

Revisiting the hunting-versus-scavenging debate at FLK Zinj: A GIS spatial analysis of bone surface modifications produced by hominins and carnivores in the FLK 22 assemblage, Olduvai Gorge, Tanzania

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ABSTRACT

This study presents a taphonomic examination of the ca. 1.84 million year old (Ma) bovid fauna from FLK Level 22 (FLK Zinj), Bed I, Olduvai Gorge using a new GIS spatial analysis approach. The FLK Zinj site contains some of the best preserved evidence for meat eating by hominins and has been used extensively in reconstructions of early hominin behavior. However, despite numerous interpretations of site function, there is currently no consensus regarding how hominins acquired carcasses at FLK Zinj. Some interpretations argue that Early Stone Age hominins had early access to fleshed carcasses through hunting or active scavenging, while others argue hominins had late access to largely defleshed carcasses through passive scavenging. In this study, GIS was used to record bone preservation in the FLK Zinj assemblage as well as in several modern, experimentally-modified bone assemblages, which are used for comparison. The placement of hominin- and carnivore-produced modifications was documented on bones from these assemblages, and the GIS Spatial Analyst was used to identify patterning in tooth mark clusters as well as patterning in cut mark locations. This analysis suggests hominins had early access to fleshed carcasses at FLK Zinj, particularly of smaller prey, which they may have acquired through hunting. Damage patterns on larger carcasses are more difficult to interpret, but are consistent with early access through hunting or aggressive scavenging. A reanalysis of carnivore tooth mark frequencies on the FLK Zinj bovid fauna also supports an early access scenario.

1. Introduction

Bone surface modifications on prey animals from Early Stone Age archaeological sites provide some of the best evidence for meat eating by early hominins. The placement and frequency of these modifications, which include hominin-produced butchery marks and carnivore-produced tooth marks, provide information on the timing of access that hominins and carnivores had to carcasses. Bone surface modifications also provide insight into the nature of competitive interactions between hominins and carnivores. It has been well established that Early Stone Age hominins were at times butchering large mammal carcasses. However, the method of carcass acquisition (i.e., hunting vs. scavenging), the timing of access to carcasses, the degree of carcass completeness at the time of hominin access (fleshed vs. defleshed), as well as the importance of meat in the diet of hominins is less certain. Research on this topic has revolved around a central debate over hunting versus scavenging (Binford, 1985; Potts, 1988; Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003). Opinions on this debate vary widely from envisioning hominins as marginal

scavengers of flesh scraps and marrow remaining on carcasses of carnivore kills (Binford, 1981, 1986, 1988; Shipman, 1986; Blumenschine, 1987, 1995; Blumenschine and Cavallo, 1992; Capaldo, 1997; Selvaggio, 1998; Pobiner, 2015) to aggressive scavengers of large mammal carcasses and possibly hunters of small mammals (Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Oliver, 1994; Domínguez-Rodrigo, 2002, 2009; Plummer, 2004; Domínguez-Rodrigo et al., 2007a; Ferraro et al., 2013; Plummer and Bishop, 2016).

Some of the best preserved archaeological evidence for meat eating by hominins comes from the ca. 1.84 Ma FLK site Level 22 (also known as FLK Zinj) from Bed I, Olduvai Gorge, Tanzania (Fig. 1). The FLK site was originally excavated by Louis and Mary Leakey following their discovery of the *Zinjanthropus* hominin cranium (since renamed *Paranthropus boisei*). The excavation exposed a number of stratigraphic levels containing stone artifacts and bone to a depth of 12 m (Potts, 1988). However, Level 22 at FLK is notable because it is the largest preserved ancient land surface of any of the Bed I sites at Olduvai and has yielded some of the best preserved fauna. All of the FLK Zinj fauna discussed here are from Leakeys' original excavation and are derived

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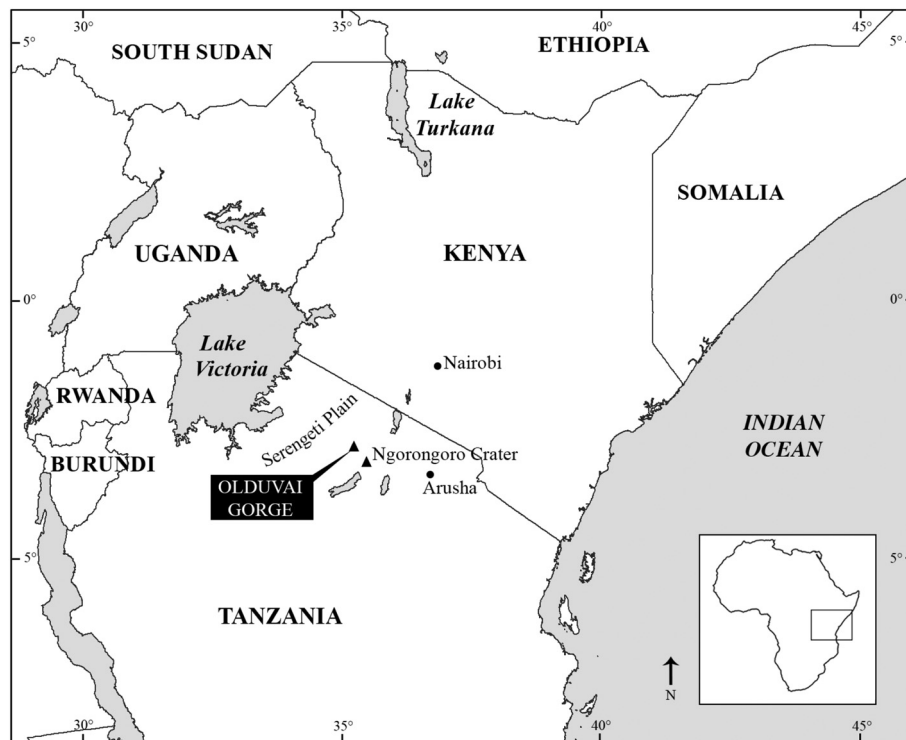


Fig. 1. Map showing the location of Olduvai Gorge in Northern Tanzania.

from this single level, which is bracketed between two volcanic tuffs, both dated to approximately 1.84 Ma (Deino, 2012; see Leakey, 1971 and Hay, 1976 for a full discussion of the geologic context of the site.)

The FLK locality was situated in a lake margin zone, approximately 1 km from the edge of a perennial lake (Potts, 1988). Bone weathering on the fossils from FLK Zinj indicates that the assemblage likely accumulated over a time range of 5–10 years (Potts, 1986). The paleoenvironment at FLK Zinj has been reconstructed as a woodland based on isotopic analyses of paleosol carbonates and phytolith analysis (Cerling and Hay, 1986; Sikes, 1994; Ashley et al., 2010; Arráiz et al., 2017). Recent excavations just north of the site but into the same stratigraphic horizon as FLK level 22 have identified carbonate deposits (tufa) deposited by a spring, indicating fresh water was also nearby (Ashley et al., 2010).

FLK Zinj contains roughly 60,000 faunal specimens (3500 of which are identifiable to at least skeletal part) representing a minimum of 48 large mammal carcasses (most of them bovid) as well as over 2500 Oldowan stone artifacts (Leakey, 1971; Bunn and Kroll, 1986; Potts, 1988; Domínguez-Rodrigo et al., 2007a). Because of the large size and exceptional preservation of the collection, the FLK Zinj assemblage has been used extensively in reconstructions of early hominin behavior. This site served as the basis for Mary Leakey's (1971) "living floor" hypothesis, which envisioned the site a base camp from which hominins dispersed from and returned to on a daily basis and which would have been the center of social activities. In the decades following Leakey's original interpretation, the site has been variously interpreted as a "home base" or "central place" at which food sharing activities may have taken place (Isaac, 1978, 1981, 1983; Bunn, 1982; Bunn and Kroll, 1986; Rose and Marshall, 1996; Domínguez-Rodrigo and Cobo-Sánchez, 2017), a place where carcasses or carcass parts obtained through hunting or more aggressive, confrontational scavenging were deposited (Bunn and Ezzo, 1993; Domínguez-Rodrigo and Pickering, 2003), and a carcass processing locale where stone for making tools was cached and carcasses were repeatedly butchered over time (Potts, 1988). The site has also been used to support behavioral models of passive scavenging,

and has been interpreted as a woodland refuge where hominins may have brought scavenged carcass remains (Blumenshine, 1991; Blumenshine et al., 1994).

Despite these numerous previous interpretations of site function at FLK Zinj, there is currently no consensus among researchers regarding the mode of carcasses acquisition by hominins at the site. While there has been much discussion on the taphonomic data from FLK Zinj and new approaches for interpreting these data (e.g., Pante et al., 2012; Domínguez-Rodrigo et al., 2014; Pante et al., 2015), there have been fewer independent studies of the actual fossils (see Oliver, 1994; Blumenshine, 1995; Domínguez-Rodrigo et al., 2007a). This paper reports on a reanalysis of the bone surface modifications on the FLK Zinj bovid fauna using a new GIS spatial analysis approach. Results from this study suggest that hominins had early access to carcasses at FLK Zinj and were not confined to passive scavenging.

2. Background: Previous research on bone surface modifications at FLK Zinj

Bunn (Bunn, 1981; Bunn and Kroll, 1986) was the first to examine bone surface damage on the FLK Zinj fossils. He argued that the butchery mark evidence was suggestive of defleshing and indicated hominins had early access to carcasses at FLK Zinj. Shortly thereafter, Binford (1986, 1988) countered this argument and proposed instead that hominins were marginal scavengers of flesh remaining on carnivore kills. Basing his argument on the preliminary data from Leakey's (1971) report, Binford cited a low frequency of meat bearing limb bones at FLK Zinj as evidence that the assemblage was a carnivore kill site subsequently scavenged by hominins for marrow. Binford's analysis was biased because it was based on a provisional dataset, but also because he excluded long bone shaft fragments from his study. Bunn and Kroll (1986) performed a lab-based analysis of skeletal part frequencies in the FLK Zinj assemblage which included limb shaft fragments, and found that the assemblage was actually dominated by limb bones, with meaty elements (humerus, radio-ulna, femur, and tibia) being more abundant

than non-meaty elements (metapodials). Bunn and Kroll argued that these skeletal element profiles provided evidence for repeated transport of carcasses by hominins to a favored place, and the abundance of cut marks on meaty limb bones indicated systematic butchery and significant meat consumption by hominins. They postulated that early access may have been achieved through confrontational scavenging of larger carcasses and possibly hunting of smaller animals. In later work, Bunn (2001) gave additional support to this argument by documenting a similarity in the anatomical patterning of cut marks between the FLK Zinj assemblage and bone refuse from carcasses processed by the present-day Hadza hunter-gatherers of Tanzania.

2.1. Application of experimental models to interpret the FLK Zinj taphonomy

Experimental modeling of bone damage patterns has increasingly become an important tool for interpreting the nature of hominin and carnivore involvement in archaeological bone assemblages. Pioneering experimental work was conducted by Blumenschine (1988, 1995), Capaldo (1998a, 1998b), and Selvaggio (1994) on hammerstone breakage of long bones as well as damage to bones by wild carnivores in the Serengeti and Ngorongoro ecosystems of Tanzania. These experiments modeled carnivore-only, hominin-only, and hominin-first access to carcasses, with the goal being to determine patterns resulting from differential access to carcasses by carnivores and hominins.

Blumenschine and colleagues (Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998) subsequently used their experimental work to argue for a three-stage (felid-hominin-hyaenid) model of carcass access to explain the bone damage patterns seen at FLK Zinj. According to this model, hominins scavenged within-bone nutrients of largely defleshed limb bones and skulls from abandoned felid kills. Following hominin consumption of brains and marrow, hyenas used their bone-cracking adaptations to scavenge the grease-rich epiphyses that remained. Blumenschine and colleagues found a high frequency of tooth marking on long bone midshafts in the FLK Zinj assemblage and interpreted this as a result of initial defleshing by felids, which do not have jaws adapted for bone cracking. They argued that hammerstone percussion marks seen on the long bones are indicative of hominin marrow processing, and that cut marks reflect the removal of flesh scraps surviving felid consumption. Finally, they argued that the low proportion of epiphyses and axial elements indicated that these portions were scavenged by bone-crunching hyenas following hominin demarrowing of long bone shafts. This three-stage model envisions hominins as marginal scavengers with secondary access to carcasses and has been recently supported by Pante et al. (2012, 2015).

2.2. Reinterpretation of the FLK Zinj tooth mark frequencies by Domínguez-Rodrigo and colleagues

The three-stage model has been challenged by Domínguez-Rodrigo and colleagues who have argued instead that hominins had early access to carcasses at FLK Zinj (Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2007a). Their argument was based on a reanalysis of carnivore tooth mark frequencies in the assemblage, as well as experimental modeling of flesh availability on modern lion kills. In their reanalysis of tooth mark frequencies in the FLK Zinj assemblage, Domínguez-Rodrigo and Barba (2006) argued that some modifications on long bone surfaces that had been identified as tooth marks by Blumenschine (1995) were actually produced through biochemical processes. They conducted experimental studies on the effects of fungus growth on modern bone and argued that the irregular grooved surface that fungus creates on bone resembles carnivore tooth marking. When the authors reanalyzed the FLK Zinj fossils, they identified tooth marks on < 20% of the specimens originally identified as tooth marked by Blumenschine. They suggested that Blumenschine's tooth mark frequencies were inflated because he had frequently misidentified

biochemical marks as tooth marks.

Domínguez-Rodrigo et al. (2007a) examined their revised tooth mark frequencies in light of the experimental framework developed by Blumenschine (1995), and found that limb shaft portions were tooth marked at frequencies similar to or below those seen in the hammerstone-to-carnivore experiments where carnivores had secondary access to carcasses first butchered by humans (< 15% of identifiable specimens). These frequencies also differed markedly from the carnivore-first models which were tooth marked much more frequently (> 70% of identifiable specimens). Additionally, Domínguez-Rodrigo and colleagues argued that the high tooth mark frequencies on metapodials, which Blumenschine interpreted as evidence for initial felid defleshing of carcasses, instead indicate secondary carnivore (mostly likely hyena) scavenging. They argued that if felids had initial access to fully fleshed carcasses, they would not likely have tooth marked the metapodials, as these contain almost no nutrition except marrow, which felids cannot access. However, if hominins had first defleshed the carcasses, bone-crunching carnivores may have been attracted to the nutrients remaining in the metapodials. Domínguez-Rodrigo et al. (2007a) have interpreted this tooth mark frequency evidence as indicative of early hominin access at FLK Zinj rather than passive scavenging as had been suggested by Blumenschine.

2.3. Flesh availability on carcasses and opportunities for scavenging

In order to further test the hypothesis of initial felid access at FLK Zinj, Domínguez-Rodrigo and colleagues also conducted experimental studies of flesh distribution on carcasses surviving felid consumption (Domínguez-Rodrigo, 1999; Domínguez-Rodrigo et al., 2007a). They observed kills made by free ranging lions in the Maasai Mara National Reserve in Kenya and examined the distribution of surviving flesh on carcasses. From these observations, they developed a “hot zone/cold zone” model. In this model, hot zones are skeletal areas where flesh typically does not survive felid consumption (mainly shaft portions of upper limb elements). Cold zones, on the other hand, are areas where flesh may survive (typically joints and distal limb elements). They suggested that cut marks found in hot zones on fossil bones should indicate hominin primary access, as felids would not have left meat in these areas for a hominin scavenger to butcher. When applying this interpretive framework to the FLK Zinj assemblage, Domínguez-Rodrigo et al. (2007a) found that cut marks often occur in hot zones. They argued that the results of their study refute the three-stage felid-hominin-hyaenid model, and indicate instead that hominins had primary access to fleshed carcasses which were later scavenged by carnivores. Domínguez-Rodrigo et al. (2007a) have argued that the combined evidence of cut marks and carnivore tooth marks suggests early access by hominins and possibly hunting of smaller mammals.

The debate over the nature of hominin and carnivore activities at FLK Zinj remains unresolved. This is partly due to disagreement over methods of identification and documentation of tooth marks (Domínguez-Rodrigo, 2009; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al., 2007). The debate outlined above underscores the need for standardization in identification and data recording methods and also highlights the necessity of having multiple observers identify bone surface modifications to try to eliminate interobserver variation. For example, the taphonomic analysis of Kanjera South, another Early Stone Age site, was conducted by a “roundtable” of three individuals, so that there was a consensus on bone surface modification frequencies in the assemblage (Ferraro et al., 2013). This previous work has also highlighted the necessity of bringing multiple lines of evidence into evaluations of site formation processes, including examining patterns as well as frequencies of bone surface modifications.

The study presented here addresses these issues through an independent reanalysis of the FLK Zinj assemblage and a GIS image analysis of bone preservation and modification patterns. GIS image analysis allows for the comparison of experimental models of carnivore

and hominin bone modification to fossil assemblages in a visual and quantifiable way, and also has the potential to tease apart more subtle patterning which may help to better interpret the competitive interactions between hominins and carnivores in the past (Parkinson, 2013; Parkinson et al., 2014, 2015).

3. Materials and methods

3.1. The FLK Zinj fossil collection

I collected data on the FLK Zinj collection during the summer of 2012 at the National Museum of Tanzania in Dar es Salaam. The FLK Zinj archeofauna had recently been repatriated from the National Museums of Kenya, where it had been housed since the Leakeys' expeditions. Because of their recent shipment, the FLK Zinj specimens were still packed in shipping boxes with fossils from other Olduvai sites. I unpacked the specimens from their boxes for analysis, but because there were no museum storage trays available at the time, they were repacked into the boxes after analysis.

I was able to locate 489 of the original bovid limb specimens from FLK Zinj. These were specimens with a maximum length > 2 cm and with good cortical surface preservation. In comparison, Domínguez-Rodrigo and Barba's (2006) sample had 699 long bone fragments, while Blumenschine's (1995) sample included 731. Hopefully the specimens missing from my study will be recovered once the collection is completely unpacked. All 489 specimens in my study were examined for bone surface modifications. Of these 489 specimens, 256 were identifiable to element and included in the GIS image analysis.

3.2. Identification of bone surface modifications

All specimens in the sample were examined with a 10× hand lens under oblique light to identify bone surface modifications. I identified bone surface modifications based on published criteria (Binford, 1981; Bunn, 1981; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994), and I verified my own reliability in mark identification using Blumenschine et al.'s (1996) modern blind test collection, on which I identified bone surface modifications with 100% accuracy. Because all potential contributing taphonomic factors are unknown in fossil assemblages, I first attempted to exclude any types of pseudo-marks (e.g., marks created by trampling, sediment abrasion, or excavation tools) (Behrensmeyer et al., 1986; Domínguez-Rodrigo and Barba, 2006). Following Oliver (1994), when mark morphology was ambiguous, I assessed the mark in light of surrounding carnivore- or hominin-induced damage. This is a conservative approach to identifying bone surface modifications, but it reduces error by examining marks as a suite of related damage points. Following Ferraro's (2007) protocol, I excluded fossils with poor surface preservation and recent breaks from the analysis. After independently identifying all hominin- and carnivore-induced modifications, I then compared my own identifications against those published by Blumenschine (1995) and Domínguez-Rodrigo et al. (2007a).

3.3. GIS image analysis

In addition to reevaluating the frequency of bone surface modifications on the FLK Zinj fauna, I have applied a GIS image analysis method to analyze the patterns that these modifications occur in, and also to visualize patterns of bone fragmentation. This GIS method was originally described by Marean et al. (2001) and expanded on by Parkinson (Parkinson, 2013; Parkinson et al., 2014, 2015). The approach essentially treats each element as a 'map' onto which the outline of bone fragments as well as bone surface modifications are recorded.

To examine bone portion survivorship, outlines of each fragment in the collection were digitally drawn as vector shapefiles over a photographic template of a complete element. Fragments were positioned on

the photo template by lining up anatomical landmarks. Because small fragments may not preserve enough landmark information, only those fragments identified to element portion and side were used ($n = 256$). Specimens were grouped by size class, and the fragment outlines were drawn over a template of similar size to reduce the potential for shape distortion. Replicability of this method has been tested by Parkinson et al. (2014) and was shown to be high. Each fragment was drawn as a separate shapefile layer. The shapefiles were then overlapped, converted to grids, and the grids were added together using the grid calculator in ArcGIS. This process produces a shaded bone survival 'map' that is a composite image illustrating which bone portions are frequently preserved and which are frequently destroyed by the agent being investigated (e.g., carnivores) (Fig. 2).

In order to examine the distribution of bone surface modifications, I spatially plotted tooth marks, cut marks, percussion marks, and percussion notches over the bone templates in ArcGIS. Each mark type was plotted in a single point or line feature class layer file for each element to produce composite images of tooth mark and butchery mark distribution by element. Data analysis was conducted in ArcGIS 9.2 using the Spatial Analyst extension following Parkinson et al. (2014). The Analyzing Patterns and Density toolsets within ArcGIS were used to analyze clustering patterns of bone modifications.

The Average Nearest Neighbor Distance (NND) tool was used to measure the distance between individual tooth marks and to test for significant spatial clusters in the composite tooth mark files. If the average distance between points (tooth marks) was less than the average for a hypothetical random distribution, the distribution was considered clustered. The NND is expressed as a ratio of the observed distance divided by the expected distance. If the index is < 1, the pattern is considered clustered. If it is > 1, the pattern is considered dispersed. The Calculate Area tool was used to constrain the study area to the bone template shapefile. The average NND was calculated using Euclidean distance for each view (e.g., anterior, posterior, etc.) separately in order to accurately represent the surface area of the bone.

The Kernel Density Spatial Analyst tool was used to visually identify where tooth mark clusters were most concentrated on specific elements (Fig. 3). This tool takes a point feature class layer and builds a rasterized image of point clustering. It uses the quadratic kernel formula to fit a smoothly tapered surface to each point, which spreads out to a specified radius around the point. The highest cell value (1) is at the point location in the center of the spread, with the value tapering to 0 at the boundary of the search radius distance. The sum of the intersecting spreads is then calculated for each cell in the output raster. Using this kernel function rather than the simple point density function effectively takes into account the margin of error that may be associated with hand-plotting the tooth mark location points on the original GIS template because it weighs cell values in a radius surrounding each point. Step by step instructions for this analysis as well as the NND analysis are outlined in the supplementary material to Parkinson et al. (2014).

Bones were sorted into two groups for all analyses. The small/medium group includes size classes 1–3a, and the large group includes size 3b (wildebeest-sized) and above. These size categories follow Bunn (1982). I have included size 3a together with smaller animals in order to make the GIS analyses easily comparable to Kanjera South (manuscript in preparation), another Early Stone Age site which has a majority of bovid specimens on the border between size 2 and 3. The grouping used here is slightly different from that used by Domínguez-Rodrigo et al.'s (2007a) study of FLK Zinj, which considered size 1 and 2 animals as small, and size 3 and 4 as large.

4. Results: Bone modification frequencies at FLK Zinj

Bone modification frequencies at FLK Zinj have been discussed and debated at length in the literature (Oliver, 1994; Blumenschine, 1995; Capaldo, 1997; Domínguez-Rodrigo, 1997; Selvaggio, 1998; Domínguez-Rodrigo and Pickering, 2003; Domínguez-Rodrigo and

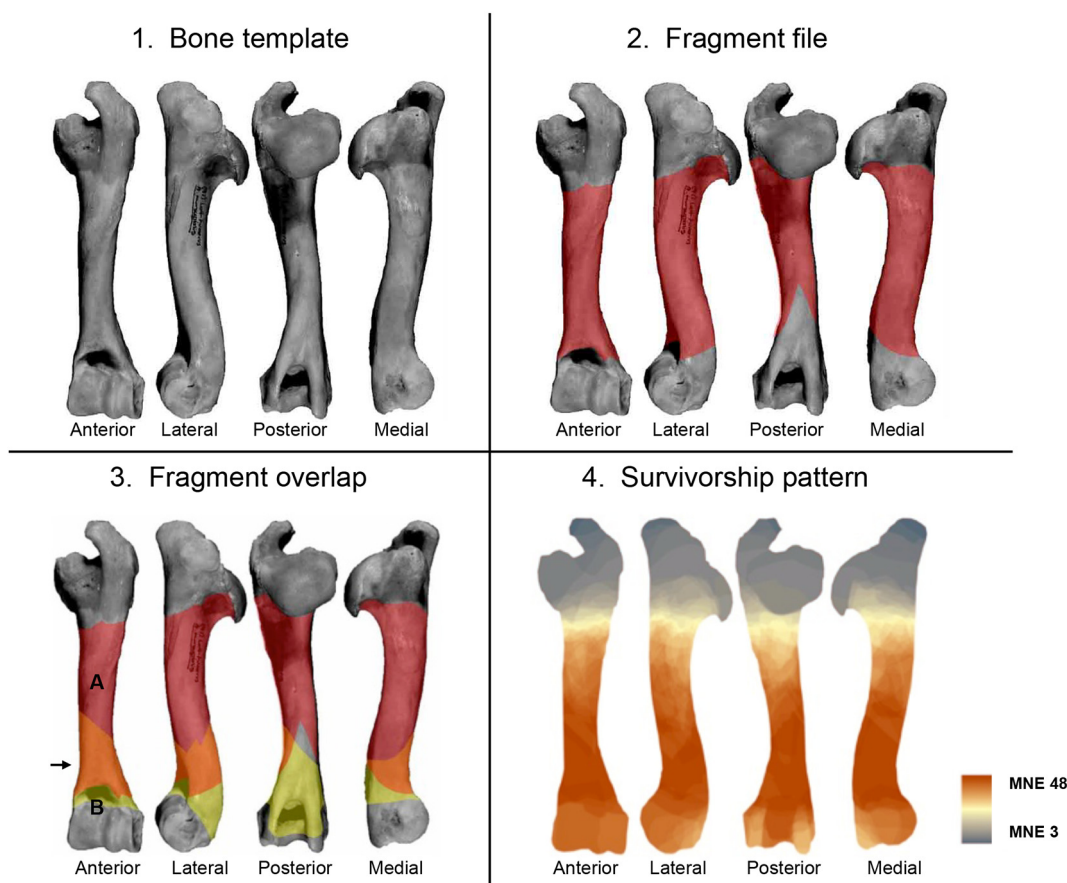


Fig. 2. GIS image analysis method – bone portion survivorship.

This image illustrates the method used to build bone portion survivorship models. Beginning with a bone template, in this example the left humerus (1), fragments are drawn as shapefiles over the template (2). Two sample fragments (A and B) are shown on the GIS template (3). Areas of fragment overlap (indicated by the arrow) provide the basis for calculating the MNE. When all fragments are entered, the resulting survivorship pattern (4) displays the bone portions most likely preserved and least likely preserved. In this example, 48 fragments are overlapping in this dark orange shaded area, so the MNE estimate is 48. The lowest number of overlapping fragments is 3.

Barba, 2006; Blumenschine et al., 2007; Domínguez-Rodrigo et al., 2007a; Pante et al., 2012; Domínguez-Rodrigo et al., 2014). Due to differences in methodology and disagreement over the identification of bone surface modifications (especially tooth marks), there is currently

no consensus on bone surface modification frequencies in the FLK Zinj assemblage. In a blind study, I independently reexamined the Zinj assemblage, and I then compared each specimen against those identified as damaged by Blumenschine (1995) and Domínguez-Rodrigo et al.

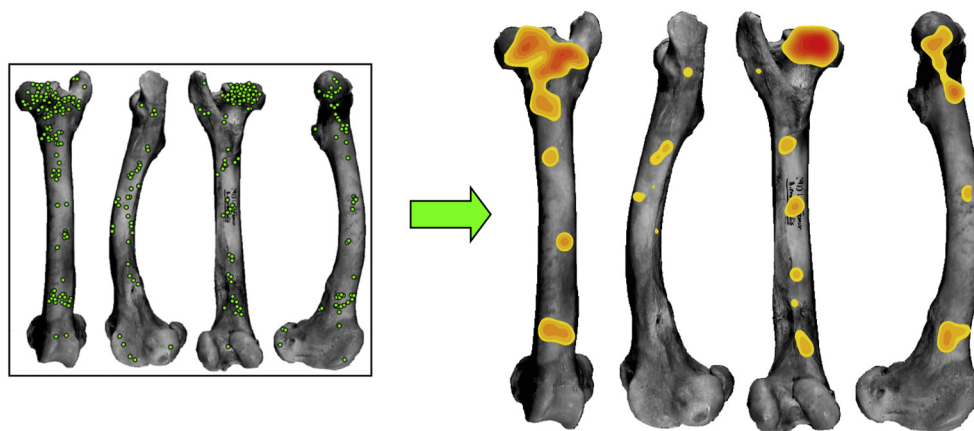


Fig. 3. GIS image analysis method – density analysis.

The image on the left shows an example of a composite plot of tooth pits in an assemblage. The Kernel Density Spatial Analyst tool takes the point layer file and builds a rasterized image of clustering (right). The red shaded areas indicate the highest concentrations of tooth pits.

Table 1

Bone surface modifications on limb specimens in this study (JAP) compared with those identified by Domínguez-Rodrigo et al. (Domínguez-Rodrigo et al., 2007a, 2007b; MDR) and Blumenschine (1995; RJB).

Tooth marks	
Sample size (NISP*) studied by both MDR and JAP**	489
NISP with TM in this sample identified by JAP	119 (24.3%)
NISP with TM in this sample identified by MDR	80 (16.4%)
% agreement of JAP with MDR	74/80 (92.5%)
Sample size (NISP) studied by both RJB and JAP	272***
NISP with TM in this sample identified by JAP	69 (25.4%)
NISP with TM in this sample identified by RJB	188 (69.1%)
% agreement of JAP with RJB =	66/188 (35.1%)
Percussion marks	
Sample size (NISP) studied by both MDR and JAP	489
NISP with PM in this sample identified by JAP	113 (23.1%)
NISP with PM in this sample identified by MDR	108 (22.1%)
% agreement of JAP with MDR	98/108 (90.7%)
Sample size (NISP) studied by both RJB and JAP	272
NISP with PM in this sample identified by JAP	82 (30.1%)
NISP with PM in this sample identified by RJB	110 (40.4%)
% agreement of JAP with RJB	67/110 (60.9%)
Cut marks	
Sample size (NISP) studied by both MDR and JAP	489
NISP with CM in this sample identified by JAP	76 (15.5%)
NISP with CM in this sample identified by MDR	71****
% agreement of JAP with MDR	62/71 (87.3%)

* Number of identifiable specimens.

** MDR lists only catalog numbers for specimens with percussion marks or tooth marks (Domínguez-Rodrigo et al., 2007a, 2007b, Appendix A,B) and does not list catalog numbers for unmodified specimens, so it is unclear whether we have examined the exact same unmodified specimens. Percussion marked specimens for MDR and JAP include notches.

*** Catalog numbers for specimens in this study were checked against those listed in Blumenschine's (1995, Appendix 1).

**** These are taken from diagrams in Domínguez-Rodrigo et al. (Domínguez-Rodrigo et al., 2007a, 2007b, figs. 54 & 55). Not all catalog numbers identified as displaying cut marks could be located from this study, but Domínguez-Rodrigo et al. (Domínguez-Rodrigo et al., 2007a, 2007b, Table 8) report total cut mark frequencies as 14.9% (size 1&2 carcasses) and 22.6% (size 3&4 carcasses).

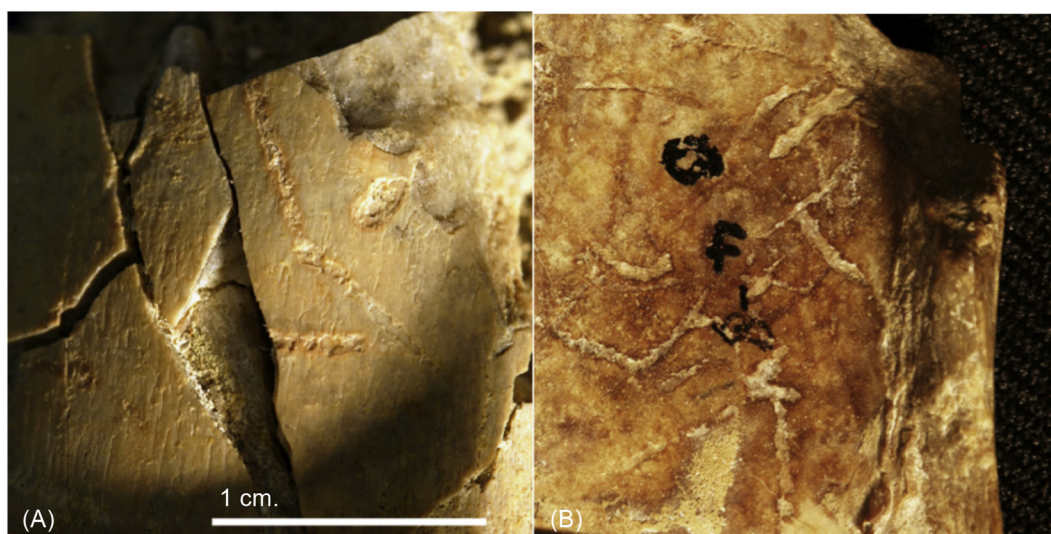
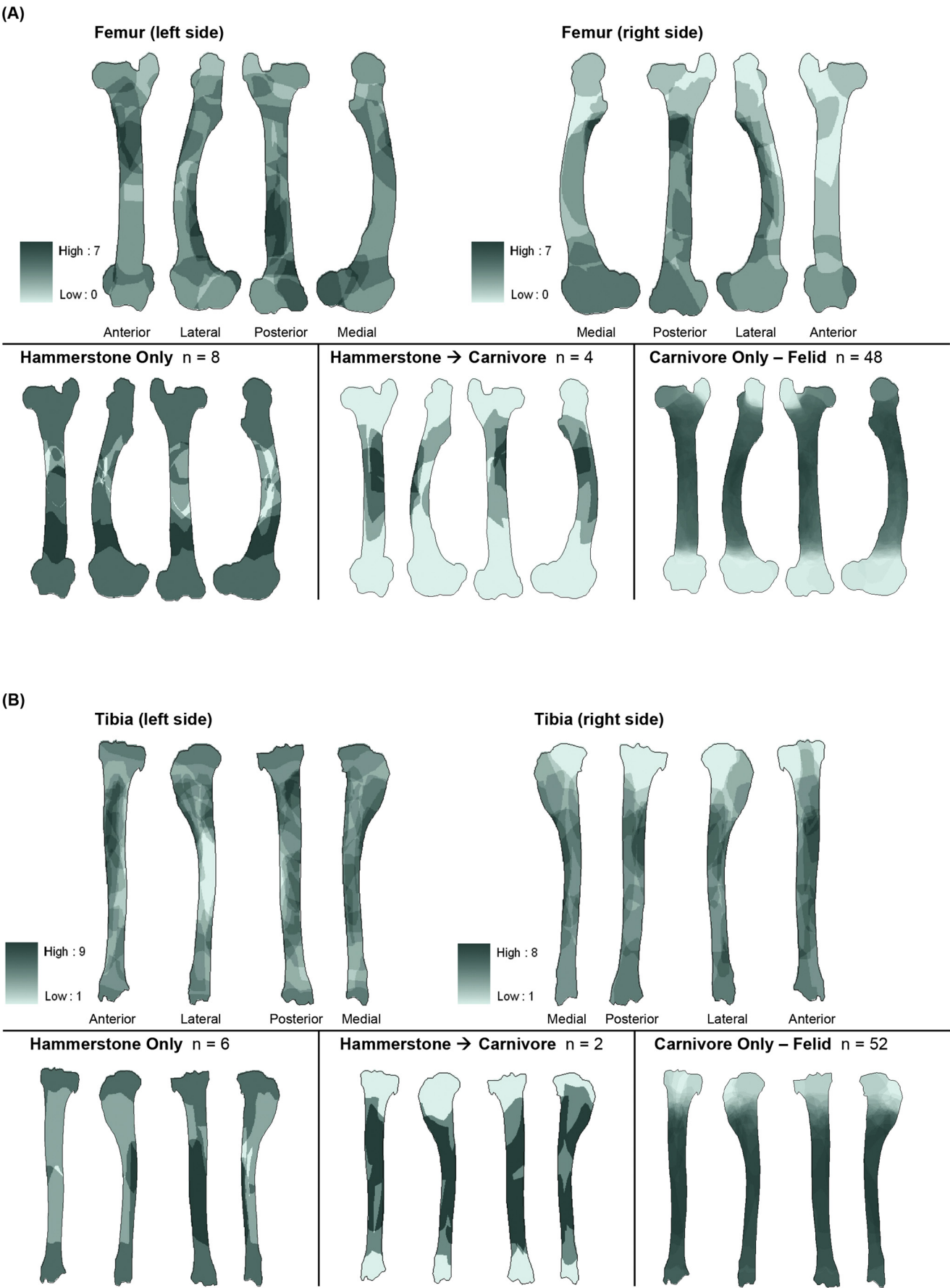


Fig. 4. Examples of biochemical marking in specimens from FLK Zinj. The image on the left (Cat.# A22) was also identified by Domínguez-Rodrigo (Domínguez-Rodrigo et al., 2007a, 2007b, Fig. 11d) as displaying biochemical marking. This specimen was not identified in Blumenschine's (1995) study as tooth marked. The image on the right (Cat.# B4–8 (84)) shows more extensive biochemical damage with intersecting scores, irregular in width. This catalog number is duplicated for several different specimens, so it is not possible to tell whether it was identified as tooth marked in previous studies. Scale is the same for both images. Scale bar is 1 cm.



(caption on next page)

Fig. 5. Preservation of small and medium bovid hindlimbs at FLK Zinj compared with experimental models of bone damage to small/medium bovinds. (A) femur, (B) tibia, (C) metatarsal. High = minimum number of elements estimate (greatest number of overlapping fragments). N = greatest number of fragment overlaps in experimental assemblages. Hammerstone Only and Hammerstone→Carnivore models are based on Blumenschine's experimental collection, and represent right/left composite images shown on a left side template. The felid model is from Parkinson et al. (2015). Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, medial.

(2007a). Percent agreement of my bone surface modification frequencies with these previous studies is reported in Table 1. Catalog numbers for modified specimens are listed in Appendices A–C.

4.1. Percussion mark and tooth mark frequencies

Of the 489 specimens examined in both this study and in Domínguez-Rodrigo's, I identified approximately 23% as percussion marked, while Domínguez-Rodrigo identified approximately 22% (note this differs slightly from Domínguez-Rodrigo's published frequency as I consider here only the sample we analyzed in common). For the sample this study shared in common with Blumenschine's study, I found a percussion mark frequency of 30%, while Blumenschine identified 40% as percussion marked. Blumenschine did not include cut marks in his study, but 87% of the cut marked specimens identified in the present study were also identified as cut marked by Domínguez-Rodrigo (the present study identified approximately 16% of the NISP as cut marked).

Carnivore tooth marking frequencies show much less concordance between researchers than do hominin-induced modifications. Of the specimens examined in both this study and in Domínguez-Rodrigo's, I identified approximately 24% as tooth marked, while Domínguez-Rodrigo identified approximately 16%. Within the shared sample analyzed by both Blumenschine and this study, I identified 25% of the NISP (number of identifiable specimens) as tooth marked, while Blumenschine identified 69%. My interpretation of the tooth marking at FLK Zinj is in agreement with Domínguez-Rodrigo in 93% of cases, while in agreement with Blumenschine in only 35% of cases. This is a significant discrepancy, and perhaps owes to the more conservative approach to tooth mark identification I have taken, where isolated marks that do not show defined characteristics of tooth mark morphology are not counted.

4.2. Biochemical/bioerosion damage

Domínguez-Rodrigo and Barba (2006) argue that some modifications originally identified as tooth marks by Blumenschine (1995) were instead equifinalities produced through biochemical processes. They cite experimental studies of fungal damage to bone showing that biochemical processes/bioerosion can superficially mimic tooth marking. They argued that misidentification of biochemical marks as tooth marks was the cause of the higher tooth mark frequency in Blumenschine's original analysis compared to their own. These differing interpretations of tooth mark frequencies have implications for understanding site function at FLK Zinj. High frequencies of tooth marking have been used by Blumenschine and colleagues to support a three-stage model of secondary access by hominins to felid kills with subsequent hyena scavenging of the food refuse left by hominins (Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998). This model, they argued, best incorporates the evidence of hammerstone breakage of long bones by hominins as well as the high frequency of carnivore tooth marking. Domínguez-Rodrigo et al. (2007a) have argued that their lower, revised tooth mark frequencies instead support early access to fleshed carcasses, and possibly hunting by hominins.

In my own analysis of the FLK Zinj assemblage, I observed biochemical damage as defined by Domínguez-Rodrigo and Barba (Fig. 4), and in many cases it does superficially resemble carnivore tooth marking. I did not conduct a thorough, quantitative examination of biochemical damage in the assemblage, but I did frequently observe its presence in the collection. I also observed staining on some bone

surfaces likely attributable to root etching (which was also identified by Blumenschine).

There have now been four separate studies of tooth marking in the Zinj assemblage (the current study; Domínguez-Rodrigo and Barba, 2006; Blumenschine, 1995; Oliver, 1994), and Blumenschine's study stands out as reporting the highest tooth mark frequency. Given that Blumenschine's study is an outlier in reporting a higher tooth mark frequency, it is likely that his study over attributed some of the marks to carnivores, when other taphonomic agents may have been responsible for some of the less defined marks. This example makes clear the hazards that potential equifinality can pose for assemblage analysis and interpretation.

5. Results: Bone portion survivorship at FLK Zinj

This section presents results of GIS analyses of bone portion survivorship. These patterns are fully illustrated in Figs. 5–8 and are compared with GIS models of several different experimental bone damage studies. These comparative GIS models are based on Blumenschine's (1988, 1995) carnivore, hammerstone, and hammerstone-to-carnivore experiments, and on my own carnivore feeding experiments conducted with felids (Parkinson et al., 2015).

5.1. Comparative experimental bone collections

Blumenschine's experiments, conducted in Tanzania's Serengeti National Park and Ngorongoro Crater, model differential access to carcasses by carnivores and humans. These collections, which were housed in the Department of Anthropology at Rutgers University at the time of study, have previously been studied in detail for evidence of bone damage (Blumenschine, 1988, 1995; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994). For this study, I independently identified bone modification traces on the experimental assemblages and input tooth mark locations as well as fragment shapes into GIS models. I entered 456 fragments into GIS out of Blumenschine's original 598 (Table 2). I excluded fragments too small to place on the GIS template and excluded experiments where carnivores other than hyenas were involved. Prey carcasses for small and medium-sized bovids in Blumenschine's collection included Grant's gazelle (*Gazella* [= *Nanger*] *granti*), Thomson's gazelle (*Gazella* [= *Eudorcas*] *thomsonii*), and impala (*Aepyceros melampus*). Large carcasses included topi (*Damaliscus lunatus*) and wildebeest (*Connochaetes taurinus*).

Blumenschine's hammerstone-only experiments include bones defleshed with a metal knife and broken using a hammerstone and anvil technique to replicate hominin-only access and marrow extraction.

The hammerstone-to-carnivore experiments, or simulated sites, replicate carnivore scavenging of hammerstone broken and demarrowed bones. For these experiments, researchers defleshed bones and broke them using hammerstone percussion as in the hammerstone-only models, but then set bones out on the landscape immediately following breakage for carnivores to feed on. Spotted hyenas (*Crocuta crocuta*) were the sole scavengers in all experiments included in the current analysis, although minor disturbance by jackals or mongooses cannot be ruled out.

Blumenschine's carnivore-only experiments include limb bones derived from carcasses scavenged by spotted hyenas in the wild. Hyenas were the sole carnivore responsible for bone fragmentation in these experiments. The original carnivore-only sample included nine assemblages. However, I have excluded two of these from my analysis due to

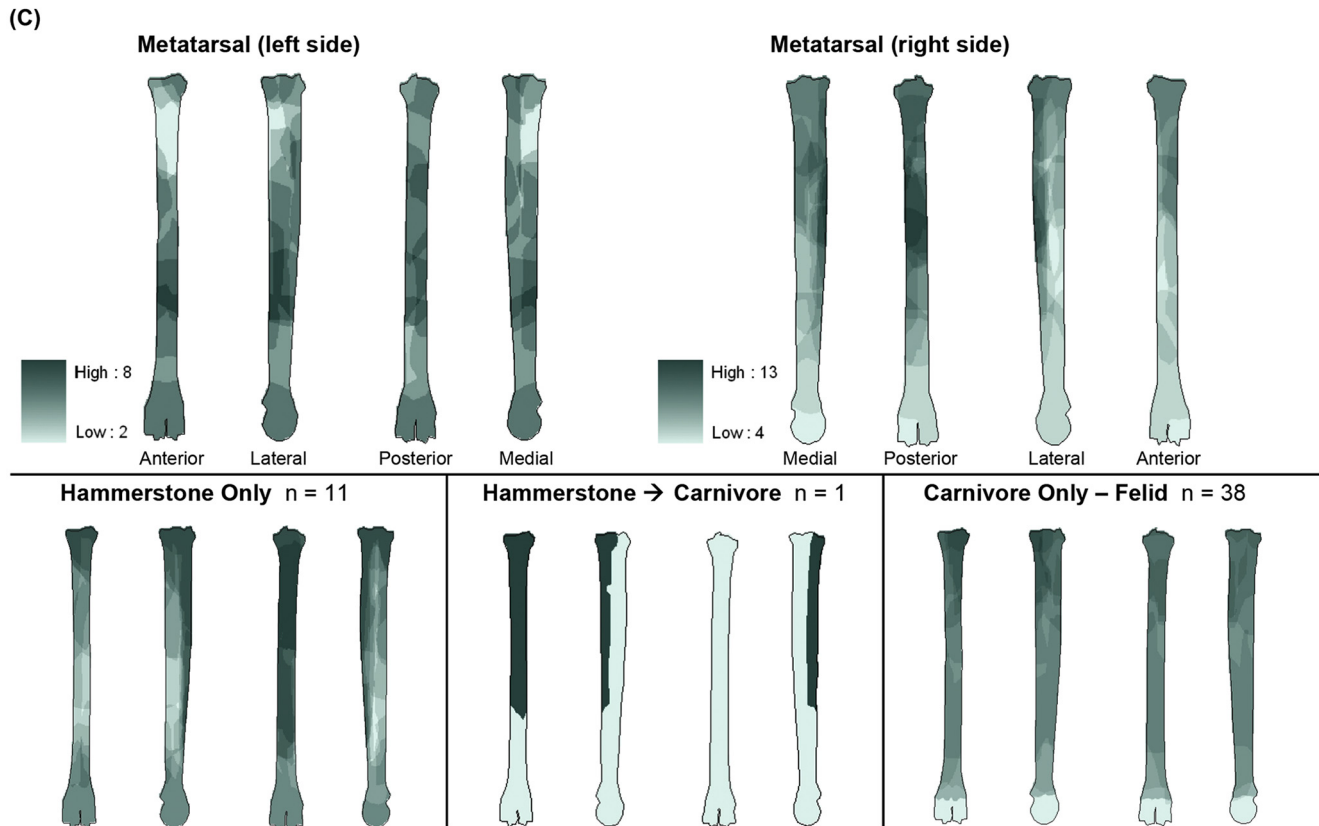


Fig. 5. (continued)

involvement by carnivores other than spotted hyenas. Because hyenas nearly completely destroyed bones from smaller carcasses, this model is only compared with the large bovid bones from FLK Zinj. It should also be noted that the sample size is extremely small for these experiments, in some cases consisting of a single fragmented bone. The sample size is partly a function of a low number of assemblages and small number of bones to begin with, but also reflects the intensive damage hyenas are capable of inflicting on bones compared to canids or felids, such that they have reduced bones to unidentifiable fragments not amenable to GIS analysis.

The felid carnivore models are based on feeding experiments conducted by Parkinson et al. (2015) with captive large felids, including tigers (*Panthera tigris*) and lions (*Panthera leo*) at the Carolina Tiger Rescue in North Carolina. The animals in these experiments are housed in natural habitat enclosures, one acre or larger in size, and are routinely fed a natural, whole carcass diet. Because of this, their carcass consumption behavior is similar to what would be expected in the wild. In this study, animals were fed whole deer (*Odocoileus virginianus*) carcasses or half carcasses obtained as road kill. Carcasses were left in the carnivore enclosures for approximately 48 h before being removed and cleaned. The detailed methodology for these experiments is described by Parkinson et al. (2015). Because felids do not typically fracture larger bones, this model is compared with the small bovid limbs from FLK Zinj.

5.2. Bone portion survivorship – FLK Zinj small and medium bovids

5.2.1. Hindlimb

Small and medium-sized femora from FLK Zinj are well-preserved, but fragmented in a pattern resembling the hammerstone damaged

experimental models (Fig. 5A). From the pattern of preservation observed, it is clear that carnivores or other density mediated agents did not completely remove the epiphyses.

The small and medium-sized tibiae at FLK Zinj (Fig. 5B) show a similar pattern of relatively even preservation across all bone regions. The highest preservation is seen in the midshafts, some proximal epiphyses are deleted, but distal epiphyses are relatively well preserved.

The pattern of preservation in the metatarsals is slightly different between the left and right sides (Fig. 5C). Both left and right metatarsals are highly fragmented, similar to the hammerstone only models. However, the right side is missing more distal epiphyses, likely due to carnivore activity. This slight variation between sides is not unexpected given the relatively small samples size. The pattern on the metatarsals overall is most consistent with the hammerstone only model, while the hammerstone-to-carnivore model is too small to make a useful comparison.

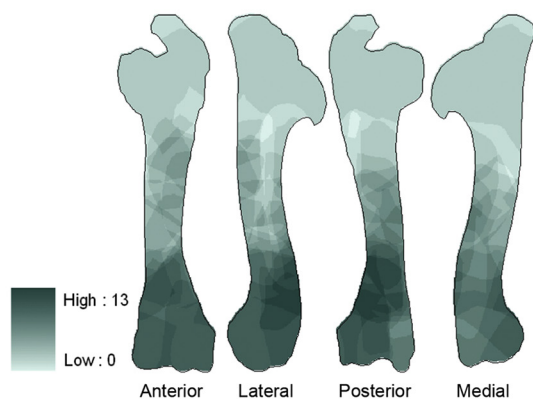
5.2.2. Forelimb

The humeri (Fig. 6A) show a similar fragmentation pattern to the hammerstone only model, but with a slightly greater degree of deletion of the proximal epiphyses. Again, this may be due to carnivore activity, as the grease-rich proximal epiphyses are also often missing in the felid carnivore only experiments. The hammerstone-to-carnivore model shows a total epiphyseal deletion of the humerus which is very different from the FLK Zinj pattern. The hammerstone-to-carnivore model has a small sample size, which may account for the lack of epiphyseal representation, but it is also important to note that the primary carnivore agents in this experiment were bone crunching hyenas which destroy epiphyses much more frequently than felids do.

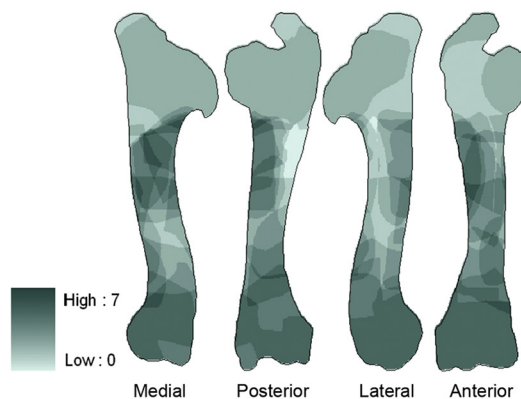
The radii (Fig. 6B) show greater preservation at the proximal end

(A)

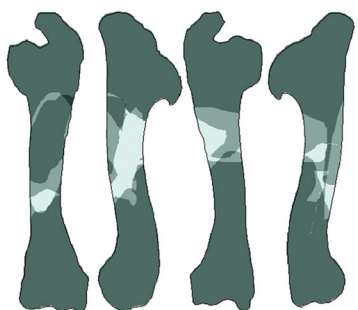
Humerus (left side)



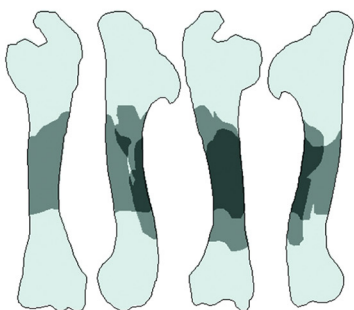
Humerus (right side)



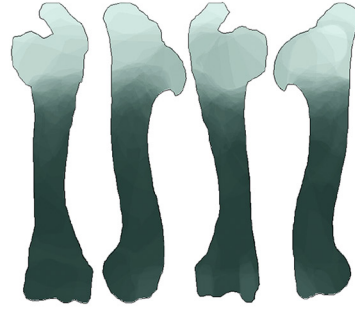
Hammerstone Only n = 7



Hammerstone → Carnivore n = 3

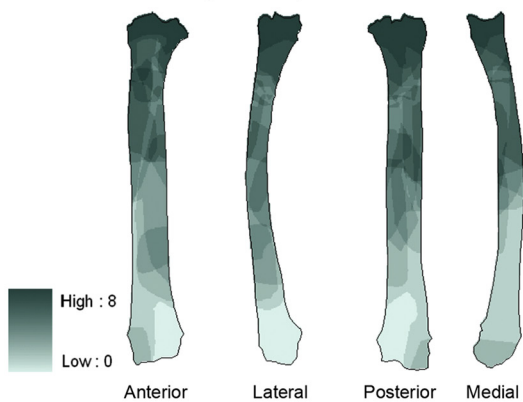


Carnivore Only – Felid n = 56

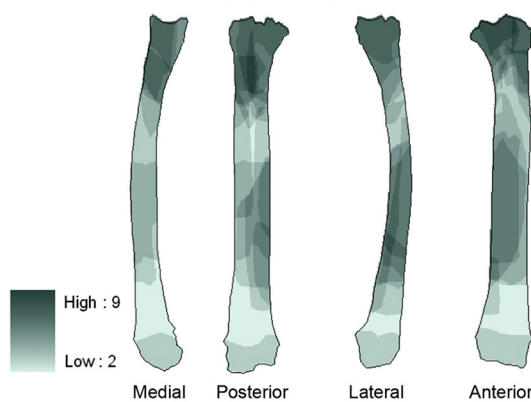


(B)

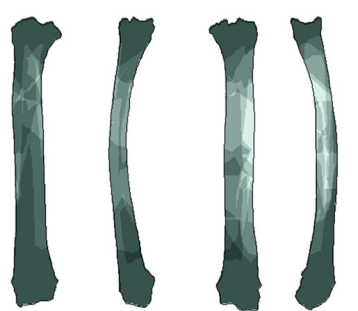
Radius (left side)



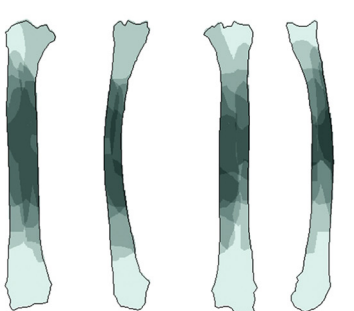
Radius (right side)



Hammerstone Only n = 11



Hammerstone → Carnivore n = 6



Carnivore Only – Felid n = 57



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Fig. 6. Preservation of small and medium bovid forelimbs at FLK Zinj compared with experimental models of bone damage to small/medium bovids. (A) humerus, (B) radius, (C) ulna (D) metacarpal. High = minimum number of elements estimate (greatest number of overlapping fragments). N = greatest number of fragment overlaps in experimental assemblages. Hammerstone Only and Hammerstone→Carnivore models are based on Blumenschine's experimental collection, and represent right/left composite images shown on a left side template. The felid model is from Parkinson et al. (2015). Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, medial.

and shaft than at the distal end. In concordance with this, the proximal ulnae are often well preserved, with intact olecranon processes (Fig. 6C). The ulnae at FLK Zinj are typically highly fragmented, similar to the hammerstone experimental models, but do not display the same degree of epiphyseal deletion seen in the hammerstone-to-carnivore experiment.

The majority of metacarpals at FLK Zinj exhibit a pattern consistent with the hammerstone only experimental model where bones are fragmented, but where all bone portions are preserved (Fig. 6D).

5.3. Bone portion survivorship – FLK Zinj large bovids

5.3.1. Hindlimb

The large, size 3b femora are highly fragmented at FLK Zinj (Fig. 7A). The majority of fragments preserved are shaft fragments, while epiphyses are generally not preserved. The size 3b sample from FLK Zinj included in the GIS analysis is poorly represented in comparison to the smaller bovid sample, so the better regional representation of fragments across the femora for smaller bovids may be related to sample size. The femora are difficult to compare to experimental models due to small sample sizes for models and lack of available hammerstone only models, but the fragmentation level is suggestive of hammerstone breakage. This is further supported by the presence of percussion notches on the large femora and absence of intensive carnivore tooth marking.

The sample size for the large tibiae at FLK Zinj is small ($n = 2$), but preserved areas include the proximal epiphysis and midshaft (Fig. 7B). The presence of a complete proximal epiphysis and lack of carnivore tooth marking on the large tibiae suggest that carnivores were not significantly involved in damaging the fossils.

Only two large metatarsal specimens from FLK Zinj were well enough preserved to place on the GIS template (Fig. 7C). One was a complete bone, the other a distal epiphysis with some shaft attached. There are no hominin or carnivore modifications on these specimens, but the presence of epiphyses is consistent with low carnivore involvement.

5.3.2. Forelimb

Preservation of the proximal epiphysis of large humeri is consistent with experimental models with little or no carnivore involvement, as this portion is often consumed by carnivores due to its low density and high grease content (Fig. 8A).

The large radio-ulnae show preservation of the midshaft and olecranon process and deletion of the distal end (Fig. 8B). This is a pattern most consistent with the hammerstone-to-carnivore experimental model.

Of the two large metacarpal specimens that could be matched to the GIS template, one was mostly complete, and the other was a proximal fragment. Although the sample size is small, the pattern of metacarpal preservation at FLK Zinj is most similar to the hammerstone-to-carnivore experimental model (Fig. 8C).

6. Results: Bone modification patterns

This section presents results of GIS analyses of the distribution of various types of hominin- and carnivore-induced damage to bones from FLK Zinj. As with the analyses of bone portion survivorship, small (size 1–3a) and large (size 3b and above) specimens are considered

separately. GIS density and cluster analyses were conducted to determine whether carnivore tooth marks occur in significant clusters. Density and cluster analyses are presented when sample sizes are large enough (> 5 tooth marks in a particular view). When sample sizes are not large enough to conduct statistical analyses, plots of individual marks on element templates are displayed.

6.1. Patterns of carnivore damage – Small and medium bovids

6.1.1. Hindlimb

Although carnivore tooth marking is reported to occur on small bovid femora from FLK Zinj at a frequency of approximately 14% (on both shaft and end fragments) by Domínguez-Rodrigo and Barba (Domínguez-Rodrigo and Barba, 2006, Table 3), femoral specimens bearing tooth marks were not amenable to GIS image analysis. For the tibiae, GIS cluster analyses show a random pattern of tooth mark distribution on the anterior, lateral, and posterior aspects, but a significant ($p \leq 0.001$) cluster proximally on the postero-medial aspect of the shaft and on the medial aspect of the midshaft (Table 3; Fig. 9). The tooth mark density distribution resembles the hammerstone-to-carnivore experimental model most closely (Supplementary Fig. 1.2). Metatarsals do not show significant clustering of tooth marks, but are gnawed on the distal ends.

6.1.2. Forelimb

The small and medium sized humeri from FLK Zinj show significantly dense clusters of tooth marks distally on the anterior shaft and trochlea as well as on the lateral shaft (Table 3; Fig. 9). Tooth marking on the trochlea is similar to what is seen in the carnivore only experimental models (Supplementary Fig. 2.1). However, the hammerstone-to-carnivore model consists of only 5 fragments (from 3 elements), and so may not be an accurate model of carnivore secondary access.

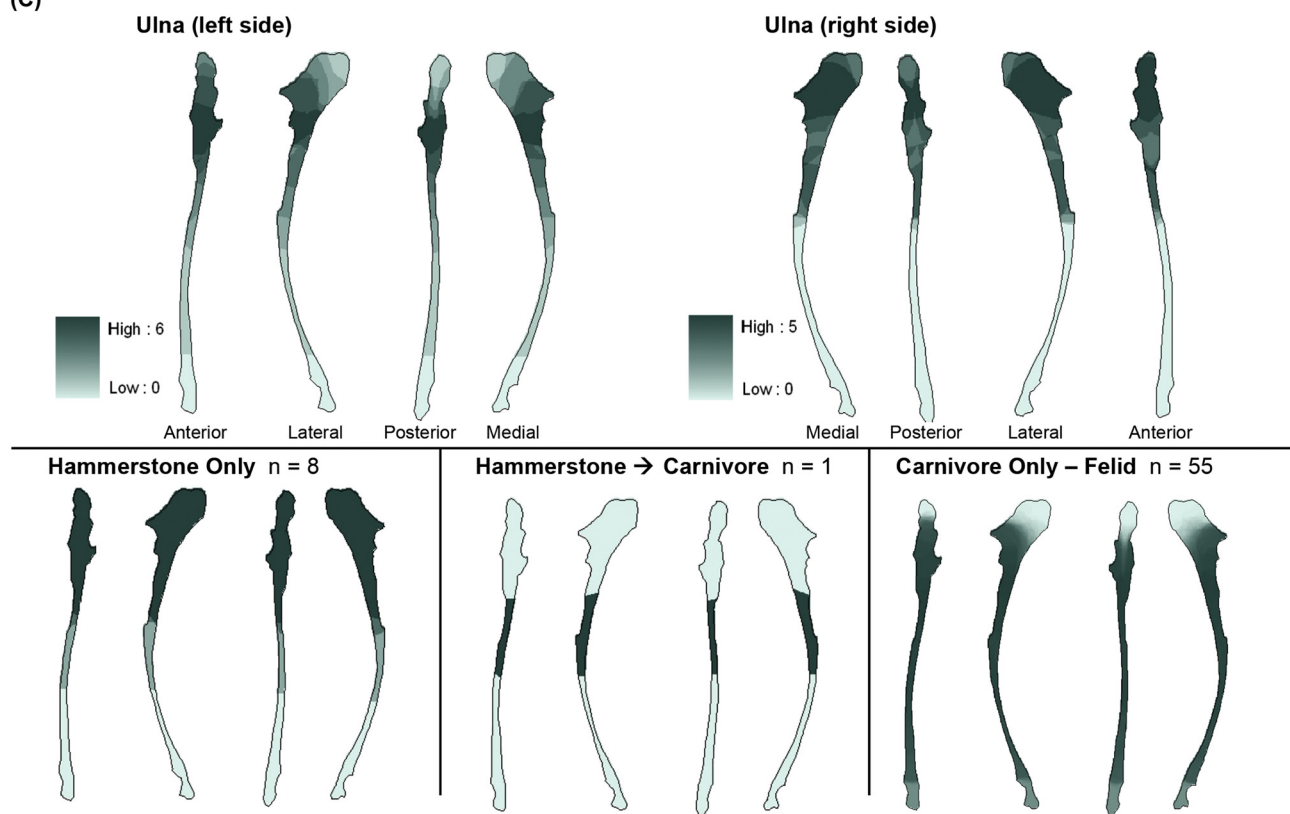
The radii and ulnae are both tooth marked, but where sample sizes are large enough to conduct cluster analyses, results show that tooth marks are randomly distributed. In the carnivore only experimental model (Supplementary Fig. 2.3), tooth marks are confined to the olecranon process of the ulna, but tooth marks on the FLK Zinj ulnae do not follow this pattern. A hammerstone-to-carnivore experimental model is not available for the radius or ulna.

The metacarpals show significant clusters of tooth marks on the posterior shaft proximally and distally, as well as on the proximal-medial shaft. These clusters also occur on the proximal-medial shaft in the carnivore only experimental model. The hammerstone-to-carnivore experimental model shows a similar tooth mark cluster on the medial shaft, however, the sample size is only 1 for this model, and so other potential areas of clustering may not have been preserved (Supplementary Fig. 2.4).

6.2. Patterns of carnivore damage – Large bovids

Only the large bovid femora and radio-ulnae from FLK Zinj were complete enough to be analyzed using the GIS method. Femora show significant clustering of tooth marks on the lateral shaft at the proximal end as well as on the medial distal condyle (Table 4; Fig. 10). Tooth marks are not clustered in these areas in either of the experimental carnivore-modified assemblages (Supplementary Fig. 3). The radius

(C)



(D)

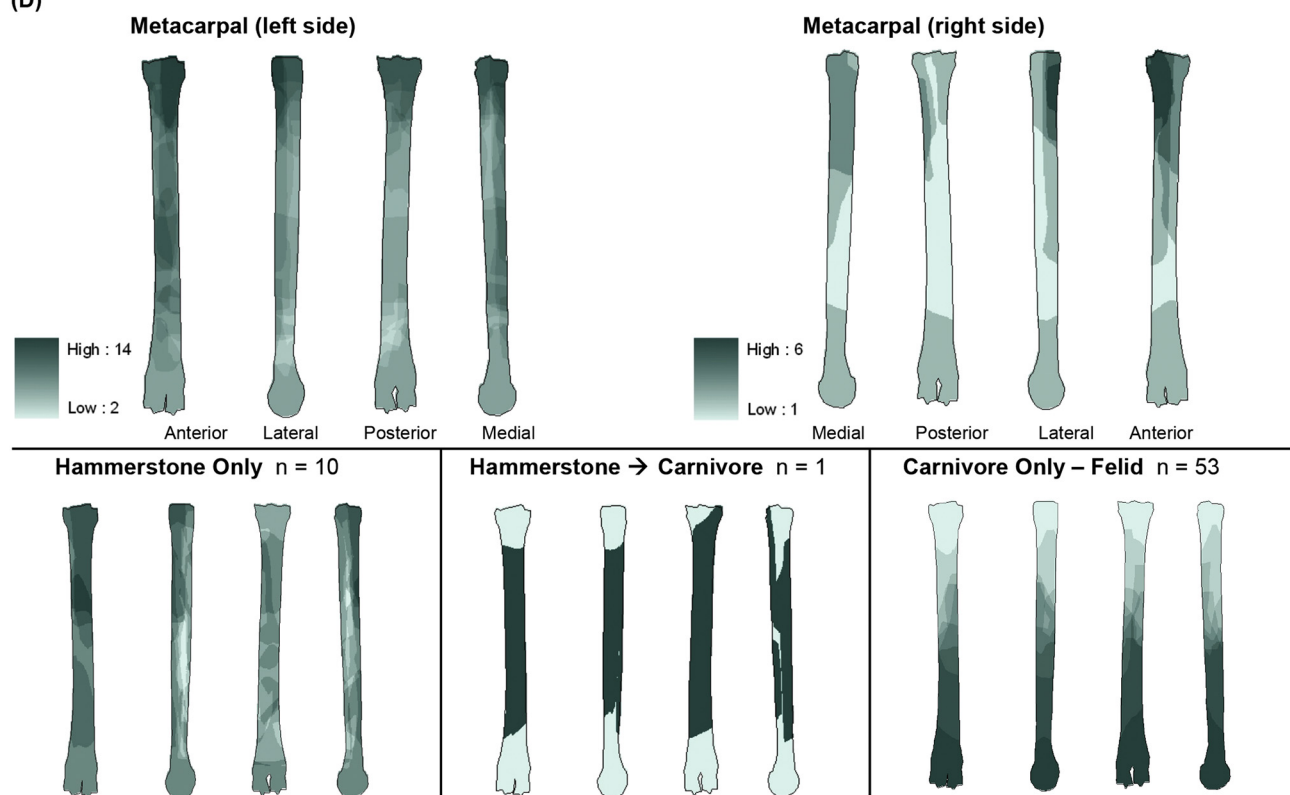
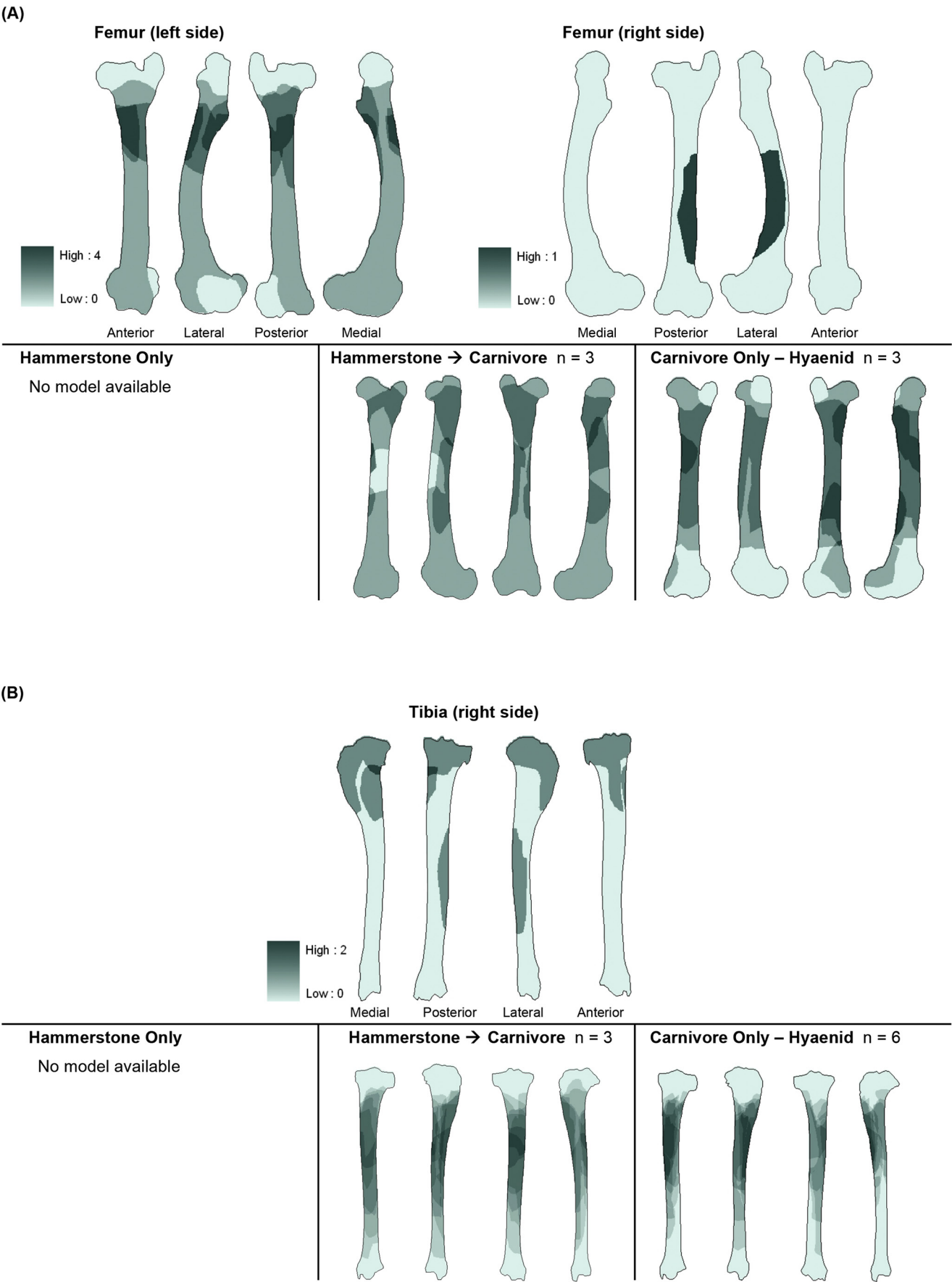


Fig. 6. (continued)



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Fig. 7. Preservation of large bovid hindlimbs at FLK Zinj compared with experimental models of bone damage to large bovids. (A) femur, (B) tibia (only right side available), (C) metatarsal (only left side available). High = minimum number of elements estimate (greatest number of overlapping fragments). N = greatest number of fragment overlaps in experimental assemblages. Hammerstone Only, Hammerstone→Carnivore, and Carnivore Only (hyaenid) models are based on Blumenschine's experimental collection, and represent right/left composite images shown on a left side template. Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, medial.

displays tooth mark clustering on the proximal end of the anterior shaft. The carnivore only experiments do not show a cluster in this area (Supplementary Fig. 4), and a hammerstone-to-carnivore experimental model is not available.

6.3. Patterns of hominin damage – Small and medium bovids

The location of hominin-produced bone surface damage was also plotted onto GIS templates (Supplementary Figs. 5–6). Cut mark distribution was analyzed following the “hot zone” approach of Domínguez-Rodrigo et al. (2007a), where cut marks seen on anatomical areas where flesh typically does not survive felid consumption indicate primary access by hominins. Regardless of cut mark frequency, it is the presence or absence of cut marks in hot zones that is most behaviorally informative because this indicates order of access to the carcass. The location of percussion marks and percussion notches is also shown in Supplementary Figs. 5–6, but it is the cut marks that indicate primary flesh removal, while percussion marks and notches indicate bone breakage after defleshing.

Cut marks occur in hot zones (unshaded areas in Supplementary Fig. 5) on both proximal (femur and humerus) and intermediate (tibia and radius) limb bones of small and medium bovids from FLK Zinj. These marks indicate flesh removal prior to felid involvement, as there would have been no flesh left to remove in these areas if felids had gained first access. Apart from some cut marks in the cold zone on the proximal radius, there do not appear to be significant disarticulation marks, which typically occur at epiphyses. Most cut marks, rather, appear to be the result of defleshing. The proximal and intermediate limbs also bear percussion marking, particularly on the tibiae, indicating bone breakage and processing for marrow. Interestingly, the location of percussion marking on the radii is heaviest on the posterior aspect, which suggests hominins may have been resting the flat posterior surface of the radius against an anvil and striking the anterior surface to break open these bones. Metapodials (not pictured) also display cut and percussion marking indicating thorough processing for marrow by hominins.

These findings corroborate Domínguez-Rodrigo et al. (2007a) study which also found cut marks in hot zones on the FLK Zinj bovid fauna. The anatomical placement of these cut marks reflects early access to fleshed carcasses by hominins prior to carnivore involvement.

6.4. Patterns of hominin damage – Large bovids

Bone surface modifications were more difficult to place on the larger bovid templates. Oliver (1994) found a cut mark frequency of 15% for large femora, but I was unable to place these marks on the GIS template. The radio-ulna was the only element I was able to anatomically place a number of hominin damage points on. As shown in Supplementary Fig. 6, the radio-ulnae are heavily cut marked, and these marks nearly all occur in hot zones, clearly demonstrating removal of tissue by hominins.

7. Discussion

7.1. Extent of hominin involvement at FLK Zinj

The GIS image analysis presented here strongly suggests hominins at FLK Zinj had early access to at least smaller bovids. This is supported by

the patterns of fragmentation. Both forelimbs and hindlimbs of small and medium bovids from the site are highly fragmented, with fracture patterns that resemble experimental models involving hammerstone breakage. However, limb bone epiphyses are preserved less often at FLK Zinj than in the hammerstone only models, while they are better preserved than in the hammerstone-to-carnivore models. The FLK Zinj limb bone fragmentation generally does not resemble the carnivore only felid model, in which fragmentation is low, limb shafts are well preserved, and there is some removal of epiphyses. The fragmentation pattern seen in the FLK Zinj small and medium bovid limbs, which is intermediate between the hammerstone only and hammerstone-to-carnivore experimental models, suggests hominin processing for marrow, but some removal of grease rich epiphyses by scavenging carnivores.

The fragmentation pattern for larger bovids at FLK Zinj is harder to interpret because of the small sample size that was amenable to GIS analysis, but the overall pattern is similar to the smaller bovid pattern: limbs are fragmented, but epiphyses are better preserved than in the hammerstone-to-carnivore models. It should be noted that Blumenschine's experiments were conducted in the Serengeti and Ngorongoro Crater, which are highly competitive ecosystems (Tappen, 1995, 2001), and the experimental models reflect this. Experimental simulations conducted in lower competition woodland environments may not show the same degree of nearly complete epiphyseal removal. Additional experimental modeling in an environment more comparable to the paleoenvironment at Olduvai may provide a better analog. The lower bone portion survivorship seen in the large bovid limbs may also be accounted for simply because there are more nutrients in large bones, so these may have been more thoroughly fragmented by hominins.

Given the number of variables that may affect the frequency of cut marking in an assemblage (e.g., degree of assemblage fragmentation, fossil surface preservation, carnivore ravaging, carcass size), it has been argued that cut mark percentages are of limited value for interpreting the nature of carcass processing by hominins (Delaney-Rivera et al., 2009). Experimental research has failed to show a consistent link between the number of cut and percussion marks and the intensity of processing (Egeland, 2003; Lyman, 2005; Pobiner and Braun, 2005; Pickering and Egeland, 2006). However, examining the anatomical placement rather than frequency of cut marks can be informative for investigating the timing of access to carcasses by hominins. For this reason, I chose to reexamine the anatomical placement of cut marks on the FLK Zinj fauna using the “hot zone” approach developed by Domínguez-Rodrigo and Barba (2006). The hot zone approach, initially based on a study of flesh availability on lion kills in the wild by Domínguez-Rodrigo (1999), was further supported in my own experiment of flesh availability following consumption of whole carcasses by captive felids (Parkinson et al., 2015).

According to my reanalysis, cut marks on small and medium bovids from FLK Zinj are located in hot zones, or areas that do not preserve flesh following lion consumption. This reanalysis of cut mark placement is consistent with what was reported by Domínguez-Rodrigo et al. (2007a). The location of cut marks in hot zones indicates butchery of fully fleshed carcasses, and removal of flesh prior to any felid involvement. This suggests hominins had primary access, because there would have been no flesh left to remove in these areas if hominins were passively scavenging. For the larger bovid limbs, only the radio-ulnae had a large enough sample size to analyze for cut mark distribution. The

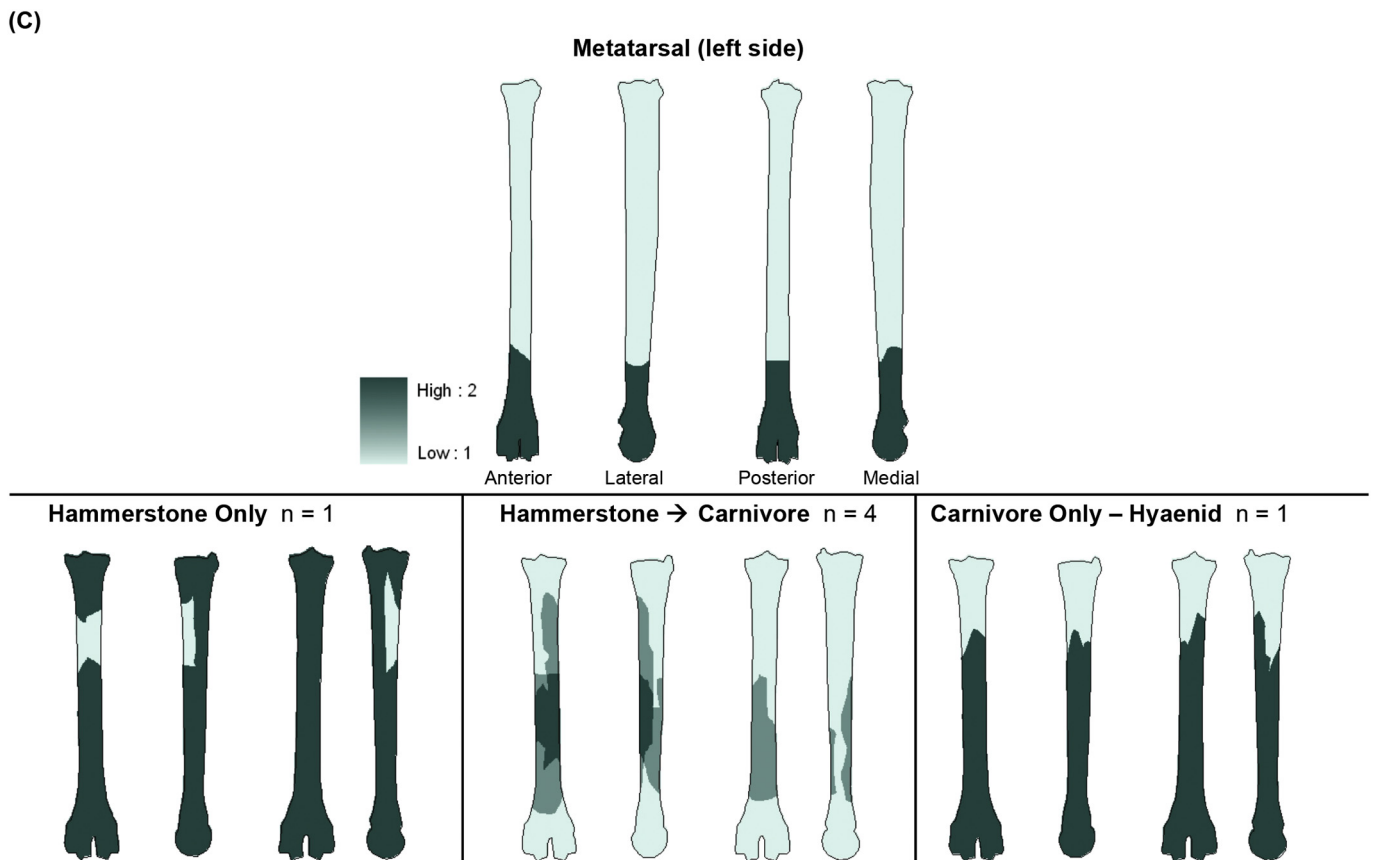


Fig. 7. (continued)

radio-ulnae also preserve cut marks in hot zones, indicating primary flesh removal by hominins. The presence of percussion markings on the FLK Zinj fauna further provides evidence of hammerstone breakage indicating full processing of carcasses by hominins, including marrow extraction. Further, the presence of some grease-rich epiphyses in the assemblage indicates low carnivore involvement.

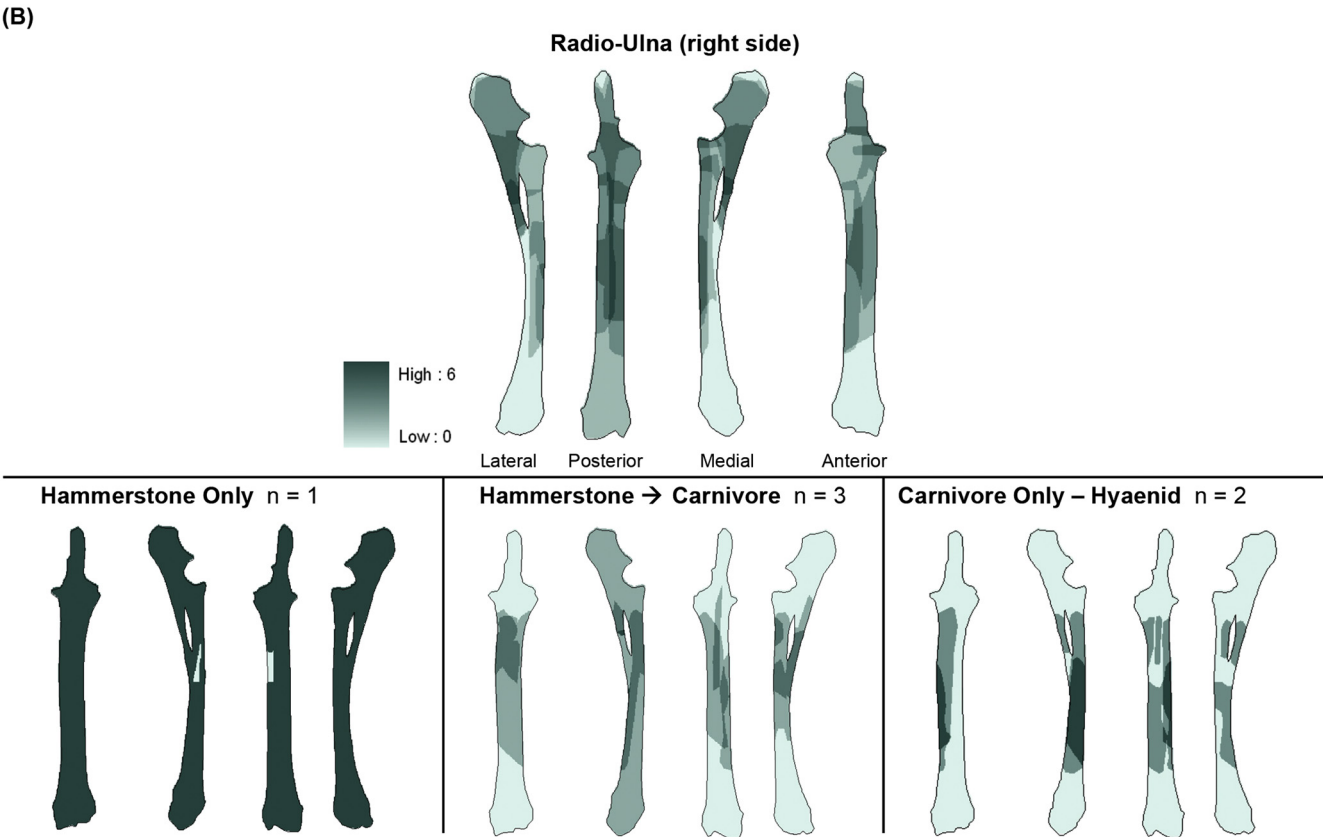
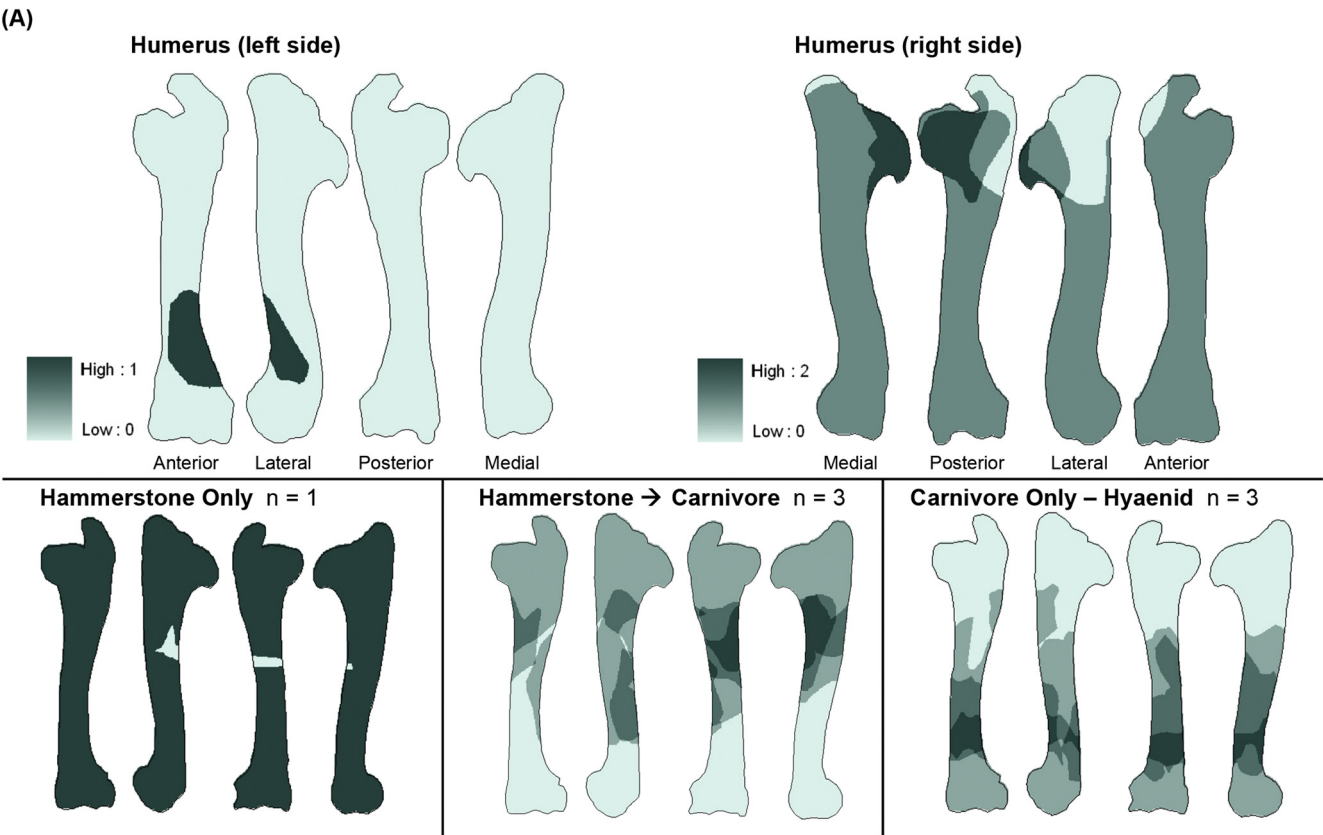
7.2. Extent of carnivore involvement at FLK Zinj

The low tooth mark frequency as well as the distribution of tooth marks on the FLK Zinj fossils suggest carnivores had secondary access. GIS cluster analyses of tooth marks on the small and medium bovid limb bones show, more often than not, a dispersed pattern of tooth marking. When clusters are identified and compared with experimental models, they most resemble the hammerstone-to-carnivore models. The larger bovid tooth marking patterns are more difficult to interpret, and only the femur and radio-ulna had sample sizes large enough to conduct cluster analyses on. The large bovid femora do show significant clusters of tooth marks, but the distribution is different from the available experimental models. This is not unexpected given that the experimental models (particularly for dual patterned assemblages: i.e., assemblages modified by multiple actors) are limited, and it is unlikely they have captured the full range of possible tooth marking patterns. The large radio-ulnae from FLK Zinj also show significant tooth mark clustering, but not in a pattern replicated in the carnivore only experimental models (a hammerstone-to-carnivore experimental GIS model is not available).

There has been considerable disagreement in the literature over tooth marking frequencies in the FLK Zinj assemblage (Domínguez-Rodrigo and Barba, 2006; Blumenschine et al., 2007; see also Oliver, 1994). Blumenschine (1995) reported an assemblage-wide tooth mark

frequency of 61% of the NISP. Domínguez-Rodrigo and colleagues have reported comparatively low tooth mark frequencies at the site (17% of the NISP). The independent reanalysis of the tooth mark frequency I report here (24% of the NISP) is more consistent with the level of carnivore damage that Domínguez-Rodrigo's group documented. In the shared sample analyzed by both Domínguez-Rodrigo and myself, my identification showed 92.5% concordance with his. This suggests that biochemical damage could potentially have been a factor in the higher tooth mark frequencies reported by Blumenschine. The tooth mark frequencies I report here fall within the 95% confidence interval of experimental models where carnivore activity followed initial hominin access (i.e., Blumenschine's hammerstone-to-carnivore model; see Blumenschine, 1995, Table 3) and also within the 95% interquartile range (bootstrapped confidence interval) for the same model reported by Pante et al., (Pante et al., 2012, Table 3). Tooth marking to the degree suggested by Blumenschine (1995) is not supported by this study, nor is the passive scavenging model of carcass access for hominins at FLK Zinj.

Although Blumenschine and others have supported the hypothesis of passive scavenging from felid kills, this hypothesis has been based on modern experimental models where humans had primary access and where hyaenas, not felids, were the primary carnivore agent involved. There have actually been no experimental taphonomic models simulating dual patterned scenarios where felids had primary access. However, in recent digital modeling of a lion-to-hammerstone scenario, Organista and colleagues (Organista et al., 2016; and see Domínguez-Rodrigo et al., 2007b) showed that tooth mark frequency on limb shaft fragments was low and overlapped the range seen in the hammerstone first models. Given this, it is clear that tooth mark frequency should not be used in isolation to indicate order of access, but rather, multiple lines of evidence, including mark distribution patterns, should be considered



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Fig. 8. Preservation of large bovid forelimbs at FLK Zinj compared with experimental models of bone damage to large bovids. (A) humerus, (B) radio-ulna, (C) metacarpal. High = minimum number of elements estimate (greatest number of overlapping fragments). N = greatest number of fragment overlaps in experimental assemblages. Hammerstone Only, Hammerstone→Carnivore, and Carnivore Only (hyaenid) models are based on Blumenschine's experimental collection, and represent right/left composite images shown on a left side template. Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, medial.

(see also Domínguez-Rodrigo et al., 2014).

7.3. Which carnivore taxa were involved in modifying the FLK Zinj assemblage?

The African large carnivore guild during the Early Pleistocene included a higher species diversity than the modern guild, and this higher diversity is accounted for mainly by felids. In addition to extant lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*), the East African carnivore guild included three now extinct sabertooth felid genera (*Dinofelis*, *Megantereon*, and *Homotherium*) which could have contributed to modifying the assemblage at FLK Zinj. The fact that we do not have extant analogs for these taxa complicates attempts to experimentally reproduce their feeding signatures. However, based on analyses of the functional morphology of sabertooth dentition, their carcass processing abilities were probably not significantly different from modern large felids (Hartstone-Rose and Wahl, 2008).

In their analysis of multiple Olduvai faunal assemblages, Domínguez-Rodrigo et al. (2007a) have identified hallmark characteristics of felid involvement in several of the FLK North sites, but not at FLK Zinj. However, some isolated tooth marked specimens from FLK Zinj are identical to those produced in my own captive felid feeding experiments described by Parkinson et al. (2015) (Fig. 11).

In an attempt to distinguish which carnivore taxon may have been involved in modifying the FLK Zinj assemblage, Domínguez-Rodrigo and Barba (2006) measured tooth pit size in the assemblage, and found that pit sizes on cortical bone surfaces fall within the range exhibited by hyenas in experimental assemblages and below the mean for lions. However, in further experiments, Delaney-Rivera et al. (2009) found that tooth pit size on cancellous, epiphyseal bone portions better discriminates between different sized carnivores than pits on cortical bone. In the FLK Zinj assemblage, the range of tooth pit sizes on cancellous bone overlaps with the range reported for hyenas and lions, and the mean is higher than that reported for leopards and cheetahs (Domínguez-Rodrigo and Barba, 2006). In a study by Selvaggio and Wilder (2001), which used a different comparative experimental sample, tooth pit size on cancellous bone from FLK Zinj was reported to fall within the range of cheetahs, leopards, and spotted hyenas. It should also be noted that tooth pit sizes on epiphyses at FLK Zinj are within the range of dogs from experiments conducted by Domínguez-Rodrigo and Piqueres (2003). While these studies make identifying specific carnivore taxon difficult due to overlap in the range of pit sizes inflicted by different carnivores, it is clear that the FLK Zinj fauna was modified by a large carnivore.

One additional possibility that should be noted is that hominins may have tooth marked some of the specimens at FLK Zinj. This is a suggestion that has previously been made by Oliver (1994). More recently, experimental work by Fernández-Jalvo and Andrews (2011) and Saladié et al. (2013) showed that humans produce an extensive array of damage that is sometimes similar to that produced by large carnivores. If hominins were responsible for some of the tooth marks at FLK Zinj, this would mean overall tooth marking frequencies due to carnivores should be somewhat lower. Further taphonomic work on the FLK Zinj assemblage would be needed in order to assess this possibility.

7.4. How did hominins gain access to carcass resources at FLK Zinj?

The evidence presented here suggests hominins had primary access

to carcasses at FLK Zinj, but it is also clear that large carnivores contributed to modifying the assemblage. Given the evidence for bone preservation patterns, cut mark distribution, tooth mark frequency and distribution, and comparison of these data with experimental models, what behavioral scenarios can be inferred for hominins at FLK Zinj?

The nature and timing of hominin access to carcass resources by early genus *Homo* has been debated for several decades, and the discussion has typically been framed as a debate over hunting versus scavenging. Scavenging hypotheses span a continuum ranging from passive to more active models of scavenging. Binford's (1981) original passive scavenging model argued that hominins obtained only occasional scraps of flesh and marrow once carnivores had fully abandoned carcasses after feeding. Blumenschine (1987) and others (Blumenschine and Cavallo, 1992; Selvaggio, 1998) have argued that hominins may have found a scavenging niche focused on marrow extraction from abandoned felid kills in woodland contexts. Bunn's (2001) active, confrontational scavenging (or power scavenging) model, where carnivores would have been actively chased from carcasses, would have yielded more substantial amounts of flesh.

Domínguez-Rodrigo and colleagues (Domínguez-Rodrigo, 1999; Domínguez-Rodrigo et al., 2007a; Gidna et al., 2014) have argued that, based on flesh availability on carcasses abandoned by lions in modern habitats, scavenging flesh from felid kills would not have been a reliable strategy for hominins, as only within-bone resources (marrow and brain) remain. My own study of flesh availability on carcasses following feeding by captive large felids (Parkinson, 2013; Parkinson et al., 2015) demonstrates a similar pattern of nearly complete defleshing of all upper limb bones, lending further support to the idea that passive scavenging would not have been a dependable strategy for hominins. However, other experimental work by Pobiner (2015) found greater survival of flesh on large carcasses following lion consumption in the wild. Pobiner found that the amount of scavengable meat remaining on large ungulate prey in her study was actually enough to meet the total daily caloric requirements of one *Homo erectus* individual. Given that the results of Pobiner's (2015) study differ from the results of Domínguez-Rodrigo (1999), Gidna et al. (2014), and Parkinson et al. (2015), it is apparent that ecosystem factors including habitat, prey size and biomass, carnivore density, and carnivore guild composition likely affect the amount of flesh surviving on felid kills and the scavenging opportunities that potentially would have been available to hominins. In woodland environmental settings such as the paleoenvironment at FLK Zinj (Arráiz et al., 2017) where competition was likely to be relatively low, passive scavenging from abandoned felid kills may have been a viable strategy, particularly for obtaining marrow and flesh scraps from larger sized carcasses. However, the taphonomic evidence indicates that hominins had early access to smaller carcasses, and potentially early access to larger carcasses as well. This evidence does not support a passive scavenging hypothesis. On the other hand, aggressive scavenging, where hominins drove large felids away from carcasses could potentially have yielded significantly greater quantities of flesh. This would have been easier for hominins if felids were solitary.

The evidence presented here from the GIS image analysis of the FLK Zinj fauna, along with the reanalysis of bone surface modification frequencies from this site, is consistent with an interpretation of early access by hominins to fleshed carcasses. The question then remains: how did hominins acquire fleshy carcasses? Hunting and/or aggressive scavenging are two potential methods of acquiring complete carcasses.

Lieberman and colleagues (Lieberman et al., 2009, and see Bramble

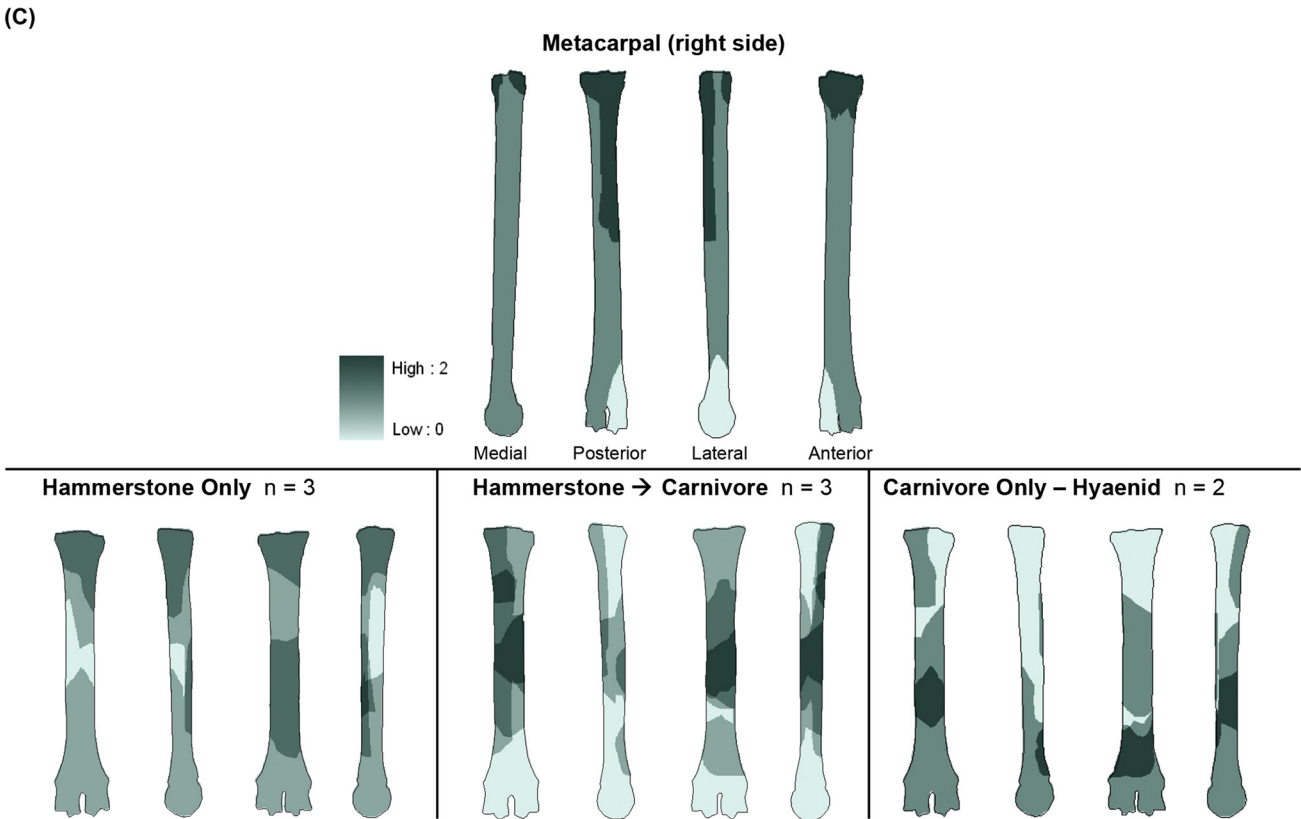


Fig. 8. (continued)

Table 2
Summary of experimental collections in GIS models.

Collection	Carnivore agent	Reference	Location	NISP*
Carnivore only	Felid	Parkinson et al., 2015	University of San Diego	435
Carnivore only	Hyaenid	Blumenschine, 1988	Rutgers University	80
Hominin → carnivore	Hyaenid	Blumenschine, 1988	Rutgers University	138
Hammerstone only	n/a	Blumenschine, 1988	Rutgers University	238

* Number of identifiable specimens.

and Lieberman, 2004) suggested that endurance running may have been selected for in early *Homo* approximately 2 Ma as an adaptation for persistence hunting, which would have allowed hominins to obtain high quality animal tissues (including meat and marrow). Endurance running may have facilitated hunting by allowing hominins to essentially run mammals to exhaustion and obtain meat without the aid of sophisticated hunting technology. Persistence hunting through endurance running has been documented in ethnographic contexts including in the Kua of the central Kalahari (Lee, 1979; Liebenberg, 2006), as well as by some Native American tribes (Lowie, 1924) and the Tarahumara of northern Mexico (Pennington, 1963).

If Early Stone Age hominins were hunting, they might have accomplished this through endurance running/persistence hunting (sensu Lieberman et al., 2009) or by ambushing prey. Both of these techniques would lead to a pattern of bone surface damage indicating early access, as found in the FLK Zinj assemblage. What might distinguish one

technique from the other is evidence from prey mortality profiles (age structure) in the fossil assemblage. Prey mortality profiles reflect the carcass access opportunities available to hominins. Mortality profiles in fossil assemblages are assessed through comparison with predicted profiles based on modern analogs for differing scenarios of hunting or scavenging. If hominins were practicing endurance running/persistence hunting to obtain carcasses, bovid mortality profiles should match what cursorial predators are known to kill: the relatively vulnerable young and old (i.e., an attritional profile following Klein, 1982). Bunn and colleagues (Bunn and Pickering, 2010; Bunn and Gurtov, 2014) have argued that the bovid mortality profile evidence from FLK Zinj does not support an endurance running technique for hunting large bovids at the site. The large bovids from FLK Zinj show a mortality pattern consisting of prime-aged adults. This is a pattern normally seen only in human-produced mortality profiles (Steele, 2003). The small bovids from FLK Zinj show a different mortality pattern consisting of mainly older individuals, which is the pattern seen for cursorial predators, such as wolves, African wild dogs, and spotted hyenas (Stiner, 1990; Steele, 2003), and the one expected to result from endurance running.

If hominins at FLK Zinj were not persistence hunting to the obtain large carcasses, perhaps they were ambushing their prey. Bunn and Pickering (2010) have argued that hominins waited in trees near game trails and speared prey that came nearby. There is currently no evidence for lethal weaponry in the archaeological record at this time, however, the absence of hunting technology does not necessarily indicate an absence of hunting capability. The absence of hunting technology in the Early Stone Age could be a taphonomic issue. We do not have a record of tools made out of perishable materials such as wood (Plummer, 2004). Bunn and Pickering believe wooden spears could have possibly been used for ambush hunting, given use-wear evidence for wood working on artifacts from Koobi Fora (Keeley and Toth, 1981) at ca. 1.5 Ma. Use-wear indicating woodworking is also found on even

Table 3
GIS cluster analysis for tooth marks on small and medium bovid limb elements from FLK Zinj.

Element	Anterior	Lateral	Posterior	Medial
Humerus				
NNI	Clustered 0.54	Clustered 0.28	Random 0.73	Random 0.72
p	0.01	0.002	0.15	0.16
Radius				
NNI	n/a	n/a	Random 0.75	n/a
p			0.247	
Ulna				
NNI	n/a	n/a	n/a	Random 1.08
p				0.714
Metacarpal				
NNI	Dispersed 1.55	n/a	Clustered 0.40	Clustered 0.62
p	0.003		< 0.001	0.081
Femur				
NNI	n/a	n/a	n/a	n/a
p				
Tibia				
NNI	Random 1.35	Random 0.95	Random 0.80	Clustered 0.400
p	0.132	0.746	0.150	< 0.001
Metatarsal				
NNI	n/a	n/a	n/a	n/a
p				

Analysis was performed on four sides of all elements. The distance between each tooth pit and its nearest neighbor was measured. The nearest neighbor index (NNI) is the observed distance divided by the average expected distance in a hypothetical random distribution. If the NNI is < 1, the pattern is considered clustered. If the NNI is > 1, the trend is toward dispersion. *P*-values indicating significant clustering of tooth pits appear in bold. Cells with n/a indicate sample sizes too small for analysis (containing < 5 individual tooth marks).

older artifacts from Kanjera South (Plummer and Bishop, 2016; Lemorini et al., 2014). Phytoliths from the edges of handaxes from Peninj, Tanzania, a locality several hundred thousand years younger than FLK Zinj, also suggest wood working (Domínguez-Rodrigo et al., 2001). Further, observations have been made in the wild of chimpanzees making and using sharpened sticks to stab bushbabies (Pruetz and Bertolani, 2007). If chimpanzees recognize that a sharpened stick can be used to stab prey, and modify and utilize such sticks for this purpose, it is not a stretch to imagine hominins using stone tools to shape branches in order to form thrusting spears.

Aggressive (power) scavenging from felid kills is an alternative explanation that could account for early access by hominins to bovids at FLK Zinj. The idea that hominins were scavenging from large felid kills is something that was originally suggested by Blumenshine and colleagues (Blumenshine, 1995; Selvaggio, 1998), although the current study and others (Bunn, 2001; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2007a) provide strong evidence against passive scavenging from large felids at FLK Zinj. Bunn and Pickering (2010) argue that the prime-dominated bovid mortality profile at FLK Zinj does not match that of modern lions (as reported by Schaller, 1972), which are less selective and tend to be biased toward older individuals, and so the FLK Zinj mortality profile cannot represent remains of large felid kills scavenged by hominins.

It should be noted, however, that although modern lion prey mortality patterns do not overlap with the large bovid pattern at FLK Zinj, the mortality profile in the non-anthropogenic “background” scatter on the Olduvai paleolandscape overlaps significantly with the mortality profile of the FLK Zinj large bovids (see Bunn and Pickering, 2010,

Fig. 3). This “background” scatter consists of the FLK N 1–2, FLK N 6, and FLK NN 2 sites, which have been argued to be primarily accumulated by extinct felids (Arriaza and Domínguez-Rodrigo, 2016; Domínguez-Rodrigo et al., 2007a). Given that a greater diversity of large felids existed in the past, we should not be too quick to assume that modern lions are an identical proxy for extinct felids which likely had different feeding ecologies. *Homotherium*, an extinct sabertooth felid that rivaled modern lions in size, has been reconstructed as a possible pack hunter and so may not have provided safe scavenging opportunities for hominins (Lewis, 1997). However, the extinct sabertooth felid *Megantereon* and the “false sabertooth” *Dinofelis* may have been solitary, ambush predators in mixed or closed habitats (Werdelin and Lewis, 2001). One can imagine that a group of hominins would have been able to drive a solitary sabertooth felid away from a kill. Further, it seems plausible that sabertooth felids adapted to ambush hunting in woodlands would have frequently killed size 3 prime adults as leopards do with smaller prey. It has also been suggested that sabertooths may have taken larger prey sizes (medium to large ungulates) because they could have made a larger killing slash with their canine than modern felids can (Emerson and Radinsky, 1980).

One additional consideration that we cannot dismiss is the potential that carnivore and hominin activities were unrelated at the site. Carnivore and hominin damage do not appear on the same individual bones, which makes inferences about interactions between these agents at the site more tenuous. FLK Zinj may represent a locale that was attractive to both tool-making hominins and carnivores, but their activities may be temporally unrelated. This “common amenity” hypothesis was first formulated by (Isaac, 1983) and recently argued to explain other Bed I Olduvai sites including DK, FLK N, and FLK NN where hominin and carnivore activities appear to be unrelated (Domínguez-Rodrigo et al., 2015).

Given the differences in the large carnivore guild structure, evidence that the FLK Zinj bovid mortality profile closely resembles the apparently felid-accumulated background scatter at Olduvai, evidence for early access to fleshed carcasses presented here and by others, and evidence for isolated damage patterns that resemble those of modern felids (Fig. 11), it seems plausible that a power scavenging scenario of hominins stealing large prey from felids could also have led to the mortality profile seen in the FLK Zinj assemblage. For smaller bovids, the evidence for early access by hominins described here and by others, coupled with the data showing an attritional mortality profile composed of mainly older adults (Bunn and Pickering, 2010), lends support to the persistence hunting hypothesis. Bunn and Pickering have argued against the persistence hunting hypothesis, but their mortality profile data for small bovids at FLK Zinj (old-adult-dominated) is more consistent with persistence hunting than it is with ambushing.

8. Conclusions

The evidence presented in this study including carnivore tooth mark frequencies, patterns of bone surface modification produced by hominins and carnivores, and patterns of bone fragmentation, indicates that hominins had early access to fleshed carcasses of small- and medium-sized bovids at FLK Zinj. The larger bovids are more difficult to interpret due to smaller sample size, but they are also suggestive of early access. The small and medium carcasses may have been acquired through hunting. Carnivores tend to destroy smaller carcasses, so active scavenging is not likely to explain hominin acquisition of relatively complete small bovids. Evidence for hominin-produced damage on larger bovids is consistent with early access, although the smaller sample size makes this difficult to interpret as confidently. Hunting cannot be ruled out, but aggressive scavenging of large bovids from felids also plausibly explains early hominin access to large bovids at FLK Zinj.

These findings have important implications for understanding the socioecology of early genus *Homo* and are directly relevant to current

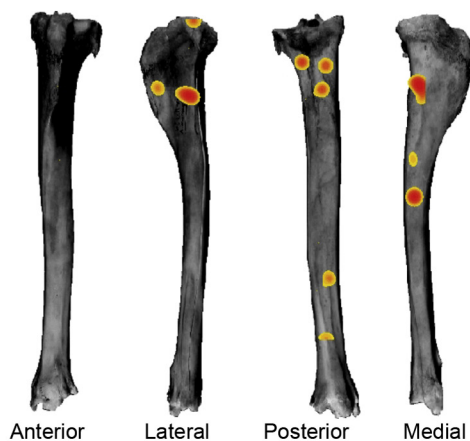
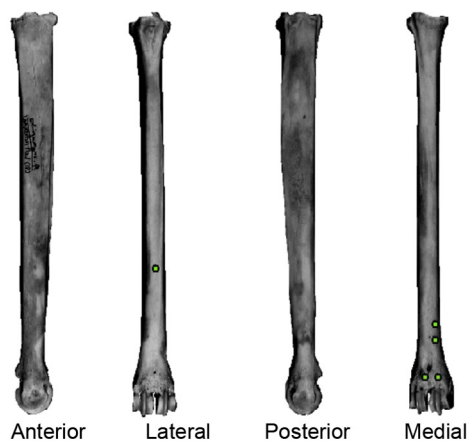
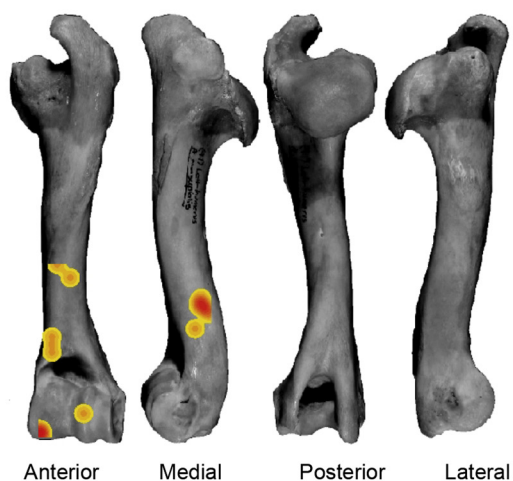
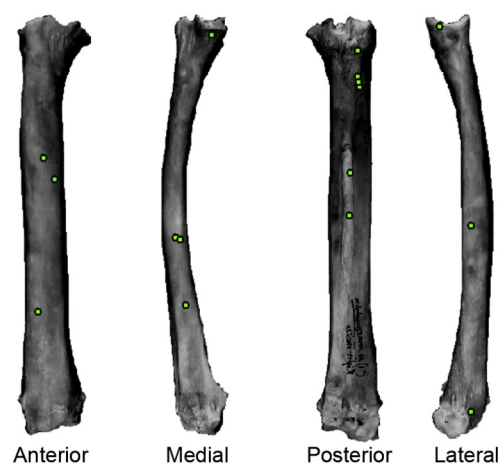
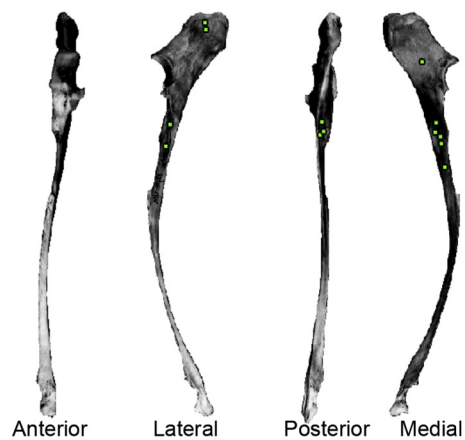
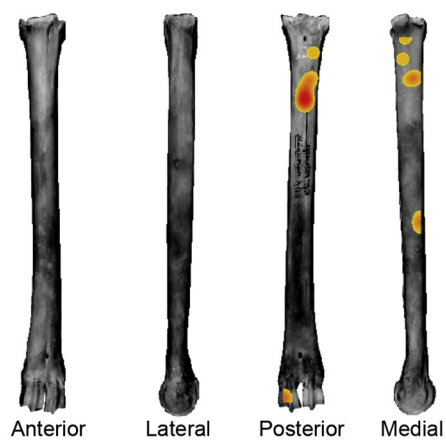
Tibia n = 20**Metatarsal** n = 5**Humerus** n = 13**Radius** n = 13**Ulna** n = 3**Metacarpal** n = 8

Fig. 9. Distribution of carnivore damage on the small and medium bovids from FLK Zinj. Figures represent composites of modifications on right and left elements shown on a left side template. Where sample sizes are large enough and clustering is significant, GIS density analyses are shown. Where sample sizes are small, distribution of individual tooth pits (green points) are shown. Tooth marking includes both pits and scores. n = the number of specimens bearing tooth marks.

Table 4
GIS cluster analysis for tooth marks on large bovid limb elements from FLK Zinj.

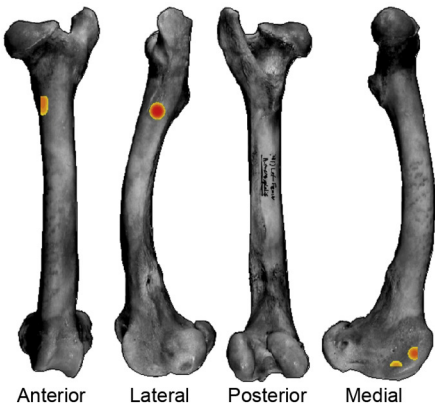
Element	Anterior	Lateral	Posterior	Medial
Radius				
NNI	Clustered	n/a	n/a	n/a
p	0.52			
	0.016			
Femur				
NNI	Dispersed	Clustered	n/a	Clustered
p	1.22	0.29		0.30
	0.010	0.002		0.003

Analysis was performed on four sides of the radius and femur, as sample sizes for other limb elements were too low (< 5 tooth marks per aspect). The distance between each tooth pit and its nearest neighbor was measured. The nearest neighbor index (NNI) is the observed distance divided by the average expected distance in a hypothetical random distribution. If the NNI is < 1, the pattern is considered clustered. If the NNI is > 1, the trend is toward dispersion. P-values indicating significant clustering of tooth pits appear in bold. Cells with n/a indicate sample sizes too small for analysis (containing < 5 individual tooth marks).

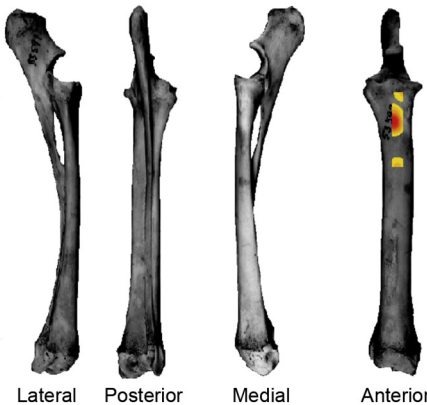
debates related to social organization, mobility patterns, and cooperative behavior in Early Stone Age hominins. The appearance of genus *Homo* approximately 2.3 Ma (and perhaps earlier) is broadly associated with an increase in brain size and a shift toward more modern body proportions as well as the development of stone tool use. Brains are metabolically expensive organs, and an increase in brain size would also have entailed an increased caloric requirement for early *Homo*. As a calorically-dense resource providing protein and fat in an easily digestible form, it is likely that meat played a key role in fulfilling these requirements. Animal tissue is not only a potentially nutritionally important resource, but also a socially important one. The evidence presented here indicating hominins had early access to carcasses at FLK Zinj implies the potential for consistent meat eating - a behavior that has also been inferred for the slightly older Oldowan site of Kanjera South. Consistent access to meat and a concurrent increase in brain size may have facilitated advances in stone tool technology and manufacture as well as spurred changes in ranging behavior. The potential food surpluses that could result from consistent meat eating may have also prompted food sharing or other cooperative behaviors that are important in modern human groups.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2018.06.044>.

Femur n = 1



Radio-Ulna n = 6



FLK Zinj **Felid Experiments**



Fig. 11. Carnivore tooth marks at FLK Zinj and in experiments conducted with modern captive felids at the Carolina Tiger Rescue (CTR). (A) distal femur (Cat. # F220) from FLK Zinj, (B) distal femur from CTR (Cat. # 221), (C) scapula from FLK Zinj, dorsal view (Cat. # C1153), (D) scapula from CTR, dorsal view (Cat. # 614).

Fig. 10. Distribution of carnivore damage on the large bovids from FLK Zinj. Figures represent composites of modifications on right and left elements shown on a left side template. Only samples for the femur and radio-ulna were available, but these were large enough to conduct density analyses, which are shown here. Tooth marking includes both pits and scores. n = the number of specimens bearing tooth marks.

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