Meat on the menu: GIS spatial distribution analysis of bone surface damage indicates that Oldowan hominins at Kanjera South, Kenya had early access to carcasses

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ABSTRACT

The shift to increased meat consumption is one of the major adaptive changes in hominin dietary evolution. Although meat eating by Oldowan hominins is well evidenced at Pleistocene archaeological sites in eastern Africa by butchery marks on bones, the methods through which carcasses were acquired (i.e., hunting vs. scavenging) and extent of their completeness (fleshed vs. defleshed) is less certain. This study addresses these issues through a geographic information systems (GIS) comparative analysis of bone modification patterns created by hominins and carnivores observed in the ca. 2.0 Ma assemblage from Kanjera South, Kenya and those of several modern, experimentally modified bone assemblages. Comparison of GIS-generated models shows that the pattern of bone preservation at Kanjera South is similar to that found in experimental bone assemblages that were first butchered and hammerstone fractured by humans, and subsequently scavenged by carnivores. The distribution of bone modifications on the

Kanjera fauna also suggests hominins had early access to small bovids. Butchery marks appear almost exclusively in ‘hot zones’—areas where flesh does not typically survive lion consumption—further suggesting Kanjera hominins were not scavenging carnivore kills. Our findings support previous claims that the Kanjera assemblage offers the earliest clear evidence of repeated butchery of antelope carcasses by Early Stone Age (Oldowan) hominins and perhaps the earliest evidence for hunting. Kanjera carnivore damage frequencies are lower than those reported for the slightly younger site of FLK Zinj (Olduvai Gorge, Tanzania), suggesting differing competitive regimes at the two sites.

Keywords: FLK Zinj; Hunting; Scavenging; Taphonomy; Carnivores; Butchery

1. Introduction

Understanding the diet and subsistence behaviors of Early Stone Age (Oldowan) hominins is central to a broader understanding of early hominin behavioral ecology. As a calorically dense resource that provides protein, fat, and many micronutrients, the importance of animal tissue in the diet and its method of acquisition are of particular interest. Early evidence for meat eating is documented by infrequent occurrences of cut marked bone from the Ethiopian locality of Gona (2.6 Ma; Domínguez-Rodrigo et al., 2005) as well as Ain Boucherit, Algeria (2.4 Ma; Sahnouni et al., 2018). More controversial evidence comes from Dikika at ca. 3.4 Ma (McPherron et al, 2010; Domínguez-Rodrigo et al., 2010) and Bouri, ca. 2.5 Ma, Ethiopia (de Heinzelin et al., 1999; Sahle et al., 2017). These limited occurrences make it unclear how frequent meat-eating was in the early Oldowan (Plummer and Finestone, 2018). After 2 Ma there seems to be more consistent evidence of meat eating at sites such as Kanjera South, Kenya

(Ferraro et al., 2013); FLK Zinj and DK, Olduvai Gorge, Tanzania; (Potts, 1988; Oliver, 1994; Blumenschine, 1995; Domínguez-Rodrigo et al., 2007a); FwJj20, Koobi Fora (McCoy, 2009; Braun et al., 2010) and other sites in East Turkana, Kenya (Pobiner et al., 2008). This evidence for a shift toward including a greater amount of animal tissue in the diet occurs at a critical time in hominin evolution and is roughly coeval with the appearance of larger bodied *Homo* (Plummer and Finestone, 2018; Swedell and Plummer, 2019), although it overlaps with the presence of *Paranthropus* as well.

Inclusion of animal tissue in the early hominin diet has been tied to a range of biological adaptations including brain enlargement, increased body mass, tooth size reduction, decreased gut size (e.g., Aiello and Wheeler, 1995; Aiello and Wells, 2002; Haeusler and McHenry, 2004; Pontzer, 2012), as well as socioecological adaptations including food sharing, changes in group structure, and hominin ability to compete with carnivores for food resources (e.g., Isaac, 1978; Oliver, 1994, 2015; Rose, 2001; see Plummer, 2004 for a review of the importance of meat in the hominin diet). Evaluation of the strength of this relationship, particularly socioecological adaptations tied to meat eating requires knowledge of how meat was acquired and the extent to which hominins competed with carnivores over this resource. Current hypotheses argue for various modes of carcass acquisition by hominins including hunting (Domínguez-Rodrigo and Pickering, 2003; Domínguez-Rodrigo and Barba, 2006; Bunn and Pickering, 2010); active scavenging, where hominins drove carnivores away from fresh kills (Bunn and Ezzo, 1993; Bunn, 2001); or passive scavenging, where hominins acquired parts late in the consumption sequence of a carcass (Blumenschine, 1988, 1995; Pante et al., 2012; Pobiner, 2015). Patterns of hominin-produced butchery marks and carnivore gnaw marks on fossil mammalian remains provide insight into these activities. However, our current understanding is largely limited to analyses of hominin and carnivore damages from a single archaeological site with a large fossil assemblage—the 1.8 Ma site of FLK Zinj, Bed I, Olduvai Gorge, Tanzania.

The 2.0 Ma Oldowan site of Kanjera South (KJS), Kenya comprises a well-preserved fossil assemblage larger than the FLK Zinj assemblage and offers an opportunity to build on our understanding of hominin carcass acquisition. Previous work has documented element representation, butchery and carnivore tooth mark frequencies, and mortality patterns indicating Kanjera hominins had early access to bovid carcasses (Ferraro et al., 2013; Oliver et al., 2019). Here we apply a GIS-based method to analyze the spatial distribution of bone modification patterns on limb elements. Using this method, we superimpose GIS shapefiles of each bone fragment, which results in a composite image of bone preservation and fragmentation for each element in an assemblage. We also examine the distribution of carnivore tooth marks and butchery marks by plotting them onto element "maps." We use modern carnivore-gnawed assemblages created under controlled conditions as a baseline for interpreting the KJS assemblage. We also apply Domínguez-Rodrigo et al.'s (2007a) hot zone model to differentiate whether carnivores or hominins had first access to bovid carcasses. This model allows evaluation of the location of butchery marks in relation to areas that are known to be stripped of meat by lion feeding. Because the KJS assemblage is dominated by green bone fractures (i.e., bones were broken while fresh, not long after deposition), this GIS-based method to examine bone fragmentation and surface damage patterns in conjunction with the "hot zone" model gives us further insight into the nature and order of hominin and carnivore involvement with the KJS assemblage.

1.1. Kanjera South site context

The approximately 2.0 Ma site of Kanjera South is located on the Homa Peninsula of Lake Victoria in Western Kenya (Fig. 1). Excavations by the Homa Peninsula Paleoanthropological Project from 1995–2001 and in 2009 recovered abundant, *in situ* Oldowan artifacts and fauna from KJS (Ditchfield et al., 1999; Plummer et al., 1999; Bishop et al., 2006; Plummer and Bishop, 2016; Ditchfield et al., 2019). Excavations 1 and 2 have yielded more than 2900 Oldowan artifacts and over 3500 identifiable fossils, including cut-marked bones, from an approximately 3 m-thick sequence of the three lowermost beds at the site, KS-1 through KS-3 (Plummer et al., 1999; Bishop et al., 2006; Ferraro, 2007; Plummer et al., 2009a; Ferraro et al., 2013). Each bed is described in detail by Ditchfield et al. (1999, 2019).

Taphonomic, zooarchaeological, and geological analyses indicate that the site formed predominantly through hominin activities with little contribution from abiotic processes (Ferraro, 2007; Plummer, 2009b; Ferraro et al., 2013; Ditchfield et al., 2019). The KS-1 through KS-3 sequence is composed primarily of sands and sandy silts deposited near an ancient lake margin by ephemerally flowing, low aspect channels. Rapid sedimentation, minimal sedimentary abrasion and bone weathering, and the absence of bone or artifact rounding suggest the fauna and artifacts in each bed accumulated relatively rapidly (Ditchfield et al., 2019). Further, KJS formed in a relatively open (C_4 grass-dominated) context, as indicated by taxonomic representation and isotopic analyses (Plummer et al., 2009b). This contrasts with most other Oldowan occurrences, including FLK Zinj, which formed in a woodland setting (Cerling and Hay, 1986; Sikes, 1994; Ashley et al., 2010) and the occurrences at Koobi Fora that are reconstructed as habitat mosaics (Quinn et al., 2007). The combined evidence indicating primary context for fossils and artifacts at KJS and its unique paleoenvironment make KJS an ideal candidate for addressing questions about early hominin foraging ecology .

1.2. Kanjera South zooarchaeology overview

Bovid remains dominate the KJS assemblage (followed by equids and suids), and represent a minimum of 56 individuals (Ferraro et al., 2013), making this one of the larger, if not the largest, Oldowan faunal assemblages. The majority of bovid individuals are small (size class 1 and 2; Bunn, 1982) or medium (size class 3) in size, and many of these (about 50%) are subadult (Ferraro, 2007; Oliver et al., 2019). Larger bovids (size 3b and above) are not well represented, and so the discussion here will mainly focus on the small and medium-sized animals. Initial zooarchaeological analysis of the KJS fauna (Ferraro, 2007; Ferraro et al., 2013; Oliver et al., 2019) concluded that hominins had early access to small (size 1 and 2) bovids at the site, probably obtained through hunting. This argument is based on element survivorship, mortality patterns, low frequency of carnivore damage, and hominin damage to bones. While there is evidence of carnivore activity at the site (Fig. 2), carnivore tooth mark frequencies are low, similar to those from experimental models where carnivores had secondary access to defleshed and demarrowed bones following hominin processing of fauna (Ferraro et al., 2013).

This study uses GIS-based methods and the hot zone model to examine the patterning of hominin- and carnivore-produced bone surface modifications on the Kanjera South fauna. Based on experimental bone damage studies and previous work at KJS, we have the following expectations:

Expectation 1: If hominins were the primary agent of bone breakage at KJS, we expect the fragmentation pattern to best match experimental models of hammerstone percussed bone rather than carnivore fragmented bone.

Expectation 2: Given evidence of minimal carnivore feeding on the assemblage (Ferraro et al., 2013), we expect moderate to high preservation of bovid limb bone epiphyses relative to experimental models of carnivore consumed bone.

Expectation 3: Given evidence of minimal carnivore feeding on the assemblage (Ferraro et al., 2013), we do not expect GIS models of tooth mark distribution to show a significant pattern of tooth mark clustering.

Expectation 4: If hominins had early access to carcasses at KJS, we should find cut marks in hot zones on bovid limb bones.

2. Materials and methods

This study applies a GIS spatial analysis method to examine bone preservation and modification patterns in the KJS assemblage. Patterns are assessed relative to visual models of cut and tooth mark distributions in experimental bone assemblages created by humans and various species of large carnivores. Although not strictly quantitative, the GIS method used provides the benefit of a clear visualization of bone surface damage patterns which can be evaluated in conjunction with previously published quantitative analyses.

2.1. Fossil collections

KJS data collection was conducted by J.A.P at the National Museums of Kenya in 2011. All limb elements from bovids of all size classes from Excavations 1 and 2 were examined. Limb specimens from the 2009 excavations (n=20) are included and reported on here for the first time. We report on the subset of the assemblage that included bovid limb bone specimens identifiable to element and side (n=318 or 53% of the Ferarro et al., 2013 sample that includes taxonomically indeterminate specimens and fragments not identifiable to limb element).

Bovid limb fragments were sorted into three size categories (small, medium, and large) with size classes following Bunn (1982). Small (size 1) bones are Thomson’s gazelle-sized

(*Gazella* [=*Eudorcas*] *thomsonii*). Medium (size 2–3a) fossils are Grants gazelle (*Gazella granti*) to topi (*Damaliscus lunatus*)-sized. Large (size 3b) bones are wildebeest-sized (*Connochaetes spp.*). No size 4 or larger specimens were included in this analysis. We have placed size 2 specimens in the medium bovid category to facilitate comparison with the available experimental assemblages, most of which are size class 2 animals.

KS-1 through KS-3 fossils were combined for most analyses because depositional processes and faunal assemblage composition of all beds are similar (Ferraro, 2007). KS-1 and KS-2 alone had sufficiently large sample sizes to allow inclusion in the GIS bone portion survivorship analyses for small and medium-sized bovids, but other analyses combine fossils from all three beds. Fossils from conglomerate facies (CP levels described in Plummer et al., 1999) are excluded from surface modification analyses due to their possible accumulation by water flow. Specimens from Excavations 1 and 2 were grouped together.

2.2. Identification of bone surface modifications

All specimens and surface damages in the sample were examined by J.A.P. with a 10× hand lens under oblique light. We used the following standard, published criteria for identifying bone surface modifications created by hominin and carnivore agents:

<u>Carnivore tooth pits</u> are circular or oval marks on bone resulting from the tooth pressing against the bone surface. <u>Tooth punctures</u> result when the cortical bone collapses under the pressure of the tooth (Binford 1981; Haynes 1980; Lyman 1994 and references therein) and are more likely in regions with substantial trabecular bone.

Tooth scores are linear marks (at least three times as long as they are wide) that result from the tooth dragging across the surface of the bone. Scores are U-shaped in cross section, lack internal striations, and are often perpendicular to the bone's long axis. (Haynes 1980; Binford 1981; Domínguez-Rodrigo and Barba 2006).

Cut marks, in general, are linear marks distinguished from carnivore tooth scores by their V-shaped cross section, presence of micro-striae within the mark, usual straight linearity, and a typical orientation oblique to the bone's long axis. Other features sometimes present on experimental cut marks and used in cut mark identification include the presence of a shoulder and chattering (aka flaking) at the juncture of the cortical surface and mark wall. To rule out tramping and sedimentary abrasion marks, features often created by these processes were considered, including: curved or multi-directional marks, presence of intersecting micro-striae, presence of flat spots in the mark base, and presence of nearby abrasions with a haphazard orientation (Binford 1981; Bunn 1981; Potts and Shipman 1981; Shipman 1981; Behrensmeyer et al., 1986; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2010; Fernández-Jalvo and Andrews, 2016. The context of the mark under evaluation, including particle size of the surrounding sediment, overall fossil preservation, presence or absence of miscellaneous scratches and/or trample marks, and associated cut marks, was also carefully considered before a mark was confidently identified as a cut mark.

Percussion marks refer to both "pits" and "striae" as defined by Blumenschine and Selvaggio (1988). Percussion pits usually have multiple small patches of micro-striations emanating from them due to bone slippage against the hammerstone or anvil during impact. Percussion marks are often associated with percussion notches.

Percussion notches are “semicircular or arcuate indentations on the fracture edge of a long bone” (Capaldo and Blumenschine 1994). These are produced by dynamic loading on the cortical surface of the bone, and display an adjacent negative flake scar on the medullary surface. Percussion notches are distinguished from tooth notches based on their broad shape in cortical view. Tooth notches tend to be more semicircular than percussion notches, and have a flake release angle closer to perpendicular compared with the obtuse release angle for hammerstone produced flakes (Capaldo and Blumenschine 1994).

Recent work indicates that crocodile tooth marks may mimic hominin-produced cut marks or percussion marks (Njau and Blumenschine, 2006; Njau and Gilbert, 2016. Sahle et al., 2017; Domínguez-Rodrigo and Baquedano, 2018). Although crocodiles are known to produce a range of pits and large and often deep scores on bones, none of the KJS fauna bear the distinctive bisected pits and punctures or hook scores associated with crocodile feeding (Njau and Blumenschine, 2006). Further, because KJS was deposited in a grassland environment with crocodile and fish fossils rarely preserved, we have ruled out crocodiles as a major taphonomic agent at the locality.

Bone modifications at KJS have previously been jointly identified by a ‘round table’ of three investigators (Ferraro et al., 2013). In this study, J.A.P. initially identified modifications independently, and then checked against the list of previous identifications. The identifications presented here are in concordance with what Ferraro et al.’s (2013) ‘round table’ (in which multiple mark features were considered and discussed before mark identification) found and were not out of the small range of variation seen among the three original observers (88.5% concordance with at least two other analysts for tooth mark identifications and 92% concordance with at least two other analysts for cut mark identifications; see Supplementary Table 1). Bone surface modifications from the 2009 excavation had not been previously analyzed and were assessed in the same three-person format by J.A.P., J.S.O., and another experienced taphonomist (F. Forrest). Fossils with poor surface preservation were excluded from the analysis .

2.3. Comparative experimental bone collections

We used GIS models of bone preservation and damage patterns based on several modern experimentally-modified bone collections previously described by Parkinson and colleagues (Parkinson et al., 2015; Parkinson, 2018). The experiments that these models are based on are described below and are summarized in Table 1.

Blumenschine's (1988) feeding experiments, conducted in Tanzania's Serengeti National Park and Ngorongoro Crater, model differential access to carcasses by carnivores and humans. These collections, housed in the Department of Anthropology at Rutgers University at the time of study, have been described in previous publications (Blumenschine, 1988, 1995; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994). This study uses GIS models of these collections created by Parkinson (2013, 2018). These models include only fragments from Blumenschine's collection that were large enough to be accurately placed on GIS templates and exclude any of Blumenschine's experiments in which carnivores other than spotted hyenas (*Crocuta crocuta*) were involved. Small (size 1) bovids were represented by Thomson's gazelle (*Gazella* [=*Eudorcas*] *thomsonii*), medium (size 2–3a) carcasses included Grant's gazelle (*Gazella* [=*Nanger*] *granti*), impala (*Aepyceros melampus*), and topi

(*Damaliscus lunatus*). Large (size 3b) carcasses were represented by wildebeest (*Connochaetes taurinus*).

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

Hammerstone-to-carnivore The hammerstone-to-carnivore experiments (simulated sites) replicate carnivore scavenging of bones broken and demarrowed by hominins. Defleshed bones were broken using hammerstone percussion and then set out on the landscape for carnivores to scavenge. Spotted hyenas (*Crocuta crocuta*) were the sole scavengers in all experiments included in the GIS models, although minor disturbance by jackals or mongooses cannot be ruled out.

Carnivore-only (hyaenid) Blumenschine's carnivore-only experiments include limb bones from carcasses scavenged by spotted hyenas in the wild. Because hyenas nearly completely destroyed bones from smaller carcasses, this model is only compared with larger bovids from KJS.

Carnivore-only (felid) The felid carnivore models are based on feeding experiments conducted by Parkinson et al. (2015) with captive large felids, including lions (*Panthera leo*) and tigers (*Panthera tigris*) at the Carolina Tiger Rescue in North Carolina. Although captive, the animals in these experiments are a good model for wild felid behavior, as they are housed in natural habitat enclosures and routinely fed a whole carcass diet. In these experiments, animals were fed whole deer (*Odocoileus virginianus*) carcasses or half carcasses obtained as road kill. The detailed methodology for these experiments is described by Parkinson et al. (2015). We chose a felid carnivore-only model to compare with the KJS small and medium bovids, as the bones in the hyaenid-only experiments exhibited far more damage than what was seen in the KJS bovid sample (Parkinson et al., 2015).

2.4. GIS image-analysis

As noted above, bones from the experimental assemblages and the fossils from KJS were sorted into three groups for analysis. The small bovid group includes size 1, the medium group includes size classes 2–3a, and the large group includes size 3b (wildebeest-sized). GIS was used to document and visualize patterns of bone fragmentation following the method of Parkinson and colleagues (Parkinson, 2013, 2018; Parkinson et al., 2014, 2015). This method, originally developed by Marean et al. (2001), treats each element as a ‘map’ onto which the bone fragment outline and any bone surface modifications are recorded. ArcGIS 9.3 and the Spatial Analyst extension were used to conduct this analysis (ESRI, 2008).

To examine bone portion survivorship, each fragment was digitally drawn as a vector shapefile over a photographic template of a complete, similarly sized element in ArcGIS. Fragments were positioned on the photo template by lining up anatomical landmarks. Only those fragments identified to element portion and side were used (n = 318). The shapefiles of each fragment were then overlapped, converted to grids (where grid cells for each fragment were assigned a value of one), and grids were added together using the grid calculator (raster calculator) in ArcGIS. This produces a shaded ‘map’ of bone survival that is a composite image of overlapping fragments illustrating which bone portions are frequently preserved and which are frequently absent. The most heavily shaded portions represent the total number of skeletal elements that occupy that space. Bone survivorship maps for the FLK Zinj assemblage and experimental assemblages were created in the same way (Parkinson, 2018). Detailed instructions for this method are outlined in Marean et al. (2001) and Parkinson et al. (2014).

In order to examine the distribution of bone surface modifications, tooth marks, cut marks, and percussion marks were plotted onto the bone templates in ArcGIS. The combined maps yielded composite images of tooth, cut, and percussion mark distribution by element. For experimental assemblages, the Kernel density estimation (ESRI, 2008) was used to identify and build models of tooth mark clustering patterns on specific elements. This tool builds a rasterized image of point clustering (where each point represents a surface modification). 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 center of the spread, with the value tapering to 0 at the boundary of the search radius distance. The sum of intersecting spreads is then calculated for each cell in the output raster. Using this kernel function rather than the simple point density function 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 are outlined in Parkinson et al. (2014)

2.5. Hot zone analysis

In addition to GIS analyses, we apply the ‘hot zone’ approach described by Domínguez-Rodrigo et al. (2007a) to assess whether hominins had initial access to carcasses or if they may have scavenged from large felid kills. A study by Domínguez-Rodrigo and colleagues documenting kills made by lions in the wild found that lions do not always consume all the flesh on bones (Domínguez-Rodrigo, 1999; Domínguez-Rodrigo et al., 2007a). They presented a model in which cut marks seen on anatomical areas where flesh *never* survives felid consumption (hot zones) indicate primary access by hominins, regardless of cutmark frequency. In contrast, ‘cold zones’ are those areas where flesh remains after felid consumption. Priority of neither hominin nor carnivore access can be inferred from cut marks in cold zones. An experiment of flesh availability following large felid consumption conducted by Parkinson et al. (2015) confirmed the ‘hot zone’ pattern observed by Domínguez-Rodrigo (1999), where upper and intermediate limb elements are typically completely defleshed and flesh scraps remain only at the joints.

Documenting the presence or absence of cut marks in hot zones allows assessment of whether Kanjera South hominins had primary access to carcass parts or were potentially scavenging from felid kills. We apply the hot zone approach to the KJS fauna by mapping bone regions that should not preserve flesh following felid consumption over the Kanjera GIS images for cut mark distribution. Hot zones only model flesh distribution on upper and intermediate limb elements (humerus, femur, radio-ulna, and tibia) —felids typically leave metapodials untouched as there is no meat on them. Hot zone images are only shown when cut marks are present, as they do not occur on every element in the KJS assemblage.

3. Results

3.1. Summary of bone portion survivorship in experimental models

<u>Hammerstone only</u> When humans are the sole modifier of an assemblage, a general pattern is apparent where limb bone epiphyses are typically preserved but limb shafts are heavily fragmented. Limb shaft fragments typically do not preserve the full circumference of the shaft.

Limb shaft fragments commonly preserved in these experiments include anterior and distal parts of the femur and humerus, posterior surface of the tibia, proximal midshaft of the radius, and posterior and medial sides of the metatarsal.

Hammerstone-to-carnivore When humans precede carnivores in processing carcasses, a pattern almost the reverse of the hammerstone model is apparent, where limb shaft fragments are preserved, but epiphyses of most lims bones are destroyed.

Carnivore-only When large felids are the sole modifier of a carcass, a mixed pattern of preservation is apparent, where the greasy, less dense epiphyseal ends are destroyed (distal femur, greater trochanter, proximal humerus, proximal tibia, olecranon process of the ulna, distal radius), but shaft cylinders remain, and denser epiphyseal ends are also preserved (distal humerus, tibia, and metatarsal) (see also Pobiner et al., 2020). When hyaenids are involved in modifying carcasses, the same general pattern is observed, but with greater fragmentation of the limb shafts.

3.2. Bone portion survivorship

Results of the GIS analyses of KJS bone portion survivorship for small and medium size bovids compared with several experimental assemblages are illustrated in Figures 3 and 4. Bone portion survivorship patterns for KJS large bovids compared with experimental assemblages are illustrated in Figures 5 and 6.

Small and medium bovids Medium-sized bovid femora at KJS show a survivorship pattern similar to the hammerstone-to-carnivore experimental model, with a high degree of preservation in the midshaft area, and a lack of complete shaft cylinders (Fig. 3a). Although slightly better preserved than in the experimental model, KJS epiphyses are not well preserved. Small bovid femora are somewhat more complete and more closely resemble the hammerstone only model.

The medium-sized tibiae at KJS also display high preservation of midshafts and distal epiphyses, but a loss of proximal epiphyses (Fig. 3b). The small bovid tibiae show greater preservation than the medium-sized tibiae. The low preservation of the distal tibia in small bovids may be due to the lack of unfused distal epiphyses in juvenile tibiae, not carnivore involvement. Juveniles account for 33% (4 out of 12) of the small bovid tibiae in this study.

Medium-sized metatarsals show higher preservation at the proximal end, but lower preservation at the distal end (Fig. 3c). This metatarsal preservation pattern is most consistent with the hammerstone-only model, while the hammerstone-to-carnivore model is too small for useful comparison. The sample of small bovid metatarsals from KJS is small, but they are mostly complete, save for one small proximal fragment.

KJS humeri are highly fragmented, and show a similar pattern to the hammerstone-only and hammerstone-to-carnivore models for both small and medium bovids. The KJS epiphyses are preserved less often than in the hammerstone-only model, perhaps indicating carnivores may have deleted some KJS epiphyses. In contrast to the humeri in the carnivore-only model, which are mainly preserved as cylinders without the proximal epiphysis, the KJS humeri are highly fragmented, preserving less than 50% of the shaft circumference (Fig. 4a).

KJS medium-sized bovid radii are highly fragmented, but preservation is highest at the proximal and distal ends—a pattern most closely resembling the hammerstone-only model (Fig. 4b). The small bovid radii are highly fragmented and preserve almost exclusively proximal ends.

Preservation of medium-sized ulnae at KJS resembles the carnivore-only models, except that the shaft in the KJS specimens shows greater destruction (Fig. 4c). The olecranon process is moderately destroyed. Preservation of the small bovid ulnae is similar. The hammerstone-to-carnivore model only contains one specimen, so it is not possible to compare it to the KJS fossil preservation.

Both medium and small metacarpals from KJS are highly fragmented (Fig. 4d) with good representation of fragments across all bone areas, though preservation is highest at the proximal end. Smaller bovids show somewhat better preservation, a pattern opposite that which would be expected if carnivores were active at KJS. The patterns at KJS follow the pattern from the hammerstone-only models although the hammerstone-to-carnivore model is difficult to use because it is comprised of a single fragment.

The fragmentation pattern of small and medium sized bovids at KJS is consistent with experimental models of hominin primary access, supporting Expectation 1. Further, the more frequent preservation of limb bone epiphyses relative to the carnivore-only models supports the prediction of minimal carnivore involvement in Expectation 2. Overall, limbs from small (size 1) carcasses are more complete, preserving epiphyses more frequently than medium-sized (size 2–3a) carcasses. This pattern seems to rule out density-mediated destruction by carnivores which are expected to more completely destroy smaller elements. Instead, these differences may reflect different hominin strategies in the transport of small and medium-sized carcasses to KJS. Ferraro et al. (2013) have made a similar argument based on their analysis of skeletal part frequencies.

Although some of the KJS small bovid limbs lack epiphyses and thus superficially resemble those from the carnivore-only experiments, many are juveniles with unfused epiphyses. These specimens account for 13% of the limb bones included in this GIS analysis (42 out of 318 limb fragments had at least one unfused epiphysis). Only 4 (<10%) of these juvenile specimens, display evidence of carnivore gnawing indicating carnivore involvement is not the main factor driving low epiphyseal representation relative to shaft representation.

<u>Large bovids</u> Large (size 3b) bovids from KJS are less well represented than small and medium bovids. Large bovids from KJS are compared in Figures 5 and 6 with GIS models based on Blumenschine's experimental assemblages. Hammerstone-only models were not available for the femora and tibiae. Blumenschine's spotted hyena damaged assemblage was used for the carnivore-only model as Parkinson's (2015) felid experiments had too small of a sample size for large animals.

The large bovid bone survivorship pattern is more difficult to assess due to small sample sizes in both the KJS fossil assemblage and experimental models, however, the data are generally consistent with Expectation 1, with fragmentation of midshafts similar to hammerstone fractured assemblages rather than carnivore fragmented assemblages. Midshafts are preserved as fragments, not cylinders as felids typically produce. Preservation of the large bovid limb bone epiphyses is less consistent with Expectation 2, indicating some likely carnivore involvement, which we discuss further below.

3.3. Bone modification patterns

The best way to interpret the contribution of hominin and carnivore activities to an assemblage is to examine multiple lines of evidence simultaneously. For this reason, we assess bone modification patterns in conjunction with the patterns of bone portion survivorship and preservation described above. Here, a spatial analysis of the distribution of various types of hominin- and carnivore-induced damage to bones from KJS is detailed and discussed within the comparative framework of GIS models based on the actualistic research described above.

The patterns and specific damages discussed below are those that occur on specimens with clear anatomical landmarks and could therefore be reliably placed on GIS element templates. As such, the GIS images represent plots of modifications that could be reliably assigned locations on element templates, and do not reflect total bone surface modification counts that have been reported previously (Ferraro, 2007; Ferraro et al., 2013). Bone surface modification data included in this spatial analysis are summarized in Table 2. We describe the location of particular surface modification patterns that are potentially informative regarding the order of access of hominins and carnivores to carcasses at KJS in light of GIS experimental models.

<u>Patterns of carnivore damage</u> Figure 8 shows plots of individual tooth marks on element templates for the KJS femora and humeri (sample sizes for tooth marks on other elements are too small to consider). Density analyses of tooth marks on experimental collections for felid experiments (Parkinson et al., 2015) and for hammerstone-to carnivore-experiments (Parkinson, 2018) are shown for comparison. Large bovids are not considered here as the sample size of tooth marks that could be reliably mapped onto GIS templates is small.

The small- and medium-sized bovid femora from KJS do not show tooth mark clustering, but the small sample size (8 tooth marks) makes this difficult to assess (Fig. 8a). Tooth marks on tibiae (not figured) also do not show clustering. This lack of identifiable tooth mark patterning is probably a reflection of the low overall tooth mark frequency, and an indication of low carnivore involvement in assemblage formation.

The carnivore damage pattern on the humeri (Fig. 8b) most closely resembles the carnivore-only experiments. One difference, however, is that more damage has been noted on the proximal humerus compared to the distal end in carnivore-only felid feeding experiments

(Pobiner et al., 2020; Parkinson et al., 2015), and the KJS tooth mark distribution shows more damage at the distal end. The sample size for the hammerstone-to-carnivore experimental model is small (consisting of 3 elements in 5 fragments). Although the small and medium bovid radii and ulnae epiphyses from KJS (not figured) have some tooth marking, it is significant that the grease-filled olecranon process is typically well-preserved (Fig. 6b). Had carnivores had sole access to this element, more intensive damage and destruction would be expected.

Taken together, these data support Expectation 3: Carnivore toothmarks show little clustering, and destruction of attractive, grease-rich epiphyses is minimal. This is consistent with minimal or secondary carnivore involvement in forming the KJS assemblage.

<u>Patterns of hominin damage</u> Hominin-induced damage to the KJS small and medium femora includes cut marks, as well as percussion marks and notches. Only one cut mark located on the femoral head, a location indicative of disarticulation (Domínguez-Rodrigo, 1997; Nilssen, 2000), occurs in a cold zone. All other cut marks found on the KJS femora occur in hot zones (Fig. 9a).

Most cut marks on small and medium bovid tibiae also occur in hot zones (Fig. 9b). The KJS tibiae preserve numerous percussion marks and percussion notches documenting marrow processing of these elements by hominins. Small and medium bovid metatarsals at KJS also display both cut marks (e.g., Ferraro et al., 2013: Fig. 2a) and percussion notches .

Cut marks do not occur on the small and medium bovid humeri, radii or ulnae examined in this study, although one humeral shaft that could not be placed on a GIS template was identified as cut marked in Ferraro’s (2007: Table 9) study. Percussion damage is present on the radii. Finally, the metacarpals at KJS show a single episode of cut marking on a posterior distal metaphysis. There is no identifiable percussion damage on metatarsals.

The only hominin-induced damage visible on size 3b bovids at KJS is on the forelimbs. Cut marking on the humerus occurs directly on the insertion point for teres major suggesting early access even though it is in a cold zone (Fig. 9c). The proximal radio-ulnae have cut marks that occur in cold zones, and are thus uninformative regarding hominin order of access. Hominin-induced damage does occur on other large (size 3–4) bovid specimens (at a frequency of 0–25% depending on observer and bed; see Ferraro, 2007: Appendix 22a–c), but the marks could not be reliably placed on element templates.

Overall, the presence of cutmarks in hot zones suggests early access by hominins to fleshed carcasses of small and medium sized bovids, supporting Expectation 4. Hominins may have practiced a more mixed strategy to access larger carcasses which we discuss below.

4. Discussion

Results of the GIS spatial analyses of bone fragmentation and surface modification patterns in the archaeofaunal assemblage from Kanjera South presented here support previous interpretations of the site, suggesting that hominins had early access to relatively complete, often juvenile, small bovids, and at least occasional access to larger bovids perhaps acquired through scavenging (Plummer, 2004; Ferraro et al., 2013; Oliver et al., 2019).

Overall, small and medium bovids at KJS exhibit a fracture pattern most consistent with the hammerstone-only experimental models. Limbs of small and medium-sized bovids show some epiphyseal deletion, but not to the extent seen in Blumenschine’s (1995) experimental hammerstone-to-carnivore models. The fact that carnivores were not completely consuming the epiphyses indicates the KJS ecosystem had a lower degree of competition than was present in Blumenschine’s experiments. It should be noted that Blumenschine’s experiments were conducted in the Serengeti and Ngorongoro crater, which are highly competitive environments (Kruuk, 1972; Schaller, 1972; Tappen, 1995, 2001), and his experimental models seem to reflect this (but see Volmer and Hertler, 2016 for a discussion of the complexities of competition). Relative to GIS models of 'carnivore-only' scenarios, the higher preservation of epiphyses at Kanjera suggests carnivores were not forming or greatly modifying the assemblage. Although carnivores were present (fossils of size 2 and 3 felids, an indeterminate hyaenid, and *Crocuta* cf. *dietrichi* have been found; Plummer et al., 2009a), there seems to have been low on-site competition at Kanjera. Further, 24% of the size 1 bovids (17/72 specimens in this study) were juveniles missing at least one unfused epiphysis. Thus, carnivores are not likely to account for size 1 bovid epiphyseal deletion.

Limbs from small carcass are better preserved than those from medium-sized carcasses. This pattern seems to rule out density-mediated destruction due to carnivore involvement because carnivores are able to destroy smaller elements more thoroughly. Smaller-sized carcasses are normally at greater risk of destruction than medium-sized carcasses, particularly in grassland contexts (like KJS) where they are typically completely consumed by lions and/or hyenas within several hours after death (Blumenschine, 1987; Domínguez-Rodrigo, 2001). The preservation differences seen between the small- and medium-sized carcasses may reflect differences in completeness of large and small bovid carcasses that impacted subsequent hominin transport and processing. Based on their study of skeletal part frequencies, Ferraro et al. (2013) also argued that hominins at KJS may have engaged in separate foraging activities for large and small carcasses. They argued that the high representation of smaller bovid elements likely reflects hominin access to and transport of complete carcasses to the locality. The higher representation of meaty limb bones and particularly head elements of medium-sized bovids suggests hominins may have at times been scavenging and transporting carcass segments rather than whole carcasses.

Carnivore secondary access is suggested by the low frequency and random distribution of carnivore tooth marking on the small and medium bovid limbs at KJS. Furthermore, the low frequency of carnivore damage but frequent preservation of epiphyseal ends at KJS suggests low on-site competition over carcasses.

The occurrence of cut marks in hot zones on the meaty hindlimb elements (“meaty” = humerus, radio-ulna, femur, and tibia following Bunn and Kroll, 1986) of small and medium bovids at KJS suggests hominins had primary access to fleshed carcasses. Flesh typically does not survive felid consumption in hot zones, so there would have been little to no flesh left to remove in these areas if hominins were scavenging from felid kills. Further, the presence of percussion marks and notches and the high degree of fragmentation (the majority of it green bone fracturing) of most of the long bones indicate hominin exploitation of within-bone resources.

For the size 3b bovids, tooth mark distribution is more difficult to interpret, as placement on the GIS templates was only possible for a single radio-ulna which was highly tooth marked (not figured). Nevertheless, the numerous tooth marks on this specimen is consistent with the interpretation that KJS hominins may have scavenged some larger bovid carcasses initially fed on by carnivores. Hominin involvement with large bovids is evidenced by cut and percussion damage to the humeri. Significantly, cut marks on these humeri are not present in hot zones, a pattern consistent with the interpretation that hominins occasionally scavenged carnivore-killed carcasses.

4.*1. How does Kanjera South compare with FLK Zinj?*

Because of its large fossil assemblage with well-preserved bone surfaces, much of the research on Oldowan hominin meat acquisition has been based on a single archaeological site: FLK Zinj, Bed I, Olduvai Gorge, Tanzania. Kanjera South has a larger fossil assemblage with comparable preservation, and thus provides an opportunity to compare two large Oldowan fossil assemblages and assess variability in carcass acquisition and processing by hominins. The sites are similar in age—FLK Zinj is slightly younger at 1.84 Ma (Deino, 2012)—and they have roughly similar faunal and lithic compositions. Significantly, however, their paleohabitats differed. While FLK Zinj formed in a woodland habitat (Arráiz et al., 2017), KJS accumulated in an open grassland (Plummer et al., 2009b). The FLK Zinj assemblage has played a central role in the hunting/scavenging debate, with some researchers suggesting hominins scavenged from felid kills at the site (Blumenschine, 1995; Capaldo, 1997; Selvaggio, 1998). Others suggest that hominins had earlier access to carcasses, and may have hunted the smaller (and perhaps the larger) bovids at FLK Zinj (Bunn, 2001; Bunn and Kroll, 1986; Oliver 1994; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2007a; Parkinson et al., 2018; Oliver et al., 2019). Key questions to consider are whether FLK Zinj represents evidence of typical Oldowan hominin carcass acquisition activities, and how environmental setting may have impacted hominin carcass acquisition strategies (Oliver et al., 2019).

<u>Bone portion survivorship at Kanjera South and FLK Zinj</u> Based on GIS image analyses of bone portion survivorship (Figs. 3–6), bones from both KJS and FLK Zinj are highly fragmented. Overall however, bones from FLK Zinj show a more even representation of fragments across element portions (including epiphyses), while elements from KJS preserve epiphyseal portions less often. As discussed above, one likely explanation for the lower epiphyseal preservation at

KJS is that a number of the small bovids are juveniles with unfused epiphyses. One other possibility is that some epiphyses were destroyed during marrow processing and consumption by hominins. The Hadza hunter gatherers of Tanzania have been observed pounding and destroying epiphyseal ends to gain access to the fat-rich cancellous tissue (Oliver, 1994)—early hominins may have done the same.

The GIS bone preservation analyses from both Kanjera and FLK Zinj are most consistent with experimental models where humans fragmented long bone midshafts and carnivores removed or destroyed epiphyses to varying degrees. When compared to experimental models, epiphyseal preservation at FLK Zinj is often higher than in the hammerstone-to-carnivore models. This may indicate lower competition in the Olduvai paleoecosystem than has been modeled experimentally.

<u>Tooth mark frequencies at Kanjera South and FLK Zinj</u> Assemblage-wide tooth mark frequencies by skeletal element calculated in this study are shown in Figure 10a and Table 3. The frequency reported here—14%—is consistent with midshaft tooth mark frequencies reported by three observers in Ferraro et al.'s study (2013; summed beds KS-1–KS-3, all size classes) which are between 8 and 14%. These frequencies all fall within or slightly below the range of experimental 'hominin first' models where carnivores had secondary access to carcass remains defleshed and demarrowed by humans (5–15% of NISP tooth marked in these experiments; Blumenschine, 1995; Capaldo, 1998; Marean et al., 2000). Tooth mark frequencies on midshafts from KJS are *well below* the range in experimental 'carnivore-only' models, in which carnivores including spotted hyenas had sole access (>75% of NISP tooth marked in these experiments; Blumenschine, 1995; Marean et al., 2000), although they are within the range produced by large

felids in experimental feeding studies reported by Parkinson et al. (2015) (Fig. 11; Supplementary Table 2).

Widely divergent tooth mark frequencies have been reported for the FLK Zinj assemblage (Oliver 1994; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al., 2007; Parkinson, 2018) (Fig. 10a). Blumenschine (1995) originally reported an assemblage-wide tooth mark frequency of 61% of the NISP, but other studies reported much lower frequencies (Oliver, 1994; Domínguez-Rodrigo and Barba, 2006; Parkinson, 2018). Some marks originally identified as tooth marks by Blumenschine (1995) may instead have been produced by biochemical processes, which Domínguez-Rodrigo and Barba (2006) identified evidence for in their study of the assemblage. An independent analysis by Parkinson (2018) also reported the presence of biochemical damage and calculated the tooth mark frequency at FLK Zinj to be 24% of the NISP—more consistent with the level of carnivore damage reported by Oliver (1994) and Domínguez-Rodrigo and Barba (2006). The shared sample analyzed by both Domínguez-Rodrigo and Barba (2006) and Parkinson showed 92.5% concordance (Parkinson, 2018). Tooth mark frequencies reported by Parkinson (2018) for FLK Zinj fall within the 95% confidence interval of experimental models where carnivore activity followed initial hominin access (Fig. 11), indicating early access by hominins.

Because it also formed in a grassland setting and contains many small bovids, another Olduvai Gorge site, HWK EE, Bed II at 1.7 Ma (Pante et al. 2018), provides an additional interesting comparison to Kanjera South. Tooth mark frequencies in the two main levels at HWK EE (Lower Augitic Sandstones [LAS] and Lemuta) are 33.7% (LAS) and 37.4% (Lemuta) for size 1–2 bovids and 25% (LAS) and 45.7% (Lemuta) for size 3–4 bovids (Pante et al., 2018). These frequencies are higher than both KJS (as described above) and FLK Zinj, and are intermediate between experimental assemblages modeling hominin first and carnivore first access (Fig. 12). Pante and colleagues (Pante et al., 2018; Pante and de la Torre, 2018) have interpreted the strong carnivore signal at the site as evidence that hominins mainly acquired carcasses through scavenging. Given that many of the cut marks on the HWK EE fauna are located near places of muscle attachment, carnivore scavenging of HWK EE hominin food refuse is equally, if not more plausible. Furthermore, HWK EE is the only other Oldowan site with an open habitat signature like KJS, and Pante et al. (2018) note that hominins appear to have obtained substantial amounts of flesh and marrow from small (size 1-2) bovids. This may indicate that like KJS hominins, the hominins forming HWK EE also had early access to small bovids.

Hominin produced damage at Kanjera South and FLK Zinj For the small and medium bovids at KJS, cut mark frequency varies between 2.0–5.9% depending on observer (Ferraro et al., 2013: Table S1). Our updated frequencies which include newly excavated material are within this range at 3.6% (Table 4). The occurrence of cut marks on meaty limb elements indicates early hominin access at KJS.

As Figure 12 illustrates, the frequency of hominin- and carnivore-induced damage is higher in the FLK Zinj assemblage than in the KJS assemblage, suggesting perhaps more thorough processing of carcasses by both hominins and carnivores at FLK Zinj despite the evidence for early hominin access at both sites. Alternatively, the lower frequency of cut marks at KJS may reflect the presence of many small bovids that were likely more easily butchered, than the larger bovids that dominate the FLK Zinj assemblage. Although cut mark frequency has not been shown to correlate with intensity of butchery in experimental scenarios (Egeland, 2003; Pobiner and Braun, 2005), we can view it as a byproduct of hominin involvement with carcasses.

Cut mark *distribution* is a better indicator of the nature of hominin involvement with carcasses (Domínguez-Rodrigo and Barba, 2007).

The GIS mapping of cut mark distribution in the KJS assemblage demonstrates that the majority of marks on size 1–3a bovids (9 out of 16 marks: 56%) fall within the 'hot zone' areas defined by Domínguez-Rodrigo et al. (2007a) as areas where flesh typically does not survive felid consumption. However, it is the presence or absence of marks in hot zones (rather than the frequency) that indicates hominin primary access. The presence of cut marks in hot zones is suggestive of early access by hominins to size 1–3a carcasses at KJS. Cut marks do not occur in hot zones on large bovids at KJS, but the sample size of size 3b bovids is small. In comparison, Domínguez-Rodrigo et al. (2007a) showed that in the FLK Zinj assemblage, cut marks also fall within hot zones. They reported 40% of marks on the femora and 20% of marks on the tibiae of small bovids occur in hot zones, and an even higher percentage occur in hot zones for medium sized bovids, suggesting early access by hominins to fleshed carcasses at this site as well.

4.2. How did hominins gain early access to carcasses at Kanjera South and FLK Zinj?

Given the evidence of early access by hominins to fleshed carcasses at Kanjera South and FLK Zinj, how would hominins have achieved this? Hunting and/or aggressive scavenging are two potential methods of acquiring complete carcasses. Oldowan hominins had a relatively limited tool kit consisting of cores and flakes, and there is no evidence for hunting technology (i.e., spears) in the archaeological record before about 500 ka (Wilkins et al., 2012). The absence of hunting technology in the Oldowan may be a preservation issue. We do not have a record of tools made out of perishable materials such as wood (Plummer, 2004). However, Lemorini et al. (2014, 2019) demonstrated that use-wear on stone tools from Kanjera South indicates tools were used for cutting and scraping wood, presumably to make wooden tools, possibly including spears. Given that wild chimpanzees have been observed making and using sharpened sticks to hunt bushbabies (Pruetz and Bertolani, 2007), it seems likely that Oldowan hominins with greater technological and cognitive abilities may have fashioned simple spears for hunting. If Oldowan hominins were hunting, they could have accomplished this through persistence hunting (i.e., running animals to exhaustion; Bramble and Lieberman, 2004) or by ambushing prey with spears. Both of these techniques would lead to a pattern of bone surface damage indicating early access similar to what is seen for smaller bovids in the KJS and FLK Zinj assemblages.

If hominins were obtaining carcasses through persistence hunting, bovid mortality profiles should match kill profiles created by modern cursorial predators such as African wild dogs or hyaenas in which relatively vulnerable young and old individuals are most numerous (i.e., an attritional profile following Bertram, 1979; Klein, 1982). On the other hand, if hominins were ambushing their prey, bovid mortality profiles should follow a pattern similar to those created by modern ambush predators such as lions and leopards: a living structure profile (Stiner, 1990).

The bovid mortality profile from KJS reported by Oliver et al. (2019) is heavily biased by juveniles, matching that created by carnivores operating in open habitats, acquiring kills via chases. The small bovids from FLK Zinj display a similar attritional pattern, although one that is dominated by old individuals. The larger bovids at FLK Zinj match the mortality profile created by ambush predators. Bunn and Gurtov (2014) and Oliver and colleagues (2019) argued that this prime dominated mortality pattern could indicate ambush hunting of larger bovids by hominins at FLK Zinj. Aggressive (power) scavenging from felid kills is an alternate explanation that could account for early access by hominins to larger bovids at FLK Zinj. Given the greater diversity of large felids that existed in the past, it is possible that they would have provided additional scavenging opportunities for hominins.

5. Conclusions

In summary, GIS image analysis and hot zone analysis of the Kanjera South bovid fauna suggest that Oldowan hominins had early access to small bovids and were habitually processing carcasses at this focal point on the landscape. Cut marks occur in hot zones on bones where flesh typically does not survive felid consumption, indicating early access to flesh by hominins. Further, the presence of percussion marking and high degree of fragmentation of the long bones indicate marrow processing by hominins. Distribution of these hominin-induced damages is consistent with GIS models based on experiments simulating early hominin access, not models of carnivore accumulated assemblages.

Carnivores were also involved in modifying carcasses to some extent, but do not appear to have been the agent of transport. This is indicated by the high survivorship of elements from small carcasses, which would likely have been completely consumed by carnivores if they had initial access. Low tooth mark frequencies and their random distribution are consistent with low carnivore involvement and suggest secondary access by carnivores. Relative to GIS models of carnivore-only scenarios, the higher preservation of epiphyses at KJS suggests carnivores were not forming or greatly modifying the assemblage. Although carnivores were present, there seems to have been lower on-site competition at Kanjera compared to FLK Zinj which has both higher tooth mark and cut mark frequencies.

Taken together, the spatial analyses presented here suggest that Kanjera South hominins had relatively early access to bovid carcasses and may have been hunting smaller bovids, confirming the results of previous studies (Ferarro et al., 2013; Oliver et al., 2019). Kanjera South thus may provide the oldest evidence of hunting in the archaeological record.

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Figure captions

Figure 1. Location of Kanjera South in relation to some other Oldowan sites.

Figure 2. Examples of bone surface modifications found in the Kanjera South assemblage: A) femur with percussion notch, view from medullary surface (#5268); B) percussion marks on long bone shaft fragment (#24844 from 2009 excavation); C) cut-marked rib (#24434); D) carnivore tooth pit on rib (#15054); E) carnivore tooth score on head of femur (#2565).

Figure 3. Preservation of small and medium bovid hindlimbs at Kanjera South compared with FLK Zinj and experimental models of bone damage to small/medium bovids: A) femur; B) tibia; C) metatarsal. *n* = greatest number of fragment overlaps. Hammerstone-only and Hammerstone-to-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). The FLK Zinj model is from Parkinson (2018). Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, and medial. Data from Kanjera specimens was recorded separately on right and left. When the sample size from the right side was larger, the right side data was transposed onto the left template for better visualization.

Figure 4. Preservation of small and medium bovid forelimbs at Kanjera South compared with FLK Zinj and experimental models of bone damage to small/medium bovids: A) humerus; B) radius; C) ulna; D) metacarpal. *n* = greatest number of fragment overlaps. Hammerstone-only

and Hammerstone-to-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). The FLK Zinj model is from Parkinson (2018). Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, and medial. Data from Kanjera specimens was recorded separately on right and left. When the sample size from the right side was larger, the right side data was transposed onto the left template for better visualization.

Figure 5. Preservation of large bovid hindlimbs at Kanjera South compared with FLK Zinj and experimental models of bone damage to large bovids: A) femur; B) tibia (only right side available); C) metatarsal. *n* = greatest number of fragment overlaps. Hammerstone-only, Hammerstone-to-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. The FLK Zinj model is from Parkinson (2018). Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, and medial. All images show damage on a left side template. Data from KJS specimens was recorded separately on right and left. When the sample size from the right side was larger, the right side data was transposed onto the left template for better visualization.

Figure 6. Preservation of large bovid forelimbs at Kanjera South compared with FLK Zinj and experimental models of bone damage to large bovids: A) humerus; B) radio-ulna; C) metacarpal. *n* = greatest number of fragment overlaps. Hammerstone-only, Hammerstone-to-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. The FLK Zinj model is from Parkinson (2018). Four views are shown for each experimental model in the following order (from left to right): anterior, lateral, posterior, and medial. Data from KJS specimens was recorded separately on right and left. When the sample size from the right side was larger, the right side data was transposed onto the left template for better visualization.

Figure 7. Example of percussion notches on large bovid humerus (#7379). Upper is cortical view, lower is medullary view.

Figure 8. Distribution of carnivore damage on the small and medium bovids from Kanjera South compared with experimental models of carnivore tooth-marking on small/medium bovids. Panels represent composites of modifications on right and left elements shown on a left side template. Distribution of individual tooth pits (green points) are shown for KJS. GIS density analyses of carnivore tooth marking are shown for experimental assemblages, which have larger sample sizes. The red shaded areas indicate highest concentrations of tooth pits. Tooth marking includes both pits and scores. *n* = number of specimens bearing tooth marks. The Hammerstone-to-Carnivore models are based on Blumenschine's experimental collection, and Carnivore-only (felid) models are from Parkinson (2018).

Figure 9. Domínguez-Rodrigo's 'cold zones' (blue shading) overlain on the KJS bovid hominin modifications: A) small bovid femur; B) small bovid tibia; C) large bovid humerus; large bovid radio-ulna. Note cut marks occur almost exclusively in hot zones (unshaded portions) for small bovids.

Figure 10. Percent of small and medium-sized tooth-marked (A) and cut marked (B) specimens from Kanjera South compared with FLK Zinj. KJS data includes Beds KS-1 through KS-3 combined and includes size classes 1-3a. Data from Tables 3 and 4. Only Blumenschine's total is plotted, as his data are not reported by anatomical part.

Figure 11. Percentage of tooth-marked (% TM) long-bone midshaft fragments (size 1-2 carcasses) for Kanjera South (mean of values for KS-1, KS-2, and KS-3 reported by Ferraro et al., 2017), FLK Zinj (Parkinson, 2018), and HWK EE (Pante et al., 2018) compared with experimental carnivore-first models (Blumenschine, 1995; Marean et al., 2000; Parkinson et al., 2015), human-first models (Blumenschine, 1995; Capaldo, 1995), and ethnographic observations of the Hadza (Lupo and O'Connell, 2002). Data listed in Supplementary Table 2. Error bars represent 95% confidence interval for modern assemblages.

Figure 12. Summary of bone surface modification frequencies at Kanjera South and FLK Zinj. Frequency data are for assemblage-wide NISP calculated in this study (KJS) and by Parkinson (2018; FLK Zinj).