

## Disentangling Early Stone Age palimpsests: determining the functional independence of hominid- and carnivore-derived portions of archaeofaunas

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### **Abstract:**

Determining the extent to which hominid- and carnivore-derived components of fossil bone palimpsests formed independently of each other can provide valuable information to paleoanthropologists interested in reconstructing the foraging adaptations of hominids. Because stone tool cutmarks, hammerstone percussion marks, and carnivore tooth marks are usually only imparted on bone during nutrient extraction from a carcass, these bone surface modifications are particularly amenable to the types of analyses that might meet this goal. This study compares the percentage of limb bone specimens that preserve evidence of both hominid- and carnivore-imparted bone damage from actualistic control samples and several Plio-Pleistocene archaeofaunas, including new data from Swartkrans Member 3 (South Africa). We argue that this procedure, which elucidates the degree of hominid-carnivore independence in assemblage formation, will allow researchers to extract for focused analyses high integrity components (hominid and carnivore) from presumably low integrity sites. Comparisons suggest that the hominid- and carnivore-derived components from sites in Olduvai Gorge Bed II (Tanzania), the ST Site Complex at Peninj (Tanzania), and Swartkrans Member 3 formed largely independent of each other, while data from the FLK 22 *Zinjanthropus* (FLK *Zinj*) site (Olduvai Gorge Bed I) indicate significant interdependence in assemblage formation. This contrast suggests that some Early Stone Age assemblages (e.g., the Olduvai Gorge Bed II sites, the Peninj ST Site Complex, and Swartkrans Member 3) are probably more useful than others (e.g., FLK *Zinj*) for assessing the maximal carcass-acquiring abilities of early hominids; in such assemblages as those in the former set, sole hominid-contribution is more confidently discerned and isolated for analysis than in assemblages such as FLK *Zinj*.

**Keywords:** early hominids; carnivores; bone surface modifications; assemblage resolution; assemblage integrity; Olduvai Gorge; Peninj; Swartkrans Member 3

### **Article:**

#### ***Introduction***

Most researchers now recognize the importance of testing the hypothesis that a number of different biological agents contributed to the formation of fossil bone assemblages. This situation is especially acute for the Early Stone Age (ESA) archaeological record, in which assessing the relative contributions of hominids and carnivores to assemblage formation is critical for inferences about hominid foraging adaptations. In his discussions of the co-occurrence of broken animal bones and stone tools at African Plio-Pleistocene sites, Isaac (1981, 1983) presented the working hypothesis that “[a]t slightly different times both tool-making hominids and carnivores may have frequented the same restricted locality” (Isaac and Crader, 1981: 84). This “common amenity” hypothesis of site formation (Isaac, 1983) predicts that, at least in some circumstances, hominid site formation behavior is temporally unrelated to previous and subsequent episodes of carnivore bone-collecting and modification at the same locale.

The recognition that ESA sites not only represent amalgamations of different processes but that these processes may have operated independently of each other is especially significant in light of proposed sequential models

of hominid/ carnivore carcass acquisition and modification in the Plio-Pleistocene (Selvaggio, 1994a,b, 1998; Capaldo, 1995, 1997, 1998; Blumenschine, 1988, 1995). While these models extensively broaden our understanding of hominid and carnivore behavior and highlight the importance of multi-patterning in the formation of faunal assemblages, their application assumes that ESA-associated faunas are composed entirely of hominid- and carnivore-derived components that are functionally interdependent (see also Dominguez-Rodrigo et al., in press). Indeed, Capaldo (1998: 312; emphasis added) is very explicit about what his dual-patterned experiments are meant to model when he states that “[t]he actualistic methods used in my study were specifically designed to document how hominids and carnivores sequentially modify bones *from the same carcass in the nutritive phase of an assemblage’s taphonomic history*”. Although actualistic and archaeological data substantiate the view that some hominid-carnivore interdependence in assemblage formation is common, if not ubiquitous (see review in Pickering et al., 2003), it seems that complete interdependence of hominid and carnivore roles in assemblage formation must be demonstrated rather than assumed. This is important because Blumenschine (1995: 28, 33-39) and others (e.g., Marean, 1991; Capaldo, 1997: 556-557, 1998: 312-314; Selvaggio, 1998: 194) have correctly stressed the importance of comparability between experimental and archaeological bone assemblages.

We propose in this study to utilize data on bone surface modifications in order to estimate the level of functional independence of the hominid- and carnivore-derived portions from several important Plio-Pleistocene archaeofaunas. Presumably low integrity palimpsest assemblages, where particular instances of carcass utilization are often rendered indistinct because of multi-event overprinting, are particularly amenable to this approach. We argue that assemblages possessing largely independent hominid and carnivore components, although characterized as relatively low integrity palimpsests, can, with the inclusion of other lines of evidence, be divided into two relatively high integrity components (one hominid and one carnivore). Once isolated, the hominid contribution to site formation is more easily characterized. This approach helps to mitigate any “taphonomic overprint” perceived in an assemblage as a whole simply because of the presence of both hominid- and carnivore-imparted bone surface modifications. Although it is not possible in all cases to differentiate individual episodes of carcass procurement and utilization, we believe that merely being able to discriminate the actions of only hominids, only carnivores, or hominids and carnivores would be an important first step for ESA zooarchaeology.

We first present a conceptual and methodological framework for inferring the level of assemblage independence. We then summarize a number of actualistic studies that report observed instances of bone modification in single interdependent sequences (hominid-to-carnivore, carnivore-to-hominid, or carnivore-to-hominid-to-carnivore), which provide expected bone surface modification frequencies in a system of hominid-carnivore resource overlap. These actualistic control samples are then compared with bone surface modification data from several ESA sites in an effort to disentangle the complicated formational processes of a palimpsest.

A conceptual and methodological framework for inferring the level of assemblage independence  
Inferring the functional independence of hominid and carnivore contributions to assemblage formation rests in part on an ability to distill from the zooarchaeological record those portions of a faunal assemblage that resulted from the actions of hominids, the actions of carnivores, and the actions of hominids *and* carnivores. Heuristically, the process of “assemblage formation” can be divided into three components: (1) carcass acquisition; (2) carcass or bone accumulation; and (3) carcass or bone modification. Acquisition involves gaining access to a carcass or carcass parts, regardless of the mode of that access (e.g., early access or late access, hunting or scavenging) or the nutritional condition of the carcass. Accumulation refers to the transport to, and deposition of, carcasses or carcass parts at a particular locale. Modification includes, either singularly or in combination, differential destruction of skeletal elements or element portions and the infliction of damage on bone surfaces—processes that result largely from the extraction of carcass nutrients by biological agents. Given this model of assemblage formation, we define “interdependence” as the utilization by hominids and carnivores of the same carcass *at any stage of assemblage formation*. This definition is flexible in that it allows for different levels of overlap in assemblage formation, from fully independent (no overlap in assemblage formation) to fully interdependent (overlap across all assemblage formation components). For example,

hominid transport of carcass parts scavenged from a felid kill would indicate interdependence in at least the acquisition component of assemblage formation, while the ravaging by carnivores of hominid food refuse would reflect interdependence during the modification component. In addition to conceding that interdependence can be reflected during different stages of assemblage formation, this conceptual framework also recognizes that the potential level of interdependence can vary within stages.

Here we focus on the modification component (recognizing that the modification can occur at any stage in the assemblage formation process) because it is the most easily inferred: bone surface damage unambiguously links both hominids and carnivores to the modification of carcasses (see below). Utilizing the modification component of assemblage formation as a starting point, we propose that it is then possible to “infer up” to the accumulation component, and, more remotely, to the acquisition component of assemblage formation.

Several decades of taphonomic research have introduced a variety of methods for distinguishing the bone-impacting activities of hominids from those of carnivores. In particular, the study of bone surface modifications, including hominid-imparted cutmarks and percussion marks and carnivore tooth marks, has proven to be the most useful method for discerning hominid and carnivore involvement in fossil bone assemblages. Our concentration here on these classes of taphonomic data expands on the framework already constructed by others for differentiating the contribution of hominids and carnivores to the modification of archaeological faunas. Several of these previous studies concentrated on the occurrence and anatomical location of bone surface modifications at the intra-skeletal and intra-bone levels to determine the timing and sequence of carcass access by hominids and carnivores (e.g., Bunn, 1982, 1983, 2001; Shipman, 1983, 1986; Bunn and Kroll, 1986, 1988; Marshall, 1986; Binford, 1988; Blumenshine, 1988, 1995; Selvaggio, 1994a,b, 1998; Capaldo, 1995, 1997, 1998; Dominguez-Rodrigo, 1997, 1999b; Lupo and O’Connell, 2002).

We utilize these bone damage data differently in an effort to understand the extent to which hominid- and carnivore-derived components of fossil bone assemblages are functionally independent. Building on previous arguments by Marean and colleagues (Marean and Kim, 1998; Marean et al., 2000) for Middle Paleolithic and Middle Stone Age (MP/MSA) archaeofaunas, we argue that the frequency of limb bone<sup>1</sup> specimens that preserve evidence of *both* hominid (cutmarks, percussion marks) *and* carnivore (tooth marks) involvement can serve as an estimate of hominid-carnivore overlap in assemblage modification. We assert that this is so because hominid butchery damage and carnivore tooth marks are usually only imparted during nutrient extraction from a carcass: a foraging hominid or carnivore is unlikely to modify a bone devoid of nutrients (exceptions include “boredom chewing” documented by Binford and Bertram [1977; see also Binford, 1981] in dog yards and wolf dens). A lack of co-occurring hominid and carnivore damage on bone specimens thus suggests a temporal gap or intensity of processing great enough to deter potential biological agents from further bone transport and/or modification. We choose at this point to focus on limb bone fragments for two reasons. First, and most importantly, limb bone shaft fragments have been shown to better survive density-mediated destructive processes, especially carnivore ravaging (e.g., Todd and Rapson, 1988; Marean and Spencer, 1991; Marean et al., 1992, 2004; Marean and Cleghorn, 2003; Pickering et al., 2003; Marean and Cleghorn, 2004). Second, current actualistic controls that model two- or three-stage sequences of hominid and carnivore involvement with bone assemblages concentrate largely on these skeletal elements (e.g., Blumenshine, 1988, 1995; Marean and Spencer, 1991; Marean et al., 1992; Blumenshine and Marean, 1993; Marean and Bertino, 1994; Selvaggio, 1994a,b, 1998; Capaldo, 1995, 1997, 1998; Dominguez-Rodrigo, 1997, 1999a,b).

### **Materials and methods Actualistic controls**

There are three actualistic studies that provide data on limb bone specimens > 2 cm that preserve both human butchery damage and carnivore tooth marks. Selvaggio (1994a, 1998) conducted several experiments with Size Class 1-4 carcasses, comprising 751 identified limb bone specimens (NISP) (for descriptions of animal Size Classes, see Brain, 1974, 1981; Bunn, 1982). Her experiments simulate two sequences of hominid and carnivore involvement: carnivore-to-hominid (NISP = 549) and carnivore-to-hominid-to-carnivore (NISP = 202). In the first sequence, limb bones were defleshed initially by various types of carnivores (lions, leopards, cheetahs, spotted hyenas, jackals), followed by human removal of flesh scraps using metal knives and marrow by

cracking open bones with hammerstones. In the second sequence, carnivores first defleshed the bones, which were then processed thoroughly by humans for all remaining flesh and marrow, followed by a final bout of ravaging by scavengers.

Capaldo (1997, 1998) conducted 69 total experiments with Size Class 1-3 carcasses, constituting a total limb bone NISP of 1910. Two different scenarios of hominid-to-carnivore involvement were modeled. First, whole-bone-to-carnivore limb bone experiments (NISP = 212) exposed humanly defleshed but unbroken, marrow-filled limb bones to carnivore ravaging. Second, in his hammerstone-to-carnivore experiments (NISP = 1698), limb bones were defleshed and demarrowed (i.e., broken open) by humans and then subjected to carnivore ravaging.

Selvaggio (1994a, 1998) and Capaldo (1997, 1998) presented the mean percentage and 95% confidence intervals (CI) of specimens across all experiments that preserved butchery damage and tooth marks.

Controlled hyena feeding experiments reported by Marean and colleagues (Marean and Spencer, 1991; Marean et al., 1992; Blumenschine and Marean, 1993; Marean and Bertino, 1994) also provide a useful actualistic reference for hominid-carnivore overlap. In these studies a total of 96 Size Class 1 and 2 sheep limb bones (femur, tibia, metatarsal) (n = 21 experiments) were stripped of flesh and cracked for marrow prior to ravaging. These hammerstone-to-carnivore experiments consist of a total limb bone NISP of 701 (Marean, personal communication). Surface mark data were presented as the percentage of this total that preserve co-occurring damage. Surface mark frequencies for this experimental sample were based only on those specimens bearing marks diagnosed as “high confidence” attributions and are therefore conservative. Marean et al. (2000: 214) argued persuasively that “high confidence” attributions are the most useful for comparative purposes considering that diagenetic processes that compromise cortical surface preservation will decrease the number of confidently identified surface marks in archaeological contexts. Table 1 summarizes the total NISP values for the actualistic controls.

It is important to note that the experimental protocol utilized in each of these actualistic studies dictates to some extent the level of assemblage interdependence, which is itself contingent on the type of consumer, the carcass parts available, and the intensity with which each of these parts is processed. For example, situations in which carnivores (especially hyenas) have access to marrow from limbs defleshed by humans will result in a higher percentage of specimens displaying both cutmarks and tooth marks. By extension, carnivore ravaging of limbs already cracked for marrow will result in a lower level of interdependence, as reflected by co-occurring damage, especially on midshaft portions. Therefore, these experimental samples provide expected bone modification frequencies across several levels of interdependence in assemblage modification.

### **Archaeological samples**

There is one assemblage from Olduvai Gorge (Tanzania) Bed I and three from Bed II for which pertinent data on bone surface modifications are published. The Bed I assemblage, from FLK 22 *Zinjanthropus* (FLK *Zinj*), is ca. 1.75 million years (myr) old and consists of a total limb bone NISP of 731. This sample includes only limb bone specimens from Size Classes 1-4 that are > 2 cm in maximum dimension, and with good surface preservation and non-recent breaks (Blumenschine, 1995; Capaldo, 1997). Blumenschine (1995: 28) noted that the removal of specimens with recent breakage “maximizes the chances that fragmentation and the attendant incidence of tooth-marked and percussion-marked fragments are attributable to hammerstone or carnivore agencies” but “does not control for the subaerial, pre-fossilization fragmentation resulting from post-consumptive processes such as trampling.” Therefore, surface mark percentages from FLK *Zinj* may be slightly depressed relative to the actualistic samples.

Monahan’s (1996) comprehensive zooarchaeological study of Bed II faunas from the sites of BK, MNK Main, and HWK East Levels 1-2, all dated between 1.2-1.7 Ma, provides detailed data on non-recent or non-geologically-broken limb bone specimens >2 cm in maximum dimension from Size Classes 1-4. (Monahan [personal communication] has confirmed that all specimens utilized in this sample are green broken and are

therefore maximally comparable to the experimental assemblages.) The relevant NISP values are: BK = 1010, MNK Main = 514, and HWK East Levels 1-2 = 218. However, Monahan (1996) also attempted to avoid the biasing effects of poor bone surface preservation by adjusting surface mark percentages based on the percentage of skeletally identifiable specimens with >50% of “unreadable” cortical surface.<sup>2</sup> Monahan’s (1996: 106, Figure 2) estimated percentages of skeletally identifiable but “unreadable” specimens for each site are: BK = 37%, MNK Main = 39%, and HWK East Levels 1-2 = 48%. Thus, we multiplied the limb bone NISP for each assemblage by Monahan’s cortical surface adjustment values and then subtracted this value from the previous NISP to arrive at the following, final values: BK = 636, MNK Main = 313, HWK East Levels 1-2 = 113.

Table 1  
Summary of limb bone number of identified specimens (NISP) and bone surface modification percentages for actualistic samples<sup>1,2</sup>

	NISP	TM+CM		TM+PM		TM+CM and/or PM		
		Mean	95% CI	Mean	95% CI	Mean	95% CI	
<b>Selvaggio</b>								
Size Class 1-4								
C-H	549	—	—	—	—	42.4	33.1-52.0	
C-H-C	202	—	—	—	—	30.0	18.0-42.1	
<b>Capaldo</b>								
Size Class 1-3								
WB-C	212	14.0	5.5-22.5	—	—	—	—	
HS-C	1698	4.8	3.5-6.1	4.9	—	—	—	
Size Class 1-2								
WB-C	—	5.8	1.5-10.1	—	—	—	—	
HS-C	—	4.1	2.5-5.7	—	—	—	—	
Size Class 3								
WB-C	—	36.8	14.7-58.9	—	—	—	—	
HS-C	—	6.4	4.3-8.5	—	—	—	—	
<b>Marean</b>								
Size Class 1-2								
HS-C	701	—	—	5.7	—	—	—	

<sup>1</sup> Abbreviations: TM = tooth marks; CM = cutmarks; PM = percussion marks; CI = confidence interval; C-H = carnivore-to-hominid; C-H-C = carnivore-to-hominid-to-carnivore; WB-C = whole bone-to-carnivore; HS-C = hammerstone-to-carnivore.

<sup>2</sup> Data sources: Selvaggio (1994a,b, 1998); Capaldo (1997, 1998); Marean (personal communication); Marean et al. (2000).

The ST Site Complex at Peninj (Tanzania) is ca. 1.5 myr old and consists of a total limb bone NISP of 154 (Domínguez-Rodrigo et al., 2002). Only specimens > 2 cm in maximum dimension from Size Classes 1-6 that display nutritive phase breakage (using criteria from Villa and Mathieu, 1991, and Alcalá, 1994) and exhibit a subaerial weathering stage (Behrensmeier, 1978) of “0” were considered.

As part of a taphonomic and zooarchaeological reassessment of the ca. 1.0 myr old faunal assemblage from Swartkrans Member 3 (South Africa), a systematic search for bone surface modifications on limb bone shaft specimens was conducted (Pickering et al., 2004, in press a,b,c). Identification of bone surface modifications was undertaken using established criteria (see Blumenschine et al., 1996). Each specimen was inspected under a strong oblique light source with the aid of at least 10x magnification, as recommended by several analysts (e.g., Bunn, 1981, 1991; Bunn and Kroll, 1986; Blumenschine and Selvaggio, 1988, 1991; Blumenschine and Marean, 1993; Blumenschine, 1995; Blumenschine et al., 1996). We extracted for in-depth analysis 1466 specimens from the ~12,500 piece limb bone shaft sub-assemblage. This subsample includes specimens ≥ 5 cm in maximum dimension and those specimens < 5 cm with observed prehistoric bone surface modifications. In order to increase comparability with actualistic controls, only specimens within the subsample from Size Class 1-4 that are >2 cm in maximum dimension, and that display green breakage (defined as a smooth release surface and a measured fracture angle of <85° or >95° [see Villa and Mathieu, 1991; Pickering et al., in press a]) and good surface preservation were considered in this study. This results in a limb bone NISP of 519 (Size Class 1-2 NISP = 323; Size Class 3-4 NISP = 196). Because limb bone shaft specimens <5 cm that do not preserve prehistoric bone surface modifications were not considered, the surface mark percentages presented in this study are slightly inflated relative to the actualistic controls. A sampling procedure to be presented elsewhere (Pickering et al., in press c) will assess the impact of diagenetic breakage and poor surface preservation on the

~11,000 specimens not considered in this study. Table 2 summarizes the total NISP values for the archaeological samples.

Once the archaeological samples were adjusted for maximal comparability with actualistic controls, the percentage of limb bone specimens preserving co-occurring hominid and carnivore damage from these Plio-Pleistocene faunas were compared to modern samples with known levels of hominid-carnivore interdependence in assemblage modification.

Table 2

Summary of limb bone number of identified specimens (NISP) and bone surface modification percentages for archaeological samples<sup>1,2</sup>

	NISP	TM + CM		TM + PM		TM + CM and/or PM	
		n	%	n	%	n	%
<b>FLK <i>Zinj</i> (Olduvai Bed I)</b>							
Size Class 1-4	731	102	14.0	125	17.1	184	25.2
Size Class 1-2	213	31	14.6	—	—	—	—
Size Class 3-4	518	71	13.7	—	—	—	—
<b>ST Site Complex (Peninj)</b>							
Size Class 1-6	154	2	1.3	2	1.3	4	2.6
<b>BK (Olduvai Bed II)</b>							
Size Class 1-4	636	1	0.2	1	0.2	2	0.3
<b>MNK Main (Olduvai Bed II)</b>							
Size Class 1-4	313	1	0.3	0	0.0	1	0.3
<b>HWK East Levels 1-2 (Olduvai Bed II)</b>							
Size Class 1-4	113	2	0.6	1	0.3	3	1.0
<b>Swartkrans Member 3</b>							
Size Class 1-4	519	9	1.7	3	0.6	12	2.3
Size Class 1-2	323	5	1.5	0	0.0	5	1.6
Size Class 3-4	196	4	2.0	3	1.5	7	3.6

<sup>1</sup> See legend to Table 1 for abbreviations.

<sup>2</sup> Data sources: FLK *Zinj*, (Blumenschine, 1995; Capaldo, 1997); ST Site Complex (this study; Domínguez-Rodrigo et al., 2002); BK, MNK Main and HWK East Levels 1-2, (Monahan, 1996); Swartkrans Member 3 (this study; Pickering et al., in press c).

## Results

Tables 1 and 2 provide, respectively, bone surface mark percentages for the actualistic and archaeological datasets. Values are presented as the percentage of NISP displaying: (1) at least one tooth mark and at least one cutmark; (2) at least one tooth mark and at least one percussion mark; or (3) at least one tooth mark and at least one cutmark and/or percussion mark.

The percentage of specimens from Olduvai Bed II, Peninj, and Swartkrans Member 3 that preserve at least one tooth mark and any evidence of hominid butchery fall below those expected if their hominid- and carnivore-derived components were modified under a high degree of interdependence. The same conclusion applies to these sites in terms of the percentage of specimens bearing at least one tooth mark and one cutmark and at least one tooth mark and one percussion mark. In contrast, the FLK *Zinj* sample exhibits percentages either within the range (for tooth-marked and cutmarked specimens) or well above the mean (for tooth-marked and percussion-marked specimens) of Capaldo's experimental sample and above the percentage of tooth-marked and percussion-marked specimens in Marean's hammerstone-to-carnivore sample.

The way in which Capaldo's experimental sample is stratified by carcass body size also allows us to examine tooth-marked and cutmarked specimen percentages for small (Size Class 1-2) and large (Size Class 3-4) carcasses. For small carcasses, the Swartkrans Member 3 sample falls at the lower end of the range of Capaldo's whole-bone-to-carnivore tooth-marked and cutmarked sample and below his hammerstone-to-carnivore tooth-marked and cutmarked sample. The FLK *Zinj* small carcass sample is situated above the 95% CI of both of the experimental sequences. The Swartkrans Member 3 tooth-marked and cutmarked large carcass sample falls below the 95% CI of both of Capaldo's experimental sequences, while the large carcass sample from FLK *Zinj*

appears above the upper range of Capaldo's hammerstone-to-carnivore experiments and below the lower range of his whole-bone-to-carnivore experiments.

These data suggest that while all of the archaeological samples represent hominid-carnivore palimpsests, the Olduvai Bed II, Peninj, and Swartkrans Member 3 samples have significantly independent hominid and carnivore components. This is in striking contrast to the FLK Zinj fauna, which more closely matches the experimental samples modeling high levels of interdependence in hominid and carnivore bone modification.

## Discussion

The bone surface modification data clearly indicate that the ESA archaeofaunas examined here were created by both hominids and large carnivores. However, there appear to be substantial differences between the assemblages in the degree to which the interdependent actions of these agents are indicated. The new data from Swartkrans Member 3 are particularly intriguing in this context. There is a common perception in paleoanthropology that South African cave sites are more informative about how early hominids died than how they lived. In particular, the difficulty associated with disentangling the complex set of non-hominid "taphonomic overprints" in the Sterkfontein Valley sites is well-documented (e.g., Brain, 1981; Pickering, 1999) and helps color this perception.

The Swartkrans Member 3 assemblage illustrates the point: within the subsample of the fauna selected for in-depth analysis, 36.3% of the specimens examined exhibit carnivore damage while only 11.1 % display hominid-imparted modifications (Pickering et al., in press c). Given these percentages, one might argue, correctly we believe, that carnivores were the more active agent in assemblage formation during Member 3 times (see also Pickering et al., 2004, in press a). However, it is likely that the predominant carnivore contribution was not at the expense of the hominid contribution, which appears to have formed largely independent of the carnivore component. This assertion is strengthened by incorporating data from limb bone fracture patterns. If carnivores modified carcass parts subsequent to hominid processing, some of those specimens should exhibit fracture surfaces that have angles within the range created by hammerstone percussion. In fact, tooth-marked limb bone specimens from the Member 3 subassemblage exhibit fracture angles that are indistinguishable from those created in experimental assemblages in which carnivore chewing (static loading) was the sole mode of fracture (Pickering et al., in press a). Together, these data suggest that the application of sequential models of carnivore-hominid bone modification to the Member 3 fauna may not be informative about the timing of hominid access to carcasses at Swartkrans. The Swartkrans Member 3 fauna thus promises to be an extremely useful datum for understanding hominid carcass foraging in a relatively "uncomplicated" taphonomic context (i.e., considered separately from the carnivore-modified component). We suspect that, given the frequencies of hominid-imparted surface modifications from the limb bone subassemblage, continued work on the remainder of the assemblage will result in the identification of even more cutmarks and percussion marks on specimens from other body regions.

Surface mark data on limb bones also suggest independently derived hominid and carnivore components for all of the Olduvai Bed II sites considered here. Monahan's (1996) independent and expanded analysis of the Bed II zooarchaeology supports this conclusion, with BK and MNK Main inferred to be primarily hominid accumulations. Furthermore, the low frequency of hominid-imparted damage co-occurring with carnivore tooth damage on specimens from the HWK East Levels 1-2 fauna support Monahan's (1996) earlier assertion that this site represents a carnivore assemblage accumulated in a relatively low competition setting. These data indicate that the HWK East Levels 1-2 fauna is almost entirely the result of carnivore activity and thus of relatively high biotic integrity. Similarly, the data from the ST Site Complex at Peninj indicate that the hominid and carnivore components of these "mini-sites" distributed across a paleolandscape formed largely independently. Dominguez-Rodrigo et al.'s (2002) zooarchaeological data support this argument, as most of the densest faunal accumulations are interpreted to have formed through hominid behavior despite the documented evidence for a high degree of carnivore activity across the paleolandscape as a whole. Similar arguments for hominid-carnivore independence have also been made for important MP/MSA cave assemblages (Marean and Kim, 1998; Marean et al., 2000).

In contrast, data from FLK *Zinj* suggest a significantly different type of assemblage. The high co-occurrence on the same specimens of hominid and carnivore damage strongly suggests that the faunal assemblage formed under a high degree of interdependence, with hominids and carnivores not only utilizing the same space, but in many cases the same carcasses. This evidence for interdependence indicates that sequential models of hominid/carnivore site formation are potentially most applicable to this site. We therefore argue that experiments modeling the sequential actions of hominids and carnivore are most productively applied only to archaeofaunas with strong interdependent formational signatures (i.e., FLK *Zinj*). Blumenschine (1995: 44) in particular has recognized this point, stressing that his sequential experiments are ideally applied only to assemblages that they are explicitly meant to model.

### **Modeling hominid-carnivore interactions during the Plio-Pleistocene**

The data presented in this study have important implications for diagnosing the extent and context of hominid-carnivore interactions in the Plio-Pleistocene, and we strongly agree with the view that “bones [including surface modifications] are barometers of the level of competition between consumers of carcass tissues” (Blumenschine et al., 1994: 201). In discussing hominid-carnivore interactions, we have relied largely on the framework and predictions offered by Blumenschine et al. (1994). By suggesting a high level of hominid-carnivore independence in assemblage formation for the Olduvai Bed II sites, the ST Site Complex at Peninj, and Swartkrans Member 3, we do not imply that hominid-carnivore interaction and competition was unimportant at these sites. Data on bone surface damage unambiguously link both hominids and carnivores to the exploitation of animal carcasses at these sites, and thus, by definition, indicate at least exploitative competition at some level (that is, use of a carcass by hominids reducing the availability of that resource to carnivores, and vice versa). In addition, it also seems likely that (at least occasionally) hominids and/or carnivores directly and aggressively denied carcass access to the other through interference competition (see, for example, Bunn and Ezzo, 1993; Bunn, 1996, 2001).

We offer here a few alternative explanations for the low frequency of specimens that exhibit both hominid and carnivore damage in some of the faunal assemblages examined in this study. Supplemental data presented on many of the assemblages discussed here strongly suggest that hominids acquired carcass parts before carnivores had a chance to modify the same bone specimens (see reviews in Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering and Domínguez-Rodrigo, in press), even though carnivore modification is much more abundant in each of the assemblages as a whole. For example, the mere presence in many of the assemblages of cutmarks on the midshaft portion of limb bones, a region that is commonly defleshed completely by feeding felids (especially for upper limb elements [i.e., humerus and femur; Domínguez-Rodrigo, 1999a]), is evidence for a significant amount of meat when the bones were butchered by hominids (Bunn, 1982; Bunn and Kroll, 1986; Domínguez-Rodrigo, 1999b, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering et al., in press b,c; Pickering and Domínguez-Rodrigo, in press).

The data further suggest that hominids, after meat and/or marrow processing, discarded bone refuse under at least two (potentially) overlapping contexts. First, hominids may have processed the bones intensely and/or completely, leaving little or no nutritious tissue to interest potential scavengers. Complete processing suggests that hominids were not under significant time constraints imposed by intense competition or predator avoidance. Whether this processing occurred during routed foraging (Binford, 1981) within relatively low competition settings, or with skeletal element transport and “refuge” (Blumenschine, 1991), or “central place” (Isaac, 1983), foraging to avoid relatively high competition settings is currently difficult to ascertain. Second, variably processed bone refuse may have been discarded in contexts in which scavenging carnivores did not discover the carcass parts before the decomposition of their nutritious components. For example, in areas of low competition and where visual cues to carcass location (e.g., circling vultures) are rare, carcasses can persist for up to seven days subsequent to abandonment by lions and, once discovered, are usually only visited by a small number of individual scavengers (Domínguez-Rodrigo, 2001; see also Blumenschine, 1986, 1987). Blumenschine (1988: 497) also reported that in some experimental cases limb bones broken by hammerstones and then discarded in riverine woodland (a habitat of relatively low competition) remained undisturbed by scavengers even after 16 days. In addition, landscape taphonomic studies indicate that complete limb bones,



signifying untapped within-bone nutrients, are encountered at higher frequencies in areas of low competition (Blumenschine, 1989; Domínguez-Rodrigo, 1996). In reference to the Swartkrans Member 3 assemblage, whether the independently derived hominid component resulted from a routed or refuge/ central place foraging strategy is difficult to determine because of the depositional nature of the Member 3 sediments. As in most South African cave deposits, the Member 3 accumulation consists primarily of secondarily deposited material derived from the cave's surface catchment. Thus, it is difficult to determine the paleoecological context of the hominid-derived component to the extent necessary to test these hypotheses rigorously.

The data on the Olduvai Bed II sites provide strong support for Monahan's (1996: 118) assertion that Olduvai hominids at that time were "able to minimize predation risk and to control carcasses until processing and consumption were accomplished." However, in order to discern whether this processing occurred under high or low competition settings, the carnivore-derived components of the BK and MNK Main assemblages must be examined in isolation for evidence of competition (e.g., epiphysis:shaft ratios, number of identified specimens:minimum number of elements ratios, epiphysis plus shaft length, epiphyseal completeness). Inference of a high competition setting would suggest that hominids actively defended carcass resources, while a reconstruction of a low competition setting might indicate that BK and MNK Main represent assemblages of carcass parts transported away from sites of acquisition, presumably to minimize competition and risk of predation.

The exposed paleolandscape of the ST Site Complex at Peninj offers a unique glimpse into hominid land-use and hominid-carnivore interactions. The landscape taphonomy of the ST Site Complex indicates that carnivore competition was relatively low near the most substantial archaeological localities, suggesting a fairly closed environment, while the area surrounding the ST Site Complex exhibits features indicating a high degree of competition characteristic of more open habitats (Domínguez-Rodrigo et al., 2001, 2002). Hominids appear to have visited the less competitive ST Site Complex area repeatedly, either by planned foraging near the intersecting river channels, or by transporting carcasses short distances from nearby open habitats.

Although FLK *Zinj* has been characterized quite variably, from a "central place" to a "near-kill location" (Binford, 1981, 1985; Bunn, 1982, 1986; Potts, 1988; Blumenschine, 1991; Bunn and Ezzo, 1993; Blumenschine et al., 1994; Rose and Marshall, 1996; O'Connell, 1997), most researchers agree that it represents an area to which hominids transported stones and carcass parts. The high frequency of specimens with both hominid and carnivore damage indicates significant resource overlap and the likelihood that neither carnivores nor hominids processed carcasses completely. Therefore, the site signifies either transport by hominids of incompletely processed carcass parts after carnivore feeding, or the ravaging by carnivores of bone refuse incompletely processed by hominids. The debate surrounding this issue is both voluminous and contentious (e.g., Binford, 1981; Bunn, 1982; Bunn and Kroll, 1986, 1988; Blumenschine, 1988, 1995; Bunn and Ezzo, 1993; Oliver, 1994; Selvaggio, 1998; Capaldo, 1997, 1998; Domínguez-Rodrigo, 1997, 1999a,b; Lupo and O'Connell, 2002). However, no proponent on either side has yet convincingly addressed why early hominids or carnivores should abandon, unprocessed, such substantial amounts of acquired carcasses.

Much of the uncertainty associated with interpretations of the FLK *Zinj* fauna emanates from the interdependent nature of its formation. We stress that this by no means renders the site useless for interpretations of early hominid foraging behavior. In fact, Marean (personal communication) has suggested that spatial analysis of the FLK *Zinj* fauna may help isolate hominid-only activity areas, as scavengers only minimally disturb the spatial integrity of hammerstone-percussed midshaft fragments (Marean and Bertino, 1994). Moreover, the uniquely interdependent nature of FLK *Zinj* makes it an invaluable datum for investigating a number of important aspects of early hominid carcass foraging that cannot be examined using assemblages characterized by largely independently derived hominid and carnivore components. We do suggest, however, that other penecontemporaneous sites with demonstrated independence of hominid and carnivore bone contributions might inform paleoanthropologists more clearly about the maximal carcass acquiring capabilities of ESA hominids. Based on the data presented here, we suggest that some of the Olduvai Bed II assemblages, the ST Site Complex, and Swartkrans Member 3 meet the requirement of demonstrated independence in their hominid-

and carnivore-derived components. Isolation of a hominid-only contribution would effectively mitigate any “taphonomic overprint” perceived in an assemblage simply because of the existence of hominid butchery damage and carnivore tooth marks. Researchers would then be in the enviable position of relying solely on direct evidence of hominid butchery (cutmarks and percussion marks) to infer the behavior of early hominids (e.g., Domínguez-Rodrigo, 1997, 1999a,b, 2002; Domínguez-Rodrigo and Pickering, 2003; Pickering et al., in press a,b,c; Domínguez-Rodrigo et al., in press; Pickering and Domínguez-Rodrigo, in press). We believe that this approach is more reliable than inferences of hominid behavior based on indirect evidence of carnivore tooth mark frequencies and distribution.

### **Conclusions and future directions**

Because cutmarks, percussion marks, and tooth marks unambiguously link hominids and carnivores to the modification of carcasses, we argue that the frequency of specimens exhibiting co-occurring damage is a meaningful estimate of the level of interdependence in assemblage formation. Actualistic assemblages of known derivation that model the sequential actions of hominids and carnivores provide a range of expectations for various levels of interdependence in assemblage modification. These data thus provide a useful framework in which fossil assemblages of unknown derivation can be compared. The results of this study indicate that the Olduvai Bed II sites, the ST Site Complex at Peninj, and Swartkrans Member 3 exhibit strong independent signatures, while the fauna from FLK *Zinj* appears to have formed under a high degree of interdependence.

The potential level of interdependence in assemblage formation is determined by a number of variables, and the procedure presented here cannot alone fully account for them all. There are three issues in particular that require further research and elaboration. First, the types of consumers and the different carcass resources targeted by them will impact the number of specimens displaying co-occurring damage. For example, the sequential actions of felid defleshing (an activity known to leave low frequencies of tooth marks on limb bones, especially midshaft portions [Domínguez-Rodrigo, 1999a; Domínguez-Rodrigo et al., in press]) and hominid marrow extraction will lower the chances of midshaft specimens preserving co-occurring damage (in this case tooth marks and percussion marks), which may in turn artificially reduce the perceived level of assemblage interdependence. Inferring the identity of carcass consumers from tooth mark dimensions (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Pickering et al., 2004) is an important alternative line of evidence that can provide expectations concerning the pattern of assemblage interdependence.

Second, our focus here on limb bone specimens (and midshafts in particular), although advantageous from a taphonomic perspective, should be expanded to other bone portions and body parts. The realization that the destruction of limb bone epiphyses by bone-crunching carnivores (or any other density-mediated destructive process) may partially obliterate previous overlap signatures is an example that highlights the importance of this issue. Inferring the intensity of carnivore ravaging in archaeofaunas may help diagnose the impact of these processes on overlap signatures.

Third, although the procedure outlined here provides an estimate of formational independence in an assemblage as a whole, inferring *which* component (hominid or carnivore) exhibits a higher level of independence is less clear. We believe a simple extension of the method presented here may illuminate this issue. Specifically, examining the number of hominid-modified specimens preserving tooth marks will provide an estimate of the level of independence in the hominid component, while examining the number of tooth-marked specimens preserving hominid damage will provide an estimate of the level of independence in the carnivore component. Although addressing this issue in depth is beyond the scope of this paper, there is at least one Stone Age assemblage (Kobeh Cave, Iran) for which the data required to investigate this question are available (Marean and Kim, 1998). Partitioning palimpsests into their constituent biotic components is an important yet complex methodological issue in zooarchaeology. Clearly, further exploration of the issues raised in this study and the incorporation of alternative lines of taphonomic data are required to fully elucidate patterns of assemblage independence. However, the conceptual and methodological framework presented here should provide a productive starting point for examining this problem.

## Notes:

<sup>1</sup> Although technically foot bones, we group the metapodials with actual limb bones because they are anatomically and functionally similar to limbs in most ungulates. Therefore, as defined here, limb bones include the ungulate humerus, radioulna, metacarpal, femur, tibia, and metatarsal. We also prefer this term to the more vague term “long bone,” which, in many systems, includes elements, such as proximal phalanges, not pertinent to our discussions (see also Pickering et al., 2003).

<sup>2</sup> Monahan’s adjustment values are not ideal for comparisons with actualistic controls for several reasons. Most importantly, because surface modifications usually appear in isolated or very restricted areas of bone specimens, it is impossible to tell how many specimens with 25, 50, or 75 percent of “unreadable” cortical surface actually did at one time possess a mark on currently “unreadable” areas. Therefore, this approach assumes that the percentage of cortical area that is “readable” is representative of the assemblage as a whole, which may not be the case. Ideally, in order to realistically compare the Bed II bone modification data with those of the actualistic controls, one would need to calculate surface mark percentages based only on that portion of the assemblage that displays relatively pristine cortical surfaces (i.e., those specimens with no, or very little, “unreadable” cortical surface). As these data are not available for the Bed II assemblages, we use the published adjustment values and note their shortcomings.

## References

- Alcalá, L., 1994. *Macromamíferos Neógenos de la Fosa de Alfambra-Teruel*. Museo Nacional de Ciencias Naturales, Madrid.
- Behrensmeier, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150-164.
- Binford, L.R., 1981. *Bones: Ancient Men and Modern Myths*. Academic Press, New York.
- Binford, L.R., 1985. Human ancestors: changing views of their behavior. *J. Anthropol. Archaeol.* 4, 292-327.
- Binford, L.R., 1988. Fact and fiction about the Zinjanthropus floor: data, arguments, and interpretations. *Curr. Anthropol.* 29, 123-149.
- Binford, L.R., Bertram, J.B., 1977. Bone frequencies - and attritional processes. In: Binford, L.R. (Ed.), *For Theory Building in Archaeology*. Academic Press, New York, pp. 77-153.
- Blumenschine, R.J., 1986. Early hominid scavenging opportunities: implications of carcass availability in the Serengeti and Ngorongoro ecosystems. *British Archaeological Reports International Series* 283, Oxford.
- Blumenschine, R.J., 1987. Characteristics of an early hominid scavenging niche. *Curr. Anthropol.* 28, 383-407.
- Blumenschine, R.J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *J. Archaeol. Sci.* 15, 483-502.
- Blumenschine, R.J., 1989. A landscape taphonomic model of the scale of prehistoric scavenging opportunities. *J. Hum. Evol.* 18, 345-371.
- Blumenschine, R.J., 1991. Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. *Phil. Trans. R. Soc. (London) B* 334, 211-221.
- Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determinations of timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 29, 21-51.
- Blumenschine, R.J., Marean, C.W., 1993. A carnivore’s view of archaeological bone assemblages. In: Hudson, J. (Ed.), *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*. Center for Archaeological Investigations, Southern Illinois University, Carbondale, IL, pp. 273-300.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behavior. *Nature* 333, 763-765.
- Blumenschine, R.J., Selvaggio, M.M., 1991. On the marks of marrow bone processing by hammerstones and hyaenas: their anatomical patterning and archaeological implications. In: Clark, J.D. (Ed.), *Cultural Beginnings: Approaches to Understanding Early Hominid Life-ways in the African Savanna*. Dr. Rudolf Habelt GmbH, Bonn, pp. 17-32.
- Blumenschine, R.J., Cavallo, J.A., Capaldo, S.D., 1994. Competition for carcasses and early hominid behavioral ecology: a case study and conceptual framework. *J. Hum. Evol.* 27, 197-213.

- Blumenschine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *J. Archaeol. Sci.* 23, 493-507.
- Brain, C.K., 1974. Some suggested procedures in the analysis of bone accumulations from southern African Quaternary sites. *Annls. Transv. Mus.* 14, 1-8.
- Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. Chicago University Press, Chicago.
- Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nature* 291, 574-577.
- Bunn, H.T., 1982. Meat-eating and human evolution: studies on the diet and subsistence patterns of Plio-Pleistocene hominids in East Africa. Ph.D. Dissertation. University of California, Berkeley.
- Bunn, H.T., 1983. Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and Olduvai Gorge, Tanzania. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology: I. Hunters and Their Prey*. British Archaeological Reports International Series 163. Oxford, pp. 21-30.
- Bunn, H.T., 1986. Patterns of skeletal part representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673-690.
- Bunn, H.T., 1991. A taphonomic perspective on the archaeology of human origins. *A. Rev. Anthropol.* 20, 433-467.
- Bunn, H.T., 1996. Comment on Rose & Marshall. *Curr. Anthropol.* 37, 321-323.
- Bunn, H.T., 2001. Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene Homo. In: Stanford, C.B., Bunn, H.T. (Eds.), *Meat-eating and Human Evolution*. Oxford University Press, Oxford, pp. 199-218.
- Bunn, H.T., Ezzo, J.A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns and behavioural implications. *J. Archaeol. Sci.* 20, 365-398.
- Bunn, H.T., Kroll, E.M., 1986. Systematic butchery by Plio/ Pleistocene hominids at Olduvai Gorge, Tanzania. *Curr. Anthropol.* 27, 431-452.
- Bunn, H.T., Kroll, E.M., 1988. Reply to Binford. *Curr. Anthropol.* 29, 135-149.
- Capaldo, S.D., 1995. Inferring hominid and carnivore behavior from dual-patterned archaeofaunal assemblages. Ph.D. Dissertation. Rutgers University, New Brunswick.
- Capaldo, S.D., 1997. Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. *J. Hum. Evol.* 33, 555-597.
- Capaldo, S.D., 1998. Simulating the formation of dual-patterned archaeofaunal assemblages with experimental control samples. *J. Archaeol. Sci.* 25, 311-330.
- Cleghorn, N., Marean, C.W., 2004. Identifying the skeletal elements useful for behavioral analysis. Paper presented at the 69<sup>th</sup> Annual Meeting of the Society for American Archaeology, Montréal, Quebec.
- Domínguez-Rodrigo, M., 1996. A landscape study of bone conservation in the Galana and Kulalu (Kenya) ecosystem. *Origini* 20, 17-38.
- Domínguez-Rodrigo, M., 1997. Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge, Tanzania: an experimental approach using cut mark data. *J. Hum. Evol.* 33, 669-690.
- Domínguez-Rodrigo, M., 1999a. Flesh availability and bone modification, in carcasses consumed by lions: palaeoecological relevance in hominid foraging patterns. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 149, 373-388.
- Domínguez-Rodrigo, M., 1999b. Meat eating and carcass procurement by hominids at the FLK Zinj 22 site, Olduvai Gorge, Tanzania: a new experimental approach to the old hunting-versus-scavenging debate. In: Ullrich, H. (Ed.), *Lifestyles and Survival Strategies in Pliocene and Pleistocene Hominids*. Edition Archaea, Schwelm, Germany, pp. 89-111.
- Domínguez-Rodrigo, M., 2001. A study of carnivore competition in riparian and open habitats of modern savannas and its implications for hominid behavioral modeling. *J. Hum. Evol.* 40, 77-98.
- Domínguez-Rodrigo, M., 2002. Hunting and scavenging in early humans: the state of the debate. *J. World Prehist.* 16, 1-52.
- Domínguez-Rodrigo, M., Pickering, T.R., 2003. Early hominid hunting and scavenging: a zooarchaeological review. *Evol. Anthropol.* 12, 275-282.

- Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *J. Archaeol. Sci.* 30, 1385-1391.
- Domínguez-Rodrigo, M., Pickering, T.R., Egeland, C.P., in press. Models of passive scavenging by early hominids: problems arising from equifinality in carnivore tooth mark frequencies and the extended concept of archaeological palimpsests. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *African Taphonomy: A Tribute to the Career of C.K. "Bob" Brain*. Stone Age Institute Press, Bloomington, IN.
- Domínguez-Rodrigo, M., Lopez-Saez, J.A., Vincens, A., Alcalá, L., Luque, L., Serrallonga, J., 2001. Fossil pollen from the Upper Humbu Formation of Peninj, (Tanzania): hominid adaptation to a dry open Plio-Pleistocene savanna environment. *J. Hum. Evol.* 40, 151-157.
- Domínguez-Rodrigo, M., de la Torre, I., de Luque, L., Alcalá, L., Mora, R., Serrallonga, J., Medina, V., 2002. The ST Site Complex at Peninj, West Lake Natron, Tanzania: implications for early human behavioural models. *J. Archaeol. Sci.* 29, 639-665.
- Isaac, G.L., 1981. Archaeological tests of alternative models of early hominid behavior: excavation and experiments. *Phil. Trans. R. Soc. (London) B* 292, 177-188.
- Isaac, G.L., 1983. Bones in contention: competing explanations for the juxtaposition of early Pleistocene artifacts and faunal remains. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology: I. Hunters and Their Prey*. British Archaeological Reports International Series 163. Oxford, pp. 3-19.
- Isaac, G.L., Crader, D., 1981. To what extent were early hominids carnivorous? An archaeological perspective. In: Harding, R.S.O., Teleki, G. (Eds.), *Omnivorous Primates: Gathering and Hunting in Human Evolution*. Columbia University Press, New York, pp. 37-103.
- Lupo, K.D., O'Connell, J.F., 2002. Cut and tooth mark distributions on large animal bones: ethnoarchaeological data from the Hadza and their implications for current ideas about early human carnivory. *J. Archaeol. Sci.* 29, 85-109.
- Marean, C.W., 1991. Measuring the post-depositional destruction of bone in archaeological assemblages. *J. Archaeol. Sci.* 18, 677-694.
- Marean, C.W., Bertino, L., 1994. Intrasite spatial analysis of bone: subtracting the effect of secondary consumers. *Am. Antiq.* 59, 748-768.
- Marean, C.W., Cleghorn, N., 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. *J. Taphonomy* 1, 15-42.
- Marean, C.W., Kim, S.Y., 1998. Mousterian large-mammal remains from Kobeh Cave: behavioral implications for Neanderthals and early modern humans. *Curr. Anthropol.* S39, S79-S 113.
- Marean, C.W., Spencer, L.M., 1991. Impact of carnivore ravaging on zooarchaeological measures of element abundance. *Am. Antiq.* 56, 645-658.
- Marean, C.W., Dominguez-Rodrigo, M., Pickering, T.R., 2004. Skeletal element equifinality begins with method. Paper presented at the 69<sup>th</sup> Annual Meeting of the Society for American Archaeology, Montréal, Quebec.
- Marean, C.W., Abe, Y., Frey, C.J., Randall, R.C., 2000. Zooarchaeological and taphonomic analysis of the Die Kelders Cave layers 10 and 11 Middle Stone Age larger mammal fauna. *J. Hum. Evol.* 38, 197-233.
- Marean, C.W., Spencer, L.M., Blumenshine, R.J., Capaldo, S.D., 1992. Captive hyena bone choice and destruction, the schlep effect and Olduvai archaeofaunas. *J. Archaeol. Sci.* 19, 101-121.
- Marshall, F., 1986. Implications of bone modification in a Neolithic faunal assemblage for the study of early hominid butchery and subsistence practices. *J. Hum. Evol.* 15, 661-672.
- Monahan, C.M., 1996. New zooarchaeological data from Bed II, Olduvai Gorge, Tanzania: implications for hominid behavior in the early Pleistocene. *J. Hum. Evol.* 31, 93-128.
- Oliver, J.S., 1994. Estimates of hominid and carnivore involvement in the FLK Zinjanthropus fossil assemblage: some socio-ecological implications. *J. Hum. Evol.* 27, 267-294.
- O'Connell, J.F., 1997. On Plio/Pleistocene archaeological sites and central places. *Curr. Anthropol.* 38, 86-88.
- Pickering, T.R., 1999. Taphonomic interpretations of the Sterkfontein early hominid site (Gauteng, South Africa) reconsidered in light of recent evidence. Ph.D. Dissertation. University of Wisconsin, Madison.

- Pickering, T.R., Dominguez-Rodrigo, M., The acquisition and use of large mammal carcasses by Oldowan hominins in eastern and southern Africa: a selected review and assessment. In: Schick, K., Toth, N. (Eds.), *The Oldowan*. Stone Age Institute Press, Bloomington, IN, in press.
- Pickering, T.R., Marean, C.W., Dominguez-Rodrigo, M., 2003. Importance of limb bone shaft fragments in zooarchaeology: a response to "On in situ attrition and vertebrate body part profiles" (2002), by M.C. Stiner. *J. Archaeol. Sci.* 30, 1469-1482.
- Pickering, T.R., Dominguez-Rodrigo, M., Egeland, C.P., Brain, C.K., 2004. Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fossil assemblage. *J. Hum. Evol.* 46, 595-604.
- Pickering, T.R., Dominguez-Rodrigo, M., Egeland, C.P., Brain, C.K. The contribution of limb bone fracture patterns to reconstructing early hominid behavior at Swartkrans Cave (South Africa): archaeological application of a new analytical method. *Int. J. Osteoarch.*, in press a.
- Pickering, T.R., Dominguez-Rodrigo, M., Egeland, C.P., Brain, C.K. New data and ideas on the foraging behaviour of Early Stone Age hominids at Swartkrans Cave, South Africa. *S. Afr. J. Sci.*, in press b.
- Pickering, T.R., Dominguez-Rodrigo, M., Egeland, C.P., Brain, C.K., Carcass foraging by early hominids at Swartkrans Cave (South Africa): a new investigation of the zooarchaeology and taphonomy of Member 3. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), *African Taphonomy: A Tribute to the Career of C.K. "Bob" Brain*. Stone Age Institute Press, Bloomington, IN, in press c.
- Potts, R., 1988. *Early Hominid Activities at Olduvai*. Aldine de Gruyter, New York.
- Rose, L., Marshall, F., 1996. Meat eating, hominid sociality, and home bases revisited. *Curr. Anthropol.* 37, 307-338.
- Selvaggio, M.M., 1994a. Identifying the timing and sequence of hominid and carnivore involvement with Plio-Pleistocene bone assemblages from carnivore tooth marks and stone-tool butchery marks on bone surfaces. Ph.D. Dissertation, Rutgers University, New Brunswick.
- Selvaggio, M.M., 1994b. Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. *J. Hum. Evol.* 27, 215-228.
- Selvaggio, M.M., 1998. Evidence for a three-stage sequence of hominid and carnivore involvement with long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *J. Archaeol. Sci.* 25, 191-202.
- Selvaggio, M.M., Wilder, J., 2001. Identifying the involvement of multiple carnivore taxa with archaeological bone assemblages. *J. Archaeol. Sci.* 28, 465-470.
- Shipman, P., 1983. Early hominid lifestyle: hunting and gathering or foraging and scavenging? In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology: I. Hunters and Their Prey*. British Archaeological Reports International Series 163. Oxford, pp. 31-49.
- Shipman, P., 1986. Scavenging or hunting in early hominids: theoretical framework and tests. *Am. Anthropol.* 88, 27-43.
- Todd, L.C., Rapson, D.J., 1988. Long bone fragmentation and interpretation of faunal assemblages: approaches to comparative analysis. *J. Archaeol. Sci.* 15, 307-325.
- Villa, P., Mathieu, E., 1991. Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27-48.