067/4092	RD	3b	TM
DK 1	067/4218.1	TH	2	TM
DK 1	067/4225.1	SC	3	TM
DK 1	067/4225.3	TA	3	TM
DK 1	067/4225.4	TA	3	TM
DK 1	067/4226.1	MC	3	TM
DK 1	067/4234.1	TA	3	TM
DK 1	067/4234.2	MC	3	TM
DK 1	067/4234.3	MC	3	TM
DK 1	067/4246	MT	3	TM
DK 1	067/4263.1	RD	1	TM
DK 2	10	LM	3b	TM
DK 2	15	RD	3a	TM
DK 2	17	TA	3b	TM
DK 2	19	MC	3	TM
DK 2	19.2	UPP	3a	TM, CM
DK 2	31.2	FM	3a	TM
DK 2	31.4	FM	3a	TM
DK 2	38.3	FM	2	TM
DK 2	43	MT	3	TM
DK 2	43.1	HM	2	TM
DK 2	43.2	RB	3	TM
DK 2	50	RD	2	TM
DK 2	69	RB	3	TM
DK 2	71	MT	3	TM
DK 2	74	LBS	5	TM
DK 2	78	TA	3a	TM
DK 2	79	HM	3a	TM
DK 2	82	RD	3	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
DK 2	86	INT	3	TM
DK 2	90	RD	3a	TM
DK 2	91	MR	3	TM
DK 2	91	CPS	3	TM
DK 2	109	RB	3	TM
DK 2	125	HM	3b	TM
DK 2	129	HM	3a	TM
DK 2	141	HM	3a	TM
DK 2	141	MT	3b	TM
DK 2	143	MC	3a	TM
DK 2	159	MT	3	TM
DK 2	163.2	UL	3b	TM
DK 2	163.3	RB	2	TM
DK 2	163.4	MC	2	TM
DK 2	163.5	TA	3	TM
DK 2	163.6	MT	3	TM
DK 2	163.7	INT	3	TM
DK 2	163.8	INT	3	TM
DK 2	163.9	TA	3a	TM
DK 2	163.11	US	US	TM
DK 2	163.12	UPP	3b	TM
DK 2	163.16	RD	2	TM
DK 2	163.20	INT	3	TM
DK 2	163.21	INT	3	PM
DK 2	163.22	TA	3	TM
DK 2	163.24	FM	3b	TM
DK 2	163.25	FM	3	TM
DK 2	163.39	HM	3	TM
DK 2	163.52	FM	3	TM
DK 2	164	HM	3b	TM
DK 2	166	RD	3b	TM
DK 2	168	HM	3a	TM
DK 2	172	TA	2	TM
DK 2	175	MC	3b	TM
DK 2	175	CL	3	TM
DK 2	175.1	RB	3	TM
DK 2	189	RD	2	TM
DK 2	195	TA	1	TM
DK 2	198	TRS	3	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
DK 2	217	CL	3	TM
DK 2	284	FM	3a	TM
DK 2	289	RD	2	TM
DK 2	290	MT	3	TM
DK 2	295	IM	3b	TM
DK 2	295.1	MR	3	TM
DK 2	299	MT	3	TM
DK 2	299.1	LBS	3b	TM
DK 2	305	AX	3b	TM
DK 2	310	MT	3	TM
DK 2	324	MC	3	TM
DK 2	338	SC	3	TM
DK 2	352	MC	3	TM
DK 2	409	FM	3	TM
DK 2	415	LBS	3	TM
DK 2	419	RD	3a	TM
DK 2	451	MC	3a	TM, CM
DK 2	453	MT	3	TM
DK 2	457	TA	3a	TM
DK 2	471	US	US	TM
DK 2	486	LM	3b	TM
DK 2	575	HM	2	TM, CM
DK 2	576	TA	3	TM, PM
DK 2	577	UL	3b	TM
DK 2	583	UPP	3b	TM
DK 2	612	TA	3b	TM
DK 2	639	MT	1	TM
DK 2	704	MR	3	TM
DK 2	780	TA	2	TM
DK 2	788	RD	3	TM
DK 2	3044.1	CRN	US	TM
DK 2	3051	FM	3b	TM
DK 2	3052	CL	3a	TM
DK 2	3053A	TA	3	TM
DK 2	3072	TA	3	TM
DK 2	3073	MT	3b	TM
DK 2	3079	TA	3a	TM
DK 2	3090	LM	2	TM
DK 2	3474	TH	3a	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
DK 2	4121	IM	3a	TM
DK 2	4137	MT	3a	TM
DK 2	4137.1	FM	3	TM
DK 2	4137.2	FM	3	TM
DK 2	4137.3	RD	3a	TM
DK 2	4137.5	HM	3	TM
DK 2	4137.6	HM	3	TM
DK 2	4137.8	UPP	3	TM
DK 2	4137.9	NUPP	3	TM
DK 2	4137.10	FM	3	TM
DK 2	4137.11	TA	5	CM
DK 2	4137.13	HM	3a	CM
DK 2	4137.14	HM	3a	TM
DK 2	4137.17	HM	3b	TM
DK 2	4137.21	RB	5	TM
DK 2	4141	MC	3a	TM
DK 2	4157	IM	3b	TM
DK 2	4181.1	RB	2	TM
DK 2	4215	FM	3a	TM
DK 2	4216	HM	3	TM
DK 2	4225	TA	3	TM
DK 2	4240	NUPP	3b	TM
DK 2	4270	MT	3b	TM
DK 2	4304	FM	3	TM
DK 2	4451	FM	3b	TM
DK 2	4536	MP	3b	TM
DK 2	5072.1	LM	3	TM
DK 2	5504	LTM	3b	TM
DK 2	5562	PHF	2	TM
DK 2	7934	SED	3	TM
DK 2	067/3093	MC	1	TM
DK 2	067/3427	LM	3	TM
DK 2	067/3465	IM	3b	TM
DK 2	067/3471	PHF	3a	TM
DK 2	067/3493	PHF	2	TM
DK 2	067/4106	MC	1	PM
DK 2	067/4107	CPI	3a	TM
DK 2	067/4109	UL	3	TM
DK 2	067/4127.1	MR	2	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
DK 2	067/4127.2	MR	3a	TM
DK 2	067/4127.4	MR	3	TM
DK 2	067/4135	MR	1	TM
DK 2	067/4140	HM	3a	TM
DK 2	067/4159.2	MT	3	PM
DK 2	067/4159.4	INT	3b	PM
DK 2	067/4159.8	TA	2	TM
DK 2	067/4159.10	IM	3	TM
DK 2	067/4159.17	INT	2	TM
DK 2	067/4191.1	MC	3	TM
DK 2	067/4191.2	MT	2	TM, CM
DK 2	067/4191.3	TA	3b	TM
DK 2	067/4191.79	TA	1	TM
DK 2	067/4193	UL	2	TM, CM
DK 2	067/4197.2	RD	3	TM
DK 2	067/4240.1	SC	3	TM
DK 2	067/4245.1	RD	3	TM
DK 2	067/4245.2	MT	2	TM
DK 2	067/4245.3	MC	3a	TM
DK 2	067/4245.4	MC	3	TM
DK 2	067/4245.5	INT	3	TM
DK 2	067/4245.7	IM	3b	TM
DK 2	067/4245.8	MC	3	TM
DK 2	067/4245.9	RD	2	TM
DK 2	067/4245.10	MT	3	TM
DK 2	067/4245.11	CE	3b	TM
DK 2	067/4245.14	FM	3	TM
DK 2	067/4245.15	RD	2	TM
DK 2	067/4245.17	UPP	3a	TM
DK 2	067/4245.26	LBS	3a	TM
DK 2	067/4245.29	LBS	3	TM
DK 2	067/4245.31	TA	3a	TM
DK 2	067/4260.1	MR	3	TM
DK 2	067/4260.2	SC	3	TM
DK 2	067/4260.4	NUPP	3	TM
DK 2	067/4260.12	RB	5	TM
DK 2	067/4260.19	RB	5	TM
DK 2	067/4260.24	FM	3b	TM
DK 3	131	FM	3a	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
DK 3	132	RB	3b	TM
DK 3	134	RB	3	TM
DK 3	136	IM	3a	TM
DK 3	144	HM	1	TM
DK 3	153	HM	3	TM
DK 3	160	RB	3	TM
DK 3	180	MT	3a	TM
DK 3	183	IM	2	TM
DK 3	188	FM	3a	TM
DK 3	203	UL	4	TM
DK 3	201	FM	3	PM
DK 3	212	TA	3b	TM
DK 3	217	RD	3	TM
DK 3	218	RB	3	TM
DK 3	222	RDU	3	TM
DK 3	223	HM	3	TM
DK 3	226	TA	3	TM
DK 3	227	SC	3a	TM
DK 3	228	MT	1	TM
DK 3	231	CL	3b	TM
DK 3	238	UL	3	TM
DK 3	243	FM	3	TM
DK 3	248	AS	3b	TM
DK 3	257	AT	3a	TM
DK 3	517	MT	3	TM
DK 3	541	CL	4	TM
DK 3	601	MT	3a	TM
DK 3	649	HM	3a	TM
DK 3	690	MC	5	TM
DK 3	777	UL	3a	TM
DK 3	864	RD	3a	TM
DK 3	866	FM	3	TM
DK 3	879	MT	3b	TM
DK 3	962A	MT	3a	TM
DK 3	1673	RB1	3a	TM
DK 3	1708	MC	3	TM
DK 3	3107	TA	3	TM
DK 3	3110	TA	1	TM
DK 3	3111	CL	3a	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
DK 3	3118	IM	3	TM
DK 3	3154	TH	3a	TM
DK 3	3201	SC	3	TM
DK 3	3230	HM	3a	TM
DK 3	3239	RD	3a	TM
DK 3	3284	HM	3a	TM
DK 3	3288.2	IM	3	TM
DK 3	3294	TA	3b	TM
DK 3	3309	IM	5	TM
DK 3	3340	TA	3	TM
DK 3	3343	US	5/6	TM
DK 3	3375	FM	3a	TM
DK 3	3394	MT	3a	TM
DK 3	3396	HM	3	TM
DK 3	4131.1	MR	1	TM
DK 3	4229	LBS	5	TM
DK 3	4277	FM	3b	TM
DK 3	4424	MR	3	TM
DK 3	4565	MR	1	TM
DK 3	5342	TRS	3a	TM
DK 3	067/3070	PHF	3	TM
DK 3	067/3071	MT	3	TM
DK 3	067/3074	MT	3	TM
DK 3	067/3075	MC	2	TM
DK 3	067/3080	MT	3a	TM
DK 3	067/4087	IM	3	TM
DK 3	067/4156	MR	3b	TM
DK 3	067/4176.2	NMP	3	TM
DK 3	067/4176.18	LBS	3	TM
DK 3	067/4176.20	RD	1	TM
DK 3	067/4176.21	US	US	TM
DK 3	067/4176.98	MT	3	TM
DK 3	067/4179	MC	2	CM
DK 3	067/4184	TA	1	TM
DK 3	067/4198.1	MT	3	TM
DK 3	067/4198.2	RD	3a	TM
DK 3	067/4198.4	TA	1	TM
DK 3	067/4198.11	MT	3a	TM
DK 3	067/4198.22	NMP	1	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
DK 3	067/4198.24	NUPP	2	TM
DK 3	067/4210.1	RB	3	TM
DK 3	067/4210.2	HM	3	TM
DK 3	067/4210.3	MP	3	TM
DK 3	067/4210.7	IM	3a	TM
DK 3	067/4210.16	RD	3	TM
DK 3	067/4210.17	MC	1	TM
DK 3	067/4211.1	LM	3	TM
FC West	246	US	US	TM
FC West	272	LBS	2	TM
FC West	319	MT	3a	TM
BK	2	MC	4	CM
BK	5	MP	3a	TM
BK	6	FM	2	PM
BK	11	INT	3b	TM
BK	18	INT	2	TM
BK	30	US	US	CM
BK	34	HY	3	CM
BK	35	US	US	TM, CM
BK	37	UPP	2	PM
BK	39	MT	3a	TM
BK	40	NUPP	2	TM
BK	41	FM	3a	PM
BK	42	NUPP	1	TM
BK	45	LBS	3	TM
BK	48	NMP	2	CM
BK	58	RD	3b	TM
BK	169	MT	2	TM, CM
BK	170	RD	3	PM
BK	171	TA	3b	TM
BK	173	MT	3a	TM
BK	310	RDU	4	TM
BK	315	RDU	3	TM
BK	374	FM	5	TM
BK	377	TA	3b	TM
BK	381	TA	4	TM
BK	382	RD	2	TM
BK	397	HM	2	TM
BK	415	FM	3a	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
BK	439	INT	3	TM
BK	440	HM	4	TM
BK	447	MT	3	TM
BK	454	MT	3a	TM
BK	457	TA	3	TM
BK	490	RD	4	TM
BK	495	HM	3a	TM
BK	528	HM	3	TM
BK	618	RD	3b	CM
BK	624	LM	3a	TM
BK	626	RB	3	CM
BK	633	HM	3b	TM, CM
BK	636	UL	3b	TM
BK	684	TA	2	TM
BK	762	IM	3b	TM, CM
BK	787	SC	3b	TM
BK	934	TA	3b	TM
BK	1270	TH	3a	TM
BK	1276	TA	3	TM
BK	1279	AX	3a	TM
BK	1616	IM	4	CM
BK	1693	SC	3b	SC
BK	1934A	TA	3	TM
BK	2230	HM	5	TM
BK	2248	TH	3b	TM
BK	2378	SAC	4	TM
BK	2484	HM	3b	CM
BK	2716	HM	2	TM, CM, PM
BK	2761	IM	3a	TM
BK	2762	HM	3b	CM
BK	2764	AX	3b	TM
BK	3036	TA	3	TM
BK	3117	TA	3	TM
BK	3140	LM	3a	CM
BK	3146	IM	1	TM
BK	3188	MT	2	TM
BK	3253	HM	1	TM
BK	6969.4	TA	3a	CM
BK	6969.26	NMP	3b	CM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
BK	6969.27	NMP	3	CM
BK	6969.28	TA	3	TM
BK	6969.78	MT	4	TM
BK	6969.112	FM	3	CM, PM
BK	6969.139	TA	4	TM
BK	6969.162	LBS	5	TM
BK	6969.417	US	5	TM
BK	6969.418	RB	3	TM
BK	6969.439	US	US	TM
BK	6969.441	SC	4	TM
BK	6969.442	UL	4	TM
BK	6969.460	MR	4	TM
BK	6969.479	RB	4	TM
BK	6969.489	US	3	TM
BK	6969.508	LBS	3	TM
BK	6969.515	US	US	TM
BK	6969.539	LBS	2	TM
BK	6969.573	US	US	TM
BK	6969.583	RD	3a	TM
BK	6969.587	RB	3	TM
BK	6969.673	US	US	TM
BK	6969.712	US	US	TM
BK	6969.718	HM	3b	TM
BK	6969.737	LBS	2	TM
BK	6969.748	NMP	3b	TM
BK	6969.756	MC	3	TM
BK	6969.759	HM	3	PM
BK	6969.773	MC	2	TM
BK	6969.795	TA	3	TM
BK	6969.807	INT	3	TM
BK	6969.829	FM	3a	TM
BK	6969.846	LBS	2	TM
BK	6969.850	TA	2	PM
BK	6969.854	FM	1	TM
BK	6969.856	NMP	2	TM
BK	6969.858	INT	2	TM
BK	6969.860	NMP	3a	TM
BK	6969.862	INT	5	CM
BK	6969.884	RD	3a	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
BK	6969.911	NUPP	3	CM
BK	6969.916	LBS	3b	TM
BK	6969.920	NMP	3	TM
BK	6969.929	TA	3a	TM
BK	6969.933	RD	3a	TM
BK	6969.934	INT	3b	TM
BK	6969.938	LBS	2	PM
BK	6969.941	TA	3	TM
BK	6969.998	INT	3	TM
BK	6969.1021	MT	3	TM
BK	6969.1027	FM	2	TM
BK	6969.1028	FM	3b	TM
BK	6969.1035	FM	2	CM
BK	6969.1065	FM	3a	TM
BK	6969.1069	HM	3b	PM
BK	6969.1076	HM	1	TM
BK	6969.1086	HM	3b	CM
BK	6969.1089	HM	4	CM
BK	6969.1096	HM	3b	PM
BK	6969.1098	HM	3a	TM, CM
BK	6969.1100	HM	3	TM
BK	6969.1108	HM	3b	TM
BK	6969.1126	HM	3a	CM
BK	6969.1127	HM	2	TM
BK	6969.1130	HM	3a	PM
BK	6969.1137	UL	3b	TM
BK	6969.1139	UL	4	TM
BK	6969.1144	RD	3a	TM
BK	6969.1146	RD	4	TM
BK	6969.1166	RD	3a	TM
BK	6969.1169	RD	4	TM
BK	6969.1170	RD	2	TM
BK	6969.1174	TA	3a	TM
BK	6969.1177	RD	3	TM
BK	6969.1180	RD	2	TM
BK	6969.1188	TA	2	TM
BK	6969.1189	TA	3a	PM
BK	6969.1193	TA	3	TM
BK	6969.1205	TA	3	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
BK	6969.1236	TA	3	PM
BK	6969.1245	TA	2	TM
BK	6969.1247	TA	3b	TM
BK	6969.1254	TA	2	TM
BK	6969.1257	LBS	3a	TM
BK	6969.1264	MC	2	TM
BK	6969.1267	MC	2	PM
BK	6969.1269	MT	3a	PM
BK	6969.1270	MC	3	TM, CM
BK	6969.1277	MP	3b	TM
BK	6969.1281	MP	3	TM
BK	6969.1284	MC	3b	PM
BK	6969.1288	MC	2	PM
BK	6969.1305	MT	3a	CM
BK	6969.1315	MT	3	CM
BK	6969.1317	MT	2	TM
BK	6969.1344	IM	3a	TM
BK	6969.1353	LM	2	TM
BK	6969.1355	LM	3a	TM
BK	6969.1376	CRN	US	TM
BK	6969.1399	MR	3	TM
BK	6969.1402	RB	3	TM
BK	6969.1404	RB	3	TM
BK	6969.1413	RB	3	CM
BK	6969.1433	RB	3	TM
BK	6969.1495	RB	4	CM
BK	067/1052	LM	3a	TM
BK	067/1598	FM	3b	TM
BK	067/1600	RD	3a	TM
BK	067/1609	TA	3b	TM
BK	067/1645	FM	2	TM
BK	067/1700	VT	4	TM
BK	067/1723	FM	3	TM
BK	067/1726	US	US	CM
BK	067/5078B	CE	3b	TM
BK	067/5079	MT	3a	PM
BK	067/5079	MT	3b	TM
BK	067/5079A	MT	3a	CM
BK	067/5080	TA	3b	TM

Table VIII.1. cont.

Site/Level	Catnum	Element	Size Class	Mark
BK	067/5085	FM	2	TM
BK	067/5090	TA	3a	TM
BK	067/5096	UL	3b	TM
BK	067/5102C	RB	3	CM
BK	067/5179	RB	5	TM
BK	068/5864	HM	3b	TM
BK	068/6680	FM	3	CM

Note: Catalog numbers with a suffix (e.g., “.1”) were added by the author because many specimens possessed the same initial catalog number.

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- 2002, 1999: Field technician, Centennial Archaeology, Inc.
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- 1999: Supervised College Teaching, Department of Anthropology, Colorado State University (AP 465: Zooarchaeology)

**PUBLICATIONS**

- Domínguez-Rodrigo, M., Barba, R., **Egeland, C.P.** (in press). Deconstructing Olduvai: A Taphonomic Study of the Bed I sites. New York: Springer.
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