

The carnivorous feeding behavior of early *Homo* at HWK EE, Bed II, Olduvai Gorge, Tanzania

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Abstract

The regular consumption of large mammal carcasses as evidenced by butchery marks on fossils recovered from Early Stone Age archaeological sites roughly coincides with the appearance of *Homo habilis*. However, the significance of this niche expansion cannot be appreciated without an understanding of hominin feeding behavior and their ecological interactions with mammalian carnivores. The Olduvai Geochronology and Archaeology Project (OGAP) has recovered a large and well-preserved fossil assemblage from the HWK EE site, which was deposited just prior to the first appearance of Acheulean technology at Olduvai Gorge and likely represents one of the last *H. habilis* sites at Olduvai. This taphonomic analysis of the larger mammal fossil assemblage excavated from HWK EE shows evidence of multiple occupations over a long period of time, suggesting the site offered affordances attractive to hominins. There was a water source indicated by the presence of fish, crocodiles and hippos, and there was possible tree cover in an otherwise open habitat. The site preserves several stratigraphic intervals with large fossil and artifact assemblages within two of these intervals. Feeding traces on bone surfaces suggest hominins at the site obtained substantial amounts of flesh and marrow, particularly from smaller size group 1-2 carcasses, and exploited a wide range of taxa, including megafauna. However, a strong carnivore signal suggests hominins scavenged much of their animal foods during the two main stratigraphic intervals. In the later of these two intervals, lower carnivore tooth mark and hammerstone percussion mark frequencies, along with high epiphyseal to shaft fragment ratios, suggest hominins and carnivores did not fully exploit bone marrow and grease, which may have been acquired from nutritionally-stressed animals that died during a dry period at Olduvai. The diversity of fauna that preserve evidence of butchery suggests the HWK EE hominins were opportunistic in their acquisition of carcass foods.

Introduction

The initial encroachment of our ancestors upon the larger carnivore guild has important implications for the feeding ecology and adaptive capabilities of our ancestors (Blumenschine and Pobiner, 2007). The regular consumption of large mammal carcasses as evidenced by butchery marks on fossils recovered from Early Stone Age archaeological sites roughly coincides with the appearance of *Homo habilis*, and has traditionally been linked to the morphological changes observed in the genus *Homo* (Milton, 1987; Shipman and Walker, 1989; Speth, 1989; Ruff and Walker, 1993; Aiello and Wheeler, 1995; Foley, 2001, 2002; Antón et al., 2002; Antón, 2003; Antón and Swisher, 2004). However, whether this niche expansion began in the form of hunting or scavenging is hotly contested, particularly for the FLK 22 (*Zinjanthropus*) level assemblage from Olduvai Gorge (Binford, 1981; 1986; 1988; Blumenschine, 1988; 1995; Bunn and Kroll, 1986; 1988; Bunn and Ezzo, 1993; Oliver, 1994; Selvaggio, 1994; 1998; Capaldo, 1995; 1997; 1998; Domínguez-Rodrigo; 1997; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al., 2007; Pobiner et al., 2008; Pante et al., 2012; 2015; Ferraro et al., 2013; Domínguez-Rodrigo et al., 2014a; Parkinson et al., 2015). Despite the apparent lack of consensus concerning the mode of carcass acquisition regularly practiced by *H. habilis*, researchers are largely in agreement that flesh and marrow were important resources to the species.

Contrary to those of *Homo habilis*, studies of assemblages associated with *Homo erectus* all suggest that the species regularly obtained early access to carcasses, possibly through hunting (Monahan, 1996; Pickering et al., 2004; Pobiner et al., 2008; Dominguez-Rodrigo et al. 2009a; 2014b; 2014c; Pante, 2013). However, the small number of assemblages on which these interpretations are based limits our ability to infer the precise timing and nature of what may

signal a pivotal progression in the predatory behavior of hominins. This limitation has historically been the result of a lack of well-preserved fossil assemblages on which the feeding traces of hominins and carnivores can be observed.

Here we report on a new and well-preserved fossil assemblage that dates to around 1.7 ma and was recovered from the HWK EE site, Olduvai Gorge, Tanzania (McHenry and Deino, this volume). The site comprises specimens from four separate archaeological trenches (i.e. Trench 1-Main Trench, T27, T28 and T29) and three stratigraphic intervals (Lemuta, Lower Augitic Sands and Tuff IIB), two of which (Lemuta and Lower Augitic Sands) are associated with Oldowan technology (Figure 1; see also de la Torre et al., this volume). Given the technology and stratigraphic position of the site, the archaeological material from HWK EE is more likely attributed to *H. habilis* than the presumed maker of Acheulean technology, *H. erectus*, and may capture the behavior of the species near the end of its existence at Olduvai. However, neither species, nor even *Paranthropus boisei*, can be ruled out as the maker and user of stone tools at the site.

The goal for this study is to provide interpretations of the carnivorous feeding behavior of the HWK EE hominins along with the ecological interactions they had with carnivores. A more general description of the assemblage taphonomy and paleoecology can be found elsewhere (de la Torre, this volume; Bibi et al., this volume). It is hypothesized that when assessed with the same methods, the HWK EE hominins will be found to have exhibited feeding strategies similar to those of the FLK *Zinjanthropus* hominins, who likely regularly obtained access to carcasses that had been partially defleshed by carnivores (Pante et al., 2012; 2015). Here, we test this hypothesis by examining the incidence and location of hominin butchery marks and carnivore tooth marks.

Methods

Experimental Controls

The HWK EE assemblage is assessed through comparison with experimental samples that were first developed by Blumenschine (1988; 1995), expanded upon by Capaldo (1995), and then refined and described in detail by Pante et al. (2012). Five feeding scenarios were modeled and characterized based on the proportions of tooth, cut and percussion marks in the assemblages. The models include two control scenarios modified by a single actor, two simulations of primary access to carcasses by hominins followed by carnivore ravaging, and one scenario that simulates passive scavenging of completely defleshed carcasses by hominins. The two control scenarios are the hammerstone only (HO) and carnivore only (CO) models, both of which simulate complete consumption of carcasses by humans or carnivores, respectively. The simulations of primary access to carcasses by hominins followed by carnivore ravaging are the hammerstone-to-carnivore (H-C) model, where hominins would have had primary access to both flesh and marrow, and the whole bone-to-carnivore (WB-C) model, which simulates primary access by hominins to flesh and subsequent carnivore consumption of grease and marrow. The simulation of scavenging is the vulture-to-hominin-to-carnivore (V-H-C) model in which carcasses were fed upon by vultures, and in some cases minimally defleshed by carnivores prior to disarticulation and marrow extraction by humans, followed by grease removal by carnivores. One additional scavenging model, the carnivore-to-hominin-to-carnivore model (C-H-C) developed by Selvaggio (1994; 1998), is considered but not directly compared with the archaeological assemblages. This model was not included with those statistically reanalyzed by Pante et al. (2012), but represents a simulation of passive scavenging from carnivores and is relevant to the interpretations of the archaeological assemblages.

When considered together on the basis of all three mark types (tooth, cut and percussion), these models become powerful tools in interpretations of hominin and carnivore feeding ecology (Pante et al., 2012). While alternative methods of interpretation based on frequencies of feeding traces in fossil assemblages have recently been proposed (Domínguez-Rodrigo et al., 2014a), their effectiveness has been questioned based on multivariate analyses that emphasize cut mark frequencies over all other feeding traces (see Pante et al., 2015). We maintain the models that are used here are more effective because they give equal attention to tooth, cut and percussion marks, and also consider specimens that preserve both tooth and butchery marks (Pante et al., 2015).

The HWK EE assemblage

The HWK EE fossil assemblage was analyzed throughout multiple field seasons at Olduvai Gorge between 2009 and 2016. All fossils were catalogued, and both taphonomic and taxonomic data were collected from the larger mammal assemblage. The teeth have been subjected to additional isotopic (Uno et al., this volume; Rivals et al., this volume) and meso/microwear (Rivals et al., this volume) analyses, while both fossils and teeth have undergone detailed taxonomic identification (Bibi et al., this volume) beyond what is presented here. A taxonomic analysis of the collection of bird fossils recovered from the site has also been conducted (Prassack et al., this volume).

Great care was taken during and after excavation to preserve the HWK EE fossil assemblage. While some fossils were found in almost pristine condition, others were embrittled, misshapen, fractured, and/or crushed. Large fossils or those in poor condition often needed to be stabilized by temporary consolidation before block lifting was carried out to remove them from the site. Cyclododecane (C₁₂H₂₄, a cyclic alkane hydrocarbon) (CDD) was used on the large

and unstable fossils because of its sublimation properties, which eliminated the need for solvent removal after excavation (Rowe & Rozeik 2008; Peters & Ohara-Anderson 2015; Peters et al. 2017). Other consolidants and adhesives were also used when CDD was not appropriate or enough to ensure that fragile or fragmented material did not suffer unnecessary damage during the excavation process. Daily temperatures oscillating between 8° and 38°C limited choices to those with higher glass transition temperatures (T_g). Paraloid B-72 (ethyl methacrylate/ methyl acrylate co-polymer) or B-44 (methylmethacrylate/ ethylacrylate) was used in these cases, with a preference to B-44 due to its higher T_g.

Specimens that needed further conservation before being studied were singled out during the excavation or cataloguing process. Treatments included mechanical removal of sedimentary accretions with a variety of dental tools and scalpels, or with rotary tools when accretions were impenetrable by hand tools. Great care was taken to avoid contact with bone surfaces during the removal of accretions. Fossils that had been consolidated or repaired in situ required further treatment when the consolidant or adhesive used in the trenches enclosed soil, or when alignment of broken pieces needed to be corrected. After the resins were reduced or removed, the finds were repaired with B-44 applied with glass capillary tubes, micro spatulas or brushes, while gap-fills were made with a mixture of B-44, acetone and glass microballoons (microscopic glass spheres used as fillers due to their low mass). All treatments were documented, photographed and entered in the conservation database.

A total of 29,808 mammal fossils were recovered in stratigraphic position from HWK EE (de la Torre et al, this volume), of which 29,115 are considered in Table 1. A subset of 6,017 were given unique coordinates, of which 5,324 are analyzed in detail here. The remaining 24,484 fragments were predominantly recovered during screening. These specimens were counted, and

those that were found to be identifiable were removed and included in the detailed taphonomic and taxonomic analyses. None of these totals include surface material, which was mapped and collected, but excluded from the analyses presented here.

The HWK EE assemblage is separated into three different stratigraphic intervals, from oldest to youngest: Lemuta, Lower Augitic Sandstone (LAS) and Tuff IIB. Lemuta and LAS are likely contemporaneous to Mary Leakey's clay and sandy conglomerate, respectively (Pante and de la Torre, this volume). Most analyses focus on the Lemuta and LAS intervals, due to the limited number of specimens recovered from Tuff IIB.

The sample of limb bones that is used for statistical comparisons with feeding trace models (comparative sample throughout) is described in Table 2. A total of 746 limb bone fragments from either the LAS or Lemuta intervals are included in this sample. The comparative sample was extracted from the larger analyzed sample of 1856 limb bone fragments to enhance comparability with feeding trace models that are limited to bovids in size groups 1-4 (see Bunn 1982 for description of size groups), and have not been subjected to the post-depositional processes experienced by the fossil assemblage, which could affect assemblage-wide frequencies of bone surface modifications (see Blumenschine, 1995; Pante, et al., 2012; Pante, 2013). Excluded specimens were 1) less than 20 mm in maximum dimension; 2) had been recently broken with more than 10% of the fragment missing, estimated based on the size of the bone fragment and the length of the broken edge; 3) had poor surface visibility due to mechanical rounding, exfoliation, and/or adhering matrix covering more than 10% of the fragment; 4) were not green broken, determined by the presence of step or transverse fractures; or 5) were known to be from an animal larger than size 4 or a taxonomic family other than bovid.

Assemblage analysis

Taxonomic and skeletal part and portion identifications were carried out using comparative collections located on-site at Olduvai Gorge and in the Zooarchaeology and Paleoanthropology Lab at Colorado State University.

Minimum number of element (MNE) calculations were conducted following the taxonomic and taphonomic analyses and are based on the taxonomic, body size, skeletal element, and element portion descriptions found therein. Refits were attempted within and between archaeological levels prior to any calculations with a total of 28 sets of refits discovered. Most refits were the result of recent breaks, and two refits were found between levels (L1/L4 and L8/LCHA). In cases of ambiguity concerning any specimen overlap, the faunal specimens were directly compared to one another. These comparisons increased MNE totals as even small areas of overlap identified the presence of multiple elements that would have been missed if previous identifications alone were consulted. These calculations were done separately for each archaeological level, and the levels within each stratigraphic interval were subsequently added together to provide the MNE estimates presented here.

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

Metric measurements collected from each specimen include length, width, thickness, and cortical thickness (for limb bones only). Measurements were recorded to the nearest mm using

digital calipers. Length was measured as the longest dimension of the specimen, width was taken perpendicular to length at the widest point and thickness perpendicular to width at the thickest point. Cortical thickness was taken from thickest portion of cortical bone exposed on limb bone fragments. Length, preserved circumference, and cortical thickness were used to help assess animal size groups from midshaft specimens.

Taphonomic analyses were conducted following Blumenschine et al. (1996) and published morphological and contextual criteria for distinguishing surface marks (e.g. Bunn, 1981; Potts and Shipman, 1981; Blumenschine and Selvaggio, 1988; Njau and Blumenschine, 2006; Blumenschine et al., 2007; Domínguez-Rodrigo et al., 2009b). Bone surfaces were inspected macroscopically under a 60w table lamp followed by closer inspection with a 10x hand lens. The orientation of the bone in relation to the light source was systematically altered to allow perception of depth for each mark, following Blumenschine (1995). Tooth, cut and percussion marks were also observed using a portable Dino-lite microscope at magnifications up to 60x. Notable marks were photographed with the portable microscope and/or a Nikon D7100 camera equipped with a 40mm macro lens and Helicon focus stacking software. In some cases, marks were also molded or scanned directly with a Nanovea ST400 white-light confocal profilometer, following Pante et al. (2017) to produce measurable 3-D models.

Percussion and tooth notches were identified and recorded following Capaldo and Blumenschine (1994). Hammerstone percussion notches were identified on the basis of having a broad and arcuate plan form while carnivore tooth notches were identified on the basis of having a semi-circular plan form. Some notches could not be assigned to either of these categories using these criteria and were considered indeterminate.

Results

The HWK EE assemblage preserves abundant traces of both hominin and carnivore feeding on large mammal carcasses. There is also evidence that hominins and carnivores occasionally fed from the same carcasses at the site. Below, the results for the assemblages from the LAS and Lemuta intervals are compared with feeding trace models.

Length of limb bone midshaft fragments in the comparative sample

The length of midshaft specimens in the LAS and Lemuta comparative assemblages from HWK EE are both strongly correlated with the H-C, CO and HO models (Table 3, Figure 2). The LAS assemblage is more strongly correlated with the models than the Lemuta assemblage, which has a minor deficiency in specimens between 20 and 30 mm in length in comparison with the models.

Skeletal part profiles

The HWK EE assemblage consists of a minimum of 941 skeletal elements with 591 coming from the LAS interval, 334 from the Lemuta interval, and 35 from the Tuff IIB interval (Table 4). These results are presented by trench and level in Supplementary Material Online 1. The most abundant elements are limb bones, followed by axial bones, compact bones, cranial bones, and pelves/scapulae. A closer look at the limb bones (Table 5) shows that their distribution is relatively even in both the LAS and Lemuta intervals when separated into animal size groups 1-2 and 3-4. The exceptions are a deficiency in the abundance of the ulnae for all but the size group 1-2 sub-sample of the LAS and a relatively low number of metatarsals for size group 3-4 of the Lemuta. The femur and humerus are also slightly underrepresented in the size group 3-4 sub-samples of both intervals.

Comparisons with feeding trace models

Fossils in the HWK EE collection exhibit percussion marks (Figure 3), mammalian carnivore and crocodile tooth marks (Figure 4), and cut marks (Figure 5). Results for the proportions of bones bearing bone surface modifications at HWK EE are based on the comparative samples, unless otherwise specified. The ‘all limb bone fragments’ category includes epiphyses, near-epiphyses, and midshaft fragments from the humerus, femur, radius, ulna, tibia, and metapodials. The proportions of bones with modifications in the LAS and Lemuta intervals can be found in Table 6, and Figures 6-9 and are summarized separately below when they differ and together when they do not.

Percussion marks

The proportion of percussion marked bones is higher in the Lemuta interval than the LAS interval (Table 6, Figure 6). However, the assemblages compare similarly to the interquartile ranges of the feeding trace models. The incidence of percussion marking for the comparative sub-samples from the LAS interval fall within the 95% interquartile ranges of all sub-samples of the V-H-C model, within both size group 3-4 sub-samples of the H-C model, and within the size group 3-4 sub-sample for midshaft fragments of the HO model. The incidence of percussion marking for the comparative sub-samples from the Lemuta interval fall within the 95% interquartile ranges of all sub-samples of the V-H-C model, within the size group 3-4 sub-sample for all limb bone fragments of the H-C model, and within the size group 3-4 sub-sample for midshaft fragments of the HO model. It falls just outside the upper range of the size group 3-4 sub-sample for midshaft fragments of the H-C model and just below the lower range of the size group 1-2 sub-sample for midshaft fragments of the HO model.

Mammalian carnivore tooth marks

The proportion of tooth-marked bones is higher in the Lemuta interval than the LAS interval (Table 6, Figure 7). However, both assemblages fall within the same interquartile ranges of the feeding trace models and are summarized together. The incidence of tooth marking for the comparative samples from the LAS and Lemuta intervals fall within the 95% interquartile ranges for both size group 1-2 sub-samples of the V-H-C model and within the large interquartile range of the size group 3-4 sub-sample for midshaft fragments of the WB-C model. In general, the proportions of tooth marked bone in the assemblages from the LAS and Lemuta intervals fall intermediate to the H-C and CO models.

Cut Marks

The proportion of cut marked bones is higher in the Lemuta interval than the LAS interval for all but size group 3-4 midshaft fragments (Table 6, Figure 8). However, the assemblages again fall within the same interquartile ranges of the feeding trace models and are summarized together. The incidence of cut marking for the all limb bone fragment sub-samples of the LAS and Lemuta intervals fall within the 95% interquartile ranges of the size group 1-2 sub-sample of the WB-C model and the size group 3-4 sub-samples of the H-C and V-H-C models. The incidence of cut marking for sub-samples of midshaft fragments for the LAS and Lemuta intervals fall within the 95% interquartile ranges of the size group 1-2 sub-samples of the HO and WB-C models and the size group 3-4 sub-samples of the HO and H-C models.

Tooth and Butchery Marks

The proportion of specimens that are both tooth and butchery marked in the LAS and Lemuta intervals is on the lower end of the ranges reported for the feeding trace models, as all sub-samples have values at or below 6.1% (Table 6, Figure 9). The intervals are similar with the

exception of the size group 3-4 sub-sample of midshaft fragments for which the LAS interval lacks any specimens that have the co-occurrence of tooth and butchery marks.

The proportion of tooth and butchery marked specimens in the LAS interval falls within all sub-samples of the V-H-C model and the size group 1-2 sub-sample for midshaft fragments of the WB-C model. The values for all sub-samples fall below 3% with the exception of the size group 3-4 sub-sample for all limb bone fragments, which has a value of 5%.

The proportion of tooth and butchery marked specimens in the Lemuta interval falls within all sub-samples of the V-H-C model, both size group sub-samples for midshaft fragments of the WB-C model, and the size group 3-4 sub-sample for all limb bone fragments of the H-C model. The size group 3-4 sub-samples have more tooth and butchery marked specimens than the size group 1-2 sub-samples.

Cut mark patterns

Cut marks on bone fragments that could be precisely located on the appendicular skeleton (Figure 10) show most cuts were inflicted to limb bone near-epiphyses or midshafts rather than epiphyses. Many cut marks occur near places of muscle attachment, such as the deltoid tuberosity of the humerus or the lesser trochanter of the femur, and cut marks appear to be concentrated in several areas like the distal tibia, distal femur and proximal humerus.

Cut marks are found on taxa in all size groups and on many parts of the skeleton (Table 7, Figure 5). Taxa that are cut marked in the assemblage include bovids in size groups 1-4, equids, suids, hippopotamids, giraffids, a proboscidean, and a hyaenid. Skeletal parts that are cut marked include mandibles, vertebrae, ribs, all limb bones, innominates, scapulae and some podials, although the majority are found on limb bones. Those found on limb bones are mostly

evenly distributed across the flesh bearing elements when sample sizes are large enough to make this assessment (Table 8).

Notches

The limb bones from both intervals of HWK EE preserve tooth and percussion notches (Table 9). The incidence of tooth notching falls well below the CO model and above the H-C model. The incidences of percussion marking falls below both the HO and H-C models.

Discussion

The large mammal fossil assemblage from HWK EE is taphonomically complex due to a fluvial component to its deposition (de la Torre et al., this volume), but it is also rich in the feeding traces of both hominins and carnivores. The assemblage offers evidence of multiple occupations at the site despite indications that the environment was highly competitive, such as the presence of carnivore remains and high carnivore tooth mark frequencies. Beyond this competition for faunal resources, hominins likely had a high risk of predation from both mammalian carnivores and crocodiles. The behavior of hominins at the site appears to have varied between the two main stratigraphic intervals represented, and this will be the focus of the interpretations presented below.

Effect of fluvial processes

Evidence for fluvial activity at HWK EE is clear in the stratigraphy of the site, particularly during the LAS interval. However, proxies such as rounding of lithic specimens, specimen length distributions, and orientation of elongated specimens show only minimal evidence of fluvial transport and abrasion of the material (de la Torre et al., this volume). The length distributions of midshaft fragments in the comparative sample (Figure 2) also suggest hydraulic processes only had a minimal effect on fossil assemblages from both the LAS and

Lemuta intervals. Both intervals are strongly correlated with the length distributions of the feeding trace models, none of which were exposed to fluvial processes. Low-energy fluvial processes can transport bone fragments differentially, with smaller fragments more likely to be transported than their larger counterparts (Pante and Blumenschine, 2010). The similarity in length distributions between HWK EE and the feeding trace models suggests the effect of fluvial processes is minimal enough to not alter interpretations based on comparisons with the models.

Transport of skeletal parts to HWK EE

Skeletal part profiles from HWK EE show that high-density limb bones are the most common elements in the assemblage, but axial, cranial, and compact bones (podials) are also well represented. This suggests that less dense elements were not transported away from the site by fluvial processes (see Voorhies, 1969; Behrensmeyer, 1975) or completely consumed by carnivores. The size group 1-2 sub-sample of the LAS interval has a relatively even distribution of limb bones, with the exception of the ulna, which is usually only represented by part of its proximal end or a portion of the midshaft fused to a radius fragment. This suggests an unbiased strategy of transport of smaller animals to the site by hominins. This is also true of the size group 1-2 sub-sample of the Lemuta interval with the exception of the femur being slightly underrepresented. The size-group 3-4 sub-sample of the LAS and Lemuta intervals are both deficient in the relatively high utility femur and humerus elements (see Metcalf and Jones, 1988 for discussion of food utility indices), suggesting they were not transported to the site as frequently as lower utility elements. This may reflect processing of these elements off-site or suggest that hominins did not have regular access to the humerus and femur when acquiring the carcasses of large animals.

The pattern of less even representation of limb bones in larger animals observed at HWK EE has also been reported for other archaeological sites, most notably for the Klasies River Mouth assemblage (Klein, 1989). It has been argued that these patterns are likely the result of the methodologies employed to reconstruct skeletal part profiles at archaeological sites (Marean and Frey, 1997; Marean and Kim, 1998; Bartram and Marean, 1999). Marrow extraction by hominins using a hammerstone-on-anvil technique fragments the bones of larger animals two to four times more than those of smaller animals due to the greater amount of force required (Bartram and Marean, 1999). When these fragmented bones are subsequently ravaged by bone crunching carnivores, those with low-density epiphyses (i.e. femur and humerus) appear to be underrepresented when midshaft fragments are not used in the reconstruction of skeletal part profiles (see also Marean and Spencer, 1991). While the HWK EE assemblage does show less even representation of limb bones in larger animals, it is not in the way that has been observed for other archaeological sites, specifically a dominance of foot bones and head bones when the complete skeleton is considered (Klein, 1989), also known as the Schlepp Effect (Perkins and Daly, 1968). The tibia and radius are well represented in both intervals and the metatarsals are actually underrepresented in the Lemuta interval. This suggests that the HWK EE skeletal part profile is not the result of the methods employed, which included attempting to refit fossils (see de la Torre et al., this volume), and considered midshaft fragments in the construction of MNEs.

The feeding behavior and ecology of hominins at HWK EE

Two of the stratigraphic intervals contained at the HWK EE site preserve substantial traces of hominin and carnivore feeding. The older Lemuta interval shows intense utilization of carcasses by both hominins and carnivores as evidenced by high frequencies of bone surface

modifications. Limb bone fragments in the younger LAS interval bear fewer traces of hominin and carnivore feeding.

There are several possibilities to explain the overall lower frequencies of bone surface modifications in the LAS interval. Lower tooth mark frequencies could be the result of reduced competition for carcass foods among carnivores or earlier access to carcasses by hominins. However, neither explains the lower rates of percussion marking in the LAS. Mark frequencies could also have been depressed by the addition of carcasses that were not associated with the hominin occupation of the site, either through fluvial transport or through time averaging, as multiple archaeological levels comprise the LAS interval. This is less likely for the Lemuta member because the majority of the assemblage came from a single archaeological level (L10 in T1-Main Trench) and some of the Lemuta layers were finer grained, suggesting a lower energy depositional environment. However, the frequencies of tooth and butchery marked bone suggests this did not have a large impact on the assemblage as they fall within ranges predicted by dual-patterned feeding trace models. The final possibility is that the Lemuta and LAS represent seasonal variations in the accumulation of the assemblages. Below we offer data that support this last hypothesis.

Seasonal variations in the accumulation of the LAS and Lemuta assemblages is indicated by isotope, mesowear and microwear data collected from bovid teeth (Rival et al., this volume). Isotopes and mesowear are long-term measures of diet, and at HWK EE they indicate that antilopin and alcelaphin bovids were predominantly grazing in both the Lemuta and LAS (Rival et al., this volume). However, dental microwear, a measure of what an animal was eating near the time of its death, suggests antilopin and alcelaphin bovids were browsing more during the

LAS (Rivals et al., this volume). This could be the result of carcasses in the LAS getting deposited during a dry period or season when grasses were in lower abundance.

Seasonality can affect the nutritional condition of animals at the time of their death, which can alter the utility of carcass parts and the feeding behavior of hominins and carnivores. Herbivores deplete fat stores in the dry season when they are more nutritionally-stressed (McNaughton and Georgiadis, 1986), and this is known to directly affect the fat content of their bone marrow (Sinclair and Duncan, 1972). Carnivores have been shown to ignore fat-depleted bones, resulting in higher epiphyseal to shaft fragment ratios and lower tooth mark frequencies (Blumenschine and Marean, 1993). A chi-square test shows that the LAS assemblage has a significantly higher epiphysis to shaft fragment ratio (.23) than the Lemuta (.15) assemblage (Table 10, $p=.0-0008$, $\chi^2=11.17$, $d.f.=1$) indicating a lower degree of carnivore ravaging in the LAS. The value for the LAS falls within the range of modern carnivore consumption of fat-depleted carcasses in the Serengeti (Blumenschine and Marean, 1993), and suggests that many of the carcasses in the LAS assemblage were likely fat-depleted at the time of death. This would likely have also affected hominin consumption of marrow, resulting in fewer percussion broken bones. Therefore, lower tooth and percussion mark frequencies in the LAS may be the result of hominin and carnivore scarcer consumption of fat-depleted carcasses.

Comparison with the feeding trace models shows that the assemblages from both intervals do not fit any one model for all sub-samples. However, nearly all size and portion sub-samples from both intervals fall within the V-H-C model. This is in part the result of the larger intervals for the V-H-C model, which occur due to smaller sample sizes of assemblages on which the model is based (see Pante et al., 2012), but it also reflects similarities in the actors that inflicted modifications on bone surfaces through feeding on carcasses. The co-occurrence of

butchery and tooth marks on individual specimens allows elimination of both the carnivore only and hammerstone only model as the sole scenarios for the behaviors that led to the accumulation of the assemblages in both intervals. However, components of each in the assemblage cannot be ruled out.

The overall incidence of percussion marking at HWK EE suggests hominins were breaking the majority of limb bones for marrow extraction at the site. However, the incidences of percussion marking for the size group 1-2 sub-samples of both intervals are relatively low and only fall within the lower end of the V-H-C model. This does not necessarily suggest hominins were not exploiting these smaller carcasses to the same extent of their larger counterparts. It is possible that some of the less conspicuous percussion marks, such as isolated patches of microstriations, were obscured by fluvial abrasion. It is also possible that hominins were breaking the limb bones of smaller animals more efficiently or in a way not replicated by the models leaving fewer impact marks. Lastly, it cannot be ruled out that at least some of the carcasses, particularly in the LAS interval, were contributed only by carnivores, which would depress frequencies of percussion and cut marks while inflating tooth mark frequencies (see Pante, 2013). None of these scenarios, nor the effect of seasonal variations in carcass consumption hypothesized above, can be eliminated based on the percussion mark data alone.

The incidence of tooth marking in the HWK EE assemblage suggests a substantial mammalian carnivore component to the consumption of carcasses at the site. This is especially true of the assemblage from the older Lemuta interval, where the incidences of tooth marking for the sub-samples double, and in some case triple, the mean values for the H-C model. The Lemuta assemblage only falls within the ranges of models where either carnivores were involved in the initial defleshing of carcasses (the V-H-C model simulates carnivore consumption of some

flesh for size 1-2 carcasses, but not size 3-4, see Pante et al., 2012 for discussion), or where carnivores had sole access to marrow from defleshed limb bones (i.e., the WB-C model). The results for tooth marking in the Lemuta interval also resemble those reported by Selvaggio (1994; 1998) for her three-stage carnivore-hominin-carnivore model (C-H-C), which simulates secondary access to carcasses by hominins and reports an incidence of tooth marking of 65% for all limb bones and 47% for midshaft fragments. When considered with the incidences of percussion marking in the assemblage, tooth mark frequencies suggest the possibility for a CO component in the accumulation of size 1-2 carcasses, but not for the size group 3-4 sub-sample, which has a percussion mark frequency at the high end of the H-C model. This suggests that the Lemuta hominins may have had earlier access to size 1-2 carcasses than the tooth mark frequencies indicate, but likely later access to larger animal carcasses.

The incidence of tooth marking for sub-samples of the LAS interval fall within the same models as those for the Lemuta interval, but in all cases, the absolute values are lower than those in the Lemuta. In fact, the incidence of tooth marking for the size group 3-4 sub-sample of midshaft fragments in the LAS interval falls just above the H-C model, suggesting hominins may have had relatively early access to these carcasses. It is also possible the lower incidence of tooth marking for the LAS interval, which follows that of percussion marking, may be attributed to other taphonomic processes such as time averaging or mixing of assemblages due to fluvial processes. However, the lower degree of carnivore ravaging in the LAS, indicated by the high epiphysis to shaft fragment ratios described above, would also result in lower tooth mark frequencies. In fact, carnivore ravaging of fat-depleted carcasses often results in a complete absence of carnivore tooth marks (Blumenschine and Marean, 1993), so the low degree of ravaging indicated for the LAS suggests that the tooth marks present in the assemblage are more

likely to have been inflicted during the initial defleshing of carcasses by carnivores refuting a hypothesis of earlier access to carcasses by hominins in the LAS interval. The incidence of tooth and percussion marking for size 1-2 carcasses in the LAS interval suggests the possibility of a substantial CO component much like those for the Lemuta interval, while the lower values of both relative to the Lemuta could again be the result of seasonal variations in the accumulation of the assemblages.

The incidence of cut marking in the HWK EE assemblage is high, especially for size group 3-4 carcasses where the values for both intervals fall within the lower ranges of the H-C model, suggesting relatively early access to flesh by hominins. Following the values for percussion marks, the frequency of cut marking for the size group 1-2 sub-samples of both intervals is lower overall. This trend of fewer hominin-induced modifications on the limb bone fragments of smaller carcasses again suggests that hominins did not have access to at least some of these animals. However, abrasive processes cannot be completely ruled out for this pattern. Our ongoing research shows that abrasion of bone surface modifications in a rock tumbler has a greater effect on cut marks than tooth marks, which is consistent with the pattern of modification observed for the HWK EE site, and could be depressing the hominin signal for size group 1-2 animals at the site.

Overall, the incidences of tooth and butchery marked bone in the HWK EE assemblage is low, but not inconsistent with the models, some of which allow for the complete absence of a co-occurrence of tooth and butchery marks on single specimens. The presence of specimens that exhibit modifications from both hominins and carnivores demonstrates conclusively that hominins and carnivores fed from the same animals and were in direct competition for carcass foods at the site. In one case from the Lemuta interval, a cut mark overlies a tooth mark,

showing secondary access by hominins to this element, a size group 1-2 femur (Figure 4C). Notably, this is one of the elements consumed first by carnivores due to its high utility (Blumenschine, 1986). While no other specimens exhibit marks that directly overlie one another, there are examples of tooth and butchery marked specimens from each limb bone element in the Lemuta and from the humerus, radius, tibia and metatarsal in the LAS.

Cut mark patterns on limb bones in the HWK EE assemblage suggest that hominins were likely skilled butchers and may have had a somewhat standardized method of butchery. Cut marks are located around muscle attachments on limb bone near-epiphyses and midshafts and, in some cases, overlap in location on specimens from separate animals (Figure 5C). Clusters of cut marks are often sub-parallel and obliquely oriented, suggesting control over the tool and perhaps defleshing skill. These butchery patterns are inconsistent with what we have observed from inexperienced students, who often leave randomly oriented and widely dispersed cut marks, but we have yet to subject the pattern observed for HWK EE to a detailed spatial comparison to the cut mark patterns left by expert and inexperienced butchers. Others have also noted that butcher experience may affect cut mark morphology and frequency (Haynes, 1991; Domínguez-Rodrigo, 1996; 1997), but further actualistic work is necessary to quantify these differences. As such, these interpretations are hypothetical and tentative, but nonetheless intriguing. Skilled butchery behavior at 1.7 mya should not be surprising given that cut marked bones appear in the archaeological record possibly as early as 3.3 mya (McPherron et al., 2010), with hominins regularly butchering animals by 2.0 mya (Ferraro et al., 2013).

The distribution of cut marks on flesh-bearing limb bones suggests hominins usually had access to at least some flesh on the humerus, femur, tibia and radius. It was shown that the FLK *Zinjanthropus* hominins more often had access to flesh on the humerus than the femur, as

indicated by a significantly higher percentage of cut marked humerus fragments when compared with femur fragments (Pante et al., 2012; 2015). This was interpreted as an indication that hominins acquired access to carcasses after the femur had been defleshed by carnivores, as it ranks higher in Blumenschine's (1986) carcass consumption sequence. However, this is not the pattern observed for HWK EE, despite other indicators of scavenging such as high tooth mark frequencies on limb bones. The relatively even distribution of cut marks across flesh-bearing limb bones suggests hominins obtained earlier access to carcasses than at the earlier FLK *Zinjanthropus* site. Tooth mark frequencies that are lower than those reported for the FLK *Zinjanthropus* site (60.7% of all limb bone fragments, see Pante et al., 2012 for further details) support this interpretation. However, sample sizes of midshaft fragments that were attributable to a particular skeletal part are low for all but the size group 1-2 sub-sample of the Lemuta interval, suggesting these results should be considered with caution. Further, the slight deficiency of the femur and humerus, observed in skeletal part profiles from the assemblage, suggests the possibility that hominins did not transport these flesh and marrow rich limb bones to the site if they had previously been defleshed by carnivores. This would result in a more even distribution of cut marks across low and high ranking limb bones.

Cut marks outside of the appendicular skeleton show that hominins at least occasionally had access to flesh from all regions of carcasses (Figure 5E), but this was not necessarily a regular occurrence, as the majority of cut marks are found on limb bones. Still, it shows that hominins could have had access to substantial amounts of flesh and marrow from carcasses at the site.

Cut marks also show hominins exploited a wide range of taxa at the site, including large fauna, such as elephants (Figure 5A), giraffes (5D), and hippos (Figure 5F), and at least one

carnivore (Figure 5B). The diversification of hominin diets and exploitation of megafauna had been previously observed at sites within Olduvai Gorge but, until now, had only been observed at sites that are younger and associated with *Homo erectus* (Domínguez-Rodrigo et al., 2014b; c). Our analysis of the fossil assemblage from the Acheulean EF-HR site also indicated *H. erectus* exploited megafauna there (de la Torre et al., this volume). The results for HWK EE show hominins were getting more regular access to a variety of fauna before the Acheulean appears at Olduvai. In regards to megafauna, our interpretation of this evidence is consistent with those of previous studies (Domínguez-Rodrigo et al., 2014b; 2014c) thus suggesting that acquisition and consumption of these massive animals was likely opportunistic and through scavenging.

The incidences of tooth and percussion notching for the HWK EE assemblage correspond with the bone surface modification results. The incidence of tooth notching is higher than predicted by the H-C model for both intervals, suggesting carnivores were breaking more limb bones than was simulated by the models. This is also supported by tooth mark frequencies that exceed the H-C model. The incidence of percussion notching for both intervals falls below that predicted by the H-C model, suggesting hominins were not the only agents responsible for breakage of the limb bones at the site. This is supported by the relatively low percussion mark frequencies for some sub-samples. These patterns suggest the possibility that the HWK EE assemblage includes CO and H-C components, or it could suggest hominins may not have broken all of the limb bones that they defleshed, implicating a WB-C component where limb bones were defleshed by hominins, but not broken for marrow consumption. As noted above, hominins may have been leaving the fat-depleted bones of nutritional-stressed animals unbroken.

Conclusions

The HWK EE site includes large and well-preserved fossil assemblages from two stratigraphic intervals deposited just prior to the first appearance of Acheulean technology at Olduvai Gorge. The site was attractive to both hominins and carnivores, with crocodiles, hyaenids and felids represented in the fossil assemblage (Bibi et al., this volume; de la Torre et al., this volume) and an abundance of feeding traces from both hominins and carnivores. Deposited just prior to the appearance of *H. erectus* at Olduvai and preserving Oldowan technology, HWK EE may represent one of the last *H. habilis* sites in the region. This implicates the site as an invaluable reference point for our understanding of the feeding behavior and ecology of the species as it continued to encroach upon the larger carnivore guild by consuming flesh and marrow from large mammals.

The HWK EE hominins regularly obtained access to flesh and marrow from all limb bones and occasionally from axial elements. They exploited a wide range of taxa, including carnivores and fauna much larger than themselves, such as elephants, hippos and giraffes, but they more regularly obtained access to bovids and less so to equids and suids. Hominin and carnivore feeding behavior appears to have varied with animal size and by stratigraphic interval. It is likely that hominins had earlier access to size 1-2 carcasses than size 3-4 carcasses in both intervals given the relatively even distribution of cut marks on size 1-2 limb bones and tooth mark frequencies that may have been inflated by CO components to the assemblages. Lower tooth and percussion mark frequencies and higher epiphysis to shaft fragment ratios in the LAS, suggest both hominins and carnivores did not fully exploit bone marrow and grease that may have been acquired from nutritionally-stressed animals that died during a dry period at Olduvai. The diversity of the fauna that hominins exploited at the site suggests opportunistic acquisition of carcasses without specialization for a particular prey size or type, a behavior that is inconsistent

with what we know of modern predators that often specialize in a particular prey size, likely due to biomechanical constraints (see Schaller, 1972; Eaton 1974; Bailey 1993; Slater et al 2009). Whether this suggests hominins scavenged much of this food or that Oldowan tools allowed them to kill prey much larger than themselves, is debatable.

The HWK EE hominins appear to have obtained earlier access to high-ranking carcass parts, such as axial elements and the flesh and marrow rich femur, than their FLK *Zinjanthropus* counterparts. Whether this was made possible through occasional hunting or a more aggressive form of scavenging (see O'Connell et al., 2002) cannot be ascertained by the available evidence. However, as noted above, the broader patterns of feeding traces at HWK EE are most consistent with hominin scavenging. The stone tools associated with the HWK EE hominins do not reveal evidence for advanced weaponry, and even if they possessed wooden spears that are not typically preserved in the archaeological record, hunting would likely have required them to be dangerously close to kill their prey. Hunting of smaller size group 1-2 prey was likely less of a risk for hominins, although the rewards would not have been as great. Feeding traces at HWK EE suggest hominins obtained earlier access to small prey than large prey during both intervals, but differential preservation of tooth, cut and percussion marks due to fluvial abrasion cannot be completely ruled out for this pattern. Regardless of whether they hunted or scavenged their food, the hominins at HWK EE were likely skilled butchers, a behavior that could have been selected for as climate became increasingly unstable, resulting in unpredictable resource availability (Antón et al., 2014).

As zooarchaeologists continue to expand upon the number of fossil assemblages that characterize the feeding behavior of our ancestors, our understanding of the importance of carnivory to the evolution of the genus *Homo* has become more apparent. It is clear that early

Homo relied on carcass foods for what was likely a substantial portion of its caloric intake, a behavior that may have allowed them to thrive during the climatic instability of the Pleistocene. HWK EE may represent the beginnings of a diversifying carnivorous diet and a continuation of an increased reliance on flesh and marrow that persisted with *Homo erectus* at Olduvai Gorge.

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Figure Captions

Figure 1) A) Location of HWK EE in Olduvai Gorge (map template after Jorayev et al, 2016). B) Aerial view of HWK EE trenches. C) Stratigraphic correlation of HWK EE trenches (simplified from de la Torre et al, this volume, Figure 20).

Figure 2) Length of limb bone midshaft fragments from the comparative samples of the Lower Augitic Sandstone (LAS) and Lemuta intervals compared with those from the feeding trace models CO, Carnivore only; HO, Hammerstone Only; H-C, Hammerstone-to-Carnivore.

Figure 3) Percussion marks on limb bones from HWK EE. A) metatarsal midshaft from a size 3 bovid (T1_LCHA_179, LAS); B) radius midshaft fragment from a size 3 bovid (T1_L2_2109, LAS); C) radius midshaft fragment from a size 4 bovid (T1_L6_174, LAS).

Figure 4) Tooth marks on fossils from HWK EE. A) Large furrows on a size 4 ilium (T1_LCHA_86, LAS); B) Crocodile tooth mark on a complete size 3 bovid radius (T1_L2_4176, LAS); C) Cut mark overlying a tooth mark on a size 1 bovid femur fragment (T1_L10_1383, Lemuta).

Figure 5) Cut marks on fossils from HWK EE. A) Proboscidean astragalus; (T1_L2_433, LAS); B) *Crocota* scapula (T1_L4_294, LAS); C) Proximal humeri of a size 2 bovid (T1_L4_330, LAS); and shaft/near epiphyses of a size 1 juvenile bovid; (T1_L4_1567, LAS); D) Tibia shaft of giraffid (T1_L6_1233, LAS); E) Complete rib from a size 3 bovid (T1_L10_1105, Lemuta); F) Mandible of a hippopotamid (T1_L6_1621, LAS).

Figure 6) Incidence of percussion marked bone for (a) animal size group 1-2, (b) animal size group 3-4. HO, Hammerstone-Only; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. Data shown for feeding trace models includes the mean and 95%

interquartile range. Data shown for LAS and Lemuta represent the proportion of percussion marked bone in the comparative samples.

Figure 7) Incidence of tooth marked bone for (a) animal size group 1-2, (b) animal size group 3-4. CO, Carnivore Only; WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. Data shown for feeding trace models includes the mean and 95% interquartile range. Data shown for LAS and Lemuta represent the proportion of tooth marked bone in the comparative samples.

Figure 8) Incidence of cut marked bone for (a) animal size group 1-2, (b) animal size group 3-4. HO, Hammerstone-Only; WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. Data shown for feeding trace models includes the mean and 95% interquartile range. Data shown for LAS and Lemuta represent the proportion of cut marked bone in the comparative samples.

Figure 9) Incidence of tooth and butchery marked bone for (a) animal size group 1-2, (b) animal size group 3-4. WB-C; Whole Bone-to-Carnivore; H-C, Hammerstone-to-Carnivore; V-H-C, Vulture-to-Hominin-to-Carnivore. Data shown for feeding trace models includes the mean and 95% interquartile range. Data shown for LAS and Lemuta represent the proportion of tooth and butchery marked bone in the comparative samples.

Figure 10) Cut mark locations and orientations on fossil bones from HWK EE. Cut marks on size 1-2 animals are represented by a blue line and regular font specimen number; cut marks on size 3-4 animals are represented by a red line and bold font specimen number; cut marks on size 5-6 animals are represented by a green line and bold italic font specimen number. Specimen numbers that are starred represent bones from the Lower Aungitic Sandstone interval, while all

others are from the Lemuta interval. Locations of cut marks are estimated based on morphological features found on the fragments that they were discovered on.

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