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## 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 resources that were 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. A strong carnivore signal suggests hominins scavenged much of their animal foods during the two main stratigraphic intervals. In the later interval, lower carnivore tooth mark and hammerstone percussion mark frequencies, in addition to 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 that the HWK EE hominins were opportunistic in their acquisition of carcass foods.

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### 1. 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; Bunn and Kroll, 1986, 1988; Blumenschine, 1988, 1995; Bunn and Ezzo, 1993; Oliver, 1994; Selvaggio, 1994, 1998; Capaldo, 1995, 1997, 1998; Domínguez-Rodrigo, 1997; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al., 2006; 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

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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 *H. 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, which was recovered from the HWK EE site, Olduvai Gorge, Tanzania (McHenry, submitted). The site comprises specimens from four separate archaeological trenches (Trench 1-Main Trench, T27, T28 and T29) and three stratigraphic intervals (Lemuta, Lower Augitic Sandstone [LAS] and Tuff IIB), two of which (Lemuta and LAS) are associated with Oldowan technology (Fig. 1; see also de la Torre et al., submitted-a). 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 (Bibi et al., submitted; de la Torre et al., submitted-a). 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 frequency and location of hominin butchery marks and carnivore tooth marks.

## 2. Methods

### 2.1. 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 include the hammerstone-to-carnivore (H–C) model, in which 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 it 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 (Dominguez-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 used here are more effective because they give equal attention to tooth, cut and percussion marks, and they also consider specimens that preserve both tooth and butchery marks (Pante et al., 2015).

### 2.2. 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 (Rivals et al., this volume; Uno et al., submitted) and meso/microwear (Rivals et al., submitted) analyses, while both fossils and teeth have undergone detailed taxonomic identification (Bibi et al., submitted) 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., submitted).

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 brittle, 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 (C<sub>12</sub>H<sub>24</sub>, 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 and Rozeik, 2008; Peters et al., 2017). Other consolidants and adhesives were used when CDD was not appropriate or when it was insufficient to ensure that fragile or fragmented material did not suffer unnecessary damage during the excavation process. Daily temperature oscillations between 8° and 38 °C limited choices to those with higher glass transition temperatures (T<sub>g</sub>). Thus, paraloid B-72 (ethyl methacrylate/methyl acrylate co-polymer) or B-44 (methylmethacrylate/ethylacrylate) were used, with a preference for B-44 due to its higher T<sub>g</sub>.

Specimens that needed further conservation before being studied were singled out during the excavation and cataloguing processes. 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

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